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THE SERBIAN LAKE SYSTEM: A STEPPING STONE FOR FRESHWATER MOLLUSCS IN THE MIDDLE MIOCENE

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Abstract: The first in-depth revision of a lacustrine freshwater mollusc fauna of the Serbian Lake System (SLS) is carried out. We describe and discuss well-preserved faunas from two localities in central and southern Serbia (Mađere and Medoševac), along with the reinvestigation of type material of several species described in the late nineteenth and early twentieth centuries. Our revision yields 14 species of gastropods, with the families Hydrobiidae (six species) and Planorbidae (four species) being most abundant, along with one species each of Neritidae, Melanopsidae, Bithyniidae and Bulinidae, as well as two dreissenid bivalve species. Three of the hydrobiid gastropods are new to science, *Prososthenia milosevici* sp. nov., *Prososthenia*? *naissensis* sp. nov., and *Prososthenia rundici* sp. nov., and so is the bivalve *Trigonipraxis madjerensis* sp. nov. The present study results in 12 lectotype designations, 10 new generic combinations, and 10 new junior synonyms. About four-fifths (81.3%) of the species are endemic to the SLS, which is slightly higher than the overall SLS endemism (71.4%). The composition at the genus and family level overlaps strongly with the slightly older faunas of the Dinaride Lake System in Croatia and Bosnia and Herzegovina, as well as that of the late Miocene Lake Pannon. Its stratigraphically intermediate position and geographical proximity suggest that the SLS was a stepping stone for many of the mollusc lineages, some of which are found only in those systems.

Key words: Gastropoda, Bivalvia, endemism, palaeobiogeography, Serbia, Dinaride Lake System.

THE Balkan Peninsula accommodated a large number of freshwater lakes during the middle Miocene (Krstić *et al.* 2003; Jiménez-Moreno *et al.* 2008, 2009; Mandic *et al.* 2009, 2011; De Leeuw *et al.* 2010, 2011, 2012; Harzhauser *et al.* 2012*a*). The palaeolakes situated in today's Croatia and Bosnia and Herzegovina are collectively termed the Dinaride Lake System (DLS; Fig. 1; Harzhauser & Mandic 2008; De Leeuw *et al.* 2012). Many of these lakes existed for several hundreds of thousands of years and harboured a diverse endemic biota (Krstić *et al.* 2003, 2012; Harzhauser & Mandic 2008; Jovanović 2012; Neubauer *et al.* 2015*a*, *b*). Most notable are the rich mollusc faunas that have attracted palaeontologists for the last 150 years (Neumayr 1869; Brusina 1897, 1902; Harzhauser & Mandic 2008). Many of the endemic mollusc faunas have been recently studied in detail because they constituted important cradles for European Miocene diversity (Neubauer *et al.* 2011, 2013*a*, *b*, 2014*a*, 2016*a*–*c*; Krstić *et al.* 2013).

Another group of lakes existed during the middle Miocene in Serbia, Kosovo and Macedonia. As for the DLS, rich mollusc faunas have also been described from these regions (Burgerstein 1877; Pavlović 1903*a*, *b*, 1931, 1932, 1933, 1935; Veselinović-Čičulić 1952; Milošević 1962, 1971, 1980, 1981, 1984; Knežević 1996; Krstić *et al.* 2007). The systematic classifications in these works suggest high similarities with the DLS faunas, but detailed descriptions or high-quality illustrations are unavailable. Moreover, fairly little was known about the palaeoenvironmental evolution and age constraints until recently, complicating faunal comparisons and inferences about evolutionary implications. Previous studies suggested the presence of a single big lake stretching from Belgrade over the Skopje and Sofia basins to northern Greece ('Serbian Lake'; Krstić *et al.* 2012). More recent investigations, however, point towards a series of lakes spread over that region, similar to the DLS: the Serbian Lake System (SLS; Sant *et al.* 2018).

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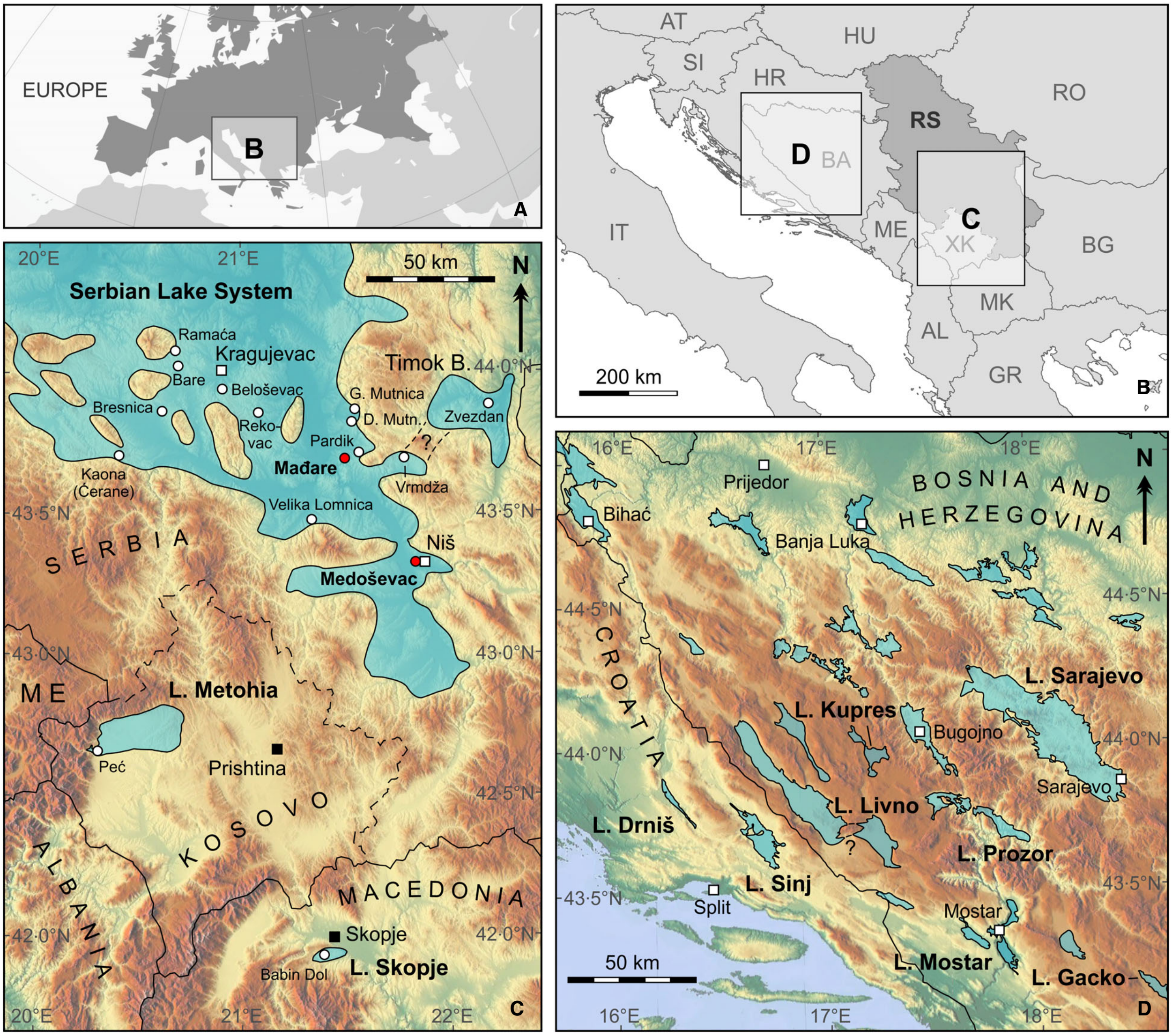

FIG. 1. Geographic overview of the Balkan Peninsula (A, B), indicating the studied localities (C), the extent of the southern part of the Serbian Lake System and nearby middle Miocene lakes (C), and the Dinaride Lake System (D). Country abbreviations in B and C follow the ISO 3166-1 Alpha-2 code. Palaeolake outlines shown in C are tentative estimations of the maximum flooding extent based on available reconstructions (Dumurdzanov *et al.* 2005; Neubauer *et al.* 2015*a*, 2017), distributions of lacustrine sediments and localities with mollusc faunas, as well as present topography. The northern boundary of the Serbian Lake System is unknown but was probably located in the Belgrade region. D was modified after Neubauer *et al.* (2016*d*); note that only major lake basins of the Dinaride Lake System are indicated in this version. *Abbreviations:* AL, Albania; AT, Austria; BA, Bosnia and Herzegovina; BG, Bulgaria; GR, Greece; HR, Croatia; HU, Hungary; IT, Italy; ME, Montenegro; MK, North Macedonia; RO, Romania; RS, Serbia; SI, Slovenia; XK, Kosovo; B., Basin; D. Mutn., Donja Mutnica; G. Mutnica, Gornja Mutnica; L., Lake. Colour online.

The aim of the present paper is to provide a detailed taxonomic description of the freshwater mollusc SLS assemblages of two localities in central and southern Serbia. We clarify the identities of previously poorly resolved taxa, designate lectotypes, and discuss potential synonyms. We compare the retrieved SLS fauna with the other middle Miocene and early late Miocene faunas to infer possible relationships. Of particular interest is the possible link to the DLS faunas.

GEOLOGICAL SETTING

The study area is situated along the southern margin of the Pannonian Basin, between the internal Dinarides and the southern Carpathian Mountains. The extension of the Pannonian Basin in Serbia and the system's faults pattern were established during the early Miocene, resulting in the formation of partly connected basins and the deposition of continental alluvial to lacustrine sediments

(Anđelković *et al.* 1991; Marović *et al.* 2002, 2007; Krstić *et al.* 2012; Stojadinović *et al.* 2013). The largest of such basins is found along the Morava River and its transversal depressions in central and southern Serbia. The basement of this so-called Velika Morava Graben is composed of Palaeozoic, Mesozoic, and Palaeogene rocks, which are partially transgressively, partially discordantly overlain by Miocene freshwater clayey silt, sand, silt, marl and marlstone, as well as by sandy limestone (Čičulić 1977; Matenco & Radivojević 2012; Sant *et al.* 2018). The freshwater environments producing these deposits have been referred to as 'Neogene lakes of Serbia', 'Serbian Lake' (Krstić *et al.* 2003, 2012) or 'Serbian Lake Systems' (Sant *et al.* 2018).

Previous estimates suggested a late early Miocene to early middle Miocene age for the freshwater deposits based on biostratigraphic comparisons of molluscs, mammals and flora (Pavlović 1930; Pantić 1956; Stevanović *et al.* 1977*a*, *b*; Alaburić & Marković 2010; Krstić *et al.* 2012). The top age is constrained by the Badenian marine transgression, flooding the region at *c.* 14.2 Ma in the north and *c.* 13.7 Ma or later in the south (Pezelj *et al.* 2013; Sant *et al.* 2018; Mandic *et al.* 2019*a*–*c*). A recent integrated study of a lacustrine sequence of the Popovac palaeolake in central Serbia has improved the chronostratigraphic framework and shed light on the palaeoenvironmental setting of the SLS (Sant *et al.* 2018). Based on biostratigraphy, cyclostratigraphy, magnetostratigraphy and radioisotope dating, the studied deposits were dated as early middle Miocene (14.61–14.16 Ma). This indicates that the SLS is slightly younger than the DLS (*c.* 18.2–14.8 Ma; De Leeuw *et al.* 2012).

MATERIAL AND METHOD

The studied material derives from the two localities Mađere and Medoševac. Mađere near Ražanj (also known as Mađari, Mađare, Maђере) is located 20 km south-south-east of Paraćin and 20 km north-east of Kruševac (Fig. 1), Medoševac (Медошевац) is a city district of Niš located 2.8 km west of its centre on the north bank of the Nišava river. The deposits in the area of Mađere consist of alluvial conglomerates and sandstones covered by yellow and grey lacustrine marls containing ostracods and the herein described molluscs (see also Veselinović *et al.* 1964, 1970). The deposits around Niš are characterized by a succession of lacustrine Miocene sediments consisting of gravels, sandstones, clay and marly beds with remains of plant fossils, ostracods and molluscs (Rakić *et al.* 1965, 1973).

The two localities were chosen because they offer well-preserved shells and type material of several species. The study site of Sant *et al.* (2018) is situated *c.* 25 km north of Mađere and contains two of the species reported in the present paper, suggesting that the studied fauna is of similar age or even originates from the deposits of Lake Popovac. The Medoševac assemblage shares several species with that of Mađere, pointing to a similar age as well.

The present study is largely based on the material deriving from the lacustrine marls at Mađere collected by B. Matejić in 1930 and studied by P. Pavlović (1931). The collection by S.A. Radovanović dating from 1897, providing the type material for *Prososthenia fuchsi* Pavlović, 1903*b* (see Pavlović 1931), is unfortunately missing. Additional material for Mađere derives from the collections of V. Milošević from 1973 and 1976, which were partly studied by Milošević (1980). The material available from the grey marly lacustrine sediments exposed at Medoševac was collected by Pavlović in July 1905.

While the material from Mađere contains an exceptionally rich gastropod fauna, the shells from Medoševac include mostly small gastropods and well-preserved dreissenid bivalves. All material is stored at the Cenozoic invertebrate collection of the Natural History Museum of Belgrade.

Scanning electron microscopy was carried out using the JEOL JSM-6610LV at the National History Museum Vienna. Macro-photographs were taken with a ZEISS Discovery.V20 stereomicroscope with attached AxioCam MRc5 using the stacking module of the software ZEISS AxioVision SE 64 4.9 to obtain throughout focused images. Photos of type specimens stored at the Croatian Natural History Museum in Zagreb studied for comparison were obtained using a Canon EOS D6. Counting of protoconch whorls follows the method of Verduin (1977).

Statistical analyses were performed using R v. 3.3.2 (R Core Team 2016) with `ade4` v. 1.7-11 (Dray & Dufour 2007; Dray *et al.* 2018) and `vegan` v. 2.5-2 (Oksanen *et al.* 2018). We carried out two cluster analyses using the unweighted pair group method with arithmetic mean to explore species and genus-level relationships of selected gastropod faunas discussed in this paper. The first analysis was based on a Dice distance matrix of species presence–absence data. The second was calculated from a Euclidean distance matrix based on the number of species per genus. Here, data were normalized by site to account for the high variation in the number of species per fauna following the procedure discussed in Borcard *et al.* (2011). The data derive from published datasets (Neubauer *et al.* 2015*b*, 2016*d*) including updates from recent revisions and the results of this paper (Neubauer *et al.* 2020). For the fauna of the Skopje and Metohia basins, only the middle Miocene parts were considered in the analyses, to avoid bias towards late Miocene and Pliocene faunas. Similarly, we included only the early lake fauna of

Lake Pannon (Phase 1 of Neubauer *et al.* 2016*d*). Subspecies and uncertain identifications were not considered.

Abbreviations. C, convexity (of a single valve); H, height; Hd, diagonal height; L, length; Ld, diagonal length; LV, left valve; P/T, protoconch/teleoconch; RV, right valve; W, largest width (perpendicular to height); Ws, second-largest width (perpendicular to both other axes).

Institutional abbreviations. CNHM, Croatian Natural History Museum, Zagreb, Croatia; NHMB, Natural History Museum of Belgrade, Serbia.

SYSTEMATIC PALAEONTOLOGY

The systematic classification for the Gastropoda follows Bouchet *et al.* (2017), bivalve systematics follow Bieler *et al.* (2014).

Note on the versions and publication dates of Brusina (1893). Brusina published his work on the Serbian Tertiary molluscs in two versions. The Serbian text appeared in two parts in *Annales Géologiques de la Péninsule Balkanique*, volume 4(1), pp. 192–208, and volume 5(1), pp. 173–202, the latter of which contains the faunas relevant to this paper. An Italian version was published in the same journal in volume 4(2), pp. 25–74. All three volumes/issues appeared in 1893 and their precedence is not established, but the volume/issue numbers suggest that the Italian version was published earlier than the corresponding Serbian text.

Class GASTROPODA Cuvier, 1795
Subclass NERITIMORPHA Golikov & Starobogatov, 1975
Order CYCLONERITIMORPHA Frýda, 1998
Superfamily NERITOIDEA Rafinesque, 1815
Family NERITIDAE Rafinesque, 1815
Subfamily NERITININAE Poey, 1852

Genus THEODOXUS Montfort, 1810

Type species. Theodoxus lutetianus Montfort, 1810 (unnecessary substitute name for *Nerita fluviatilis* Linnaeus, 1758); by original designation. Recent, Europe.

Theodoxus zivkovici (Pavlović, 1903*b*)
Figure 2A–I

* 1903*b* *Neritodonta Živkovići* Pavlović, p. 324, pl. 9, figs 9–10.
1931 *Neritodonta* cf. *xanthozona* Brusina; Pavlović, p. 28, pl. 11, figs 38–41 [non *Neritodonta xanthozona* Brusina, 1884].
1929 *Theodoxus* (*Calvertia*) *živkovići* (Pavlović); Wenz, p. 2985.
1962 *Neritodonta živkovići* Pavl.; Milošević, p. 30, pl. 1, fig. 1.

Types. The syntypes from the middle Miocene (?) of Zvezdan are stored at NHMB. We designate the specimen illustrated by Pavlović (1903*b*) as the lectotype (NHMB 1329, formerly NHMB 2505).

Material. 73 specimens from Mađere (NHMB 2504, 7119–7122, 7124, 7125), 11 juvenile specimens from Medoševac (NHMB 7123).

Description. Large, regularly rounded, hemispherical shell; more globular in early stages. Apex entirely immersed in young individuals; becomes weakly raised in fully grown specimens. Peristome sharp, regularly semilunar, with very weakly convex inner lip. Callus pad weakly thickened, not well delimited from last whorl. Most typical feature is weak, irregular, locally confined crenulation at centre of callus pad margin (Fig. 2D, G). Colour pattern highly variable, showing changes through ontogeny, which can be observed on many shells (particularly on apical region): juveniles have bright white shells covered with dark, thin spiral bands; later, additional, light brown patterns develop, covering bands as well as interspaces; shells at that stage typically expose mottled patterns, with large or small, usually irregularly sized white spots on light brown background; this pattern grades into densely spaced zigzag lines or broad zigzag bands grading into each other in fully grown individuals; in many specimens, previous spiral bands are still visible, often expressed as local variation of colouration or amplitude of zigzag lines. In a few adult specimens, bands are still very prominent and broad (Fig. 2E). Occasionally, distinct growth lines cover shell (Fig. 2G–I).

Dimensions. H 7.33 mm, W 8.16 mm, Ws 6.54 mm (NHMB 7121; Fig. 2A–C); H 7.64 mm, W 8.77 mm, Ws 6.79 mm (NHMB 7120; Fig. 2D–F); H 3.92 mm, W 4.49 mm, Ws 3.61 mm (juvenile specimen, NHMB 7119; Fig. 2G–I); largest specimen found: H 10.2 mm, W 10.4 mm, Ws 7.65 mm (NHMB 2881/2506).

Remarks. The present material closely resembles shells of *Theodoxus zivkovici* (Pavlović, 1903*b*) from supposedly coeval strata of Zvezdan concerning overall shell shape and the low and broad spire. The Zvezdan species shows a pattern of spiral colour bands, which occurs only in juvenile specimens of the present material. Adult specimens have a variety of colour patterns, including thin axial zigzag lines, mixed axial lines and spiral bands, mottled, and almost completely plain-coloured. Given that colouration in *Theodoxus* is generally considered a variable character that depends on the environmental conditions (Glöer & Pešić 2015), the colour variability of the studied shells does not allow taxonomic differentiation.

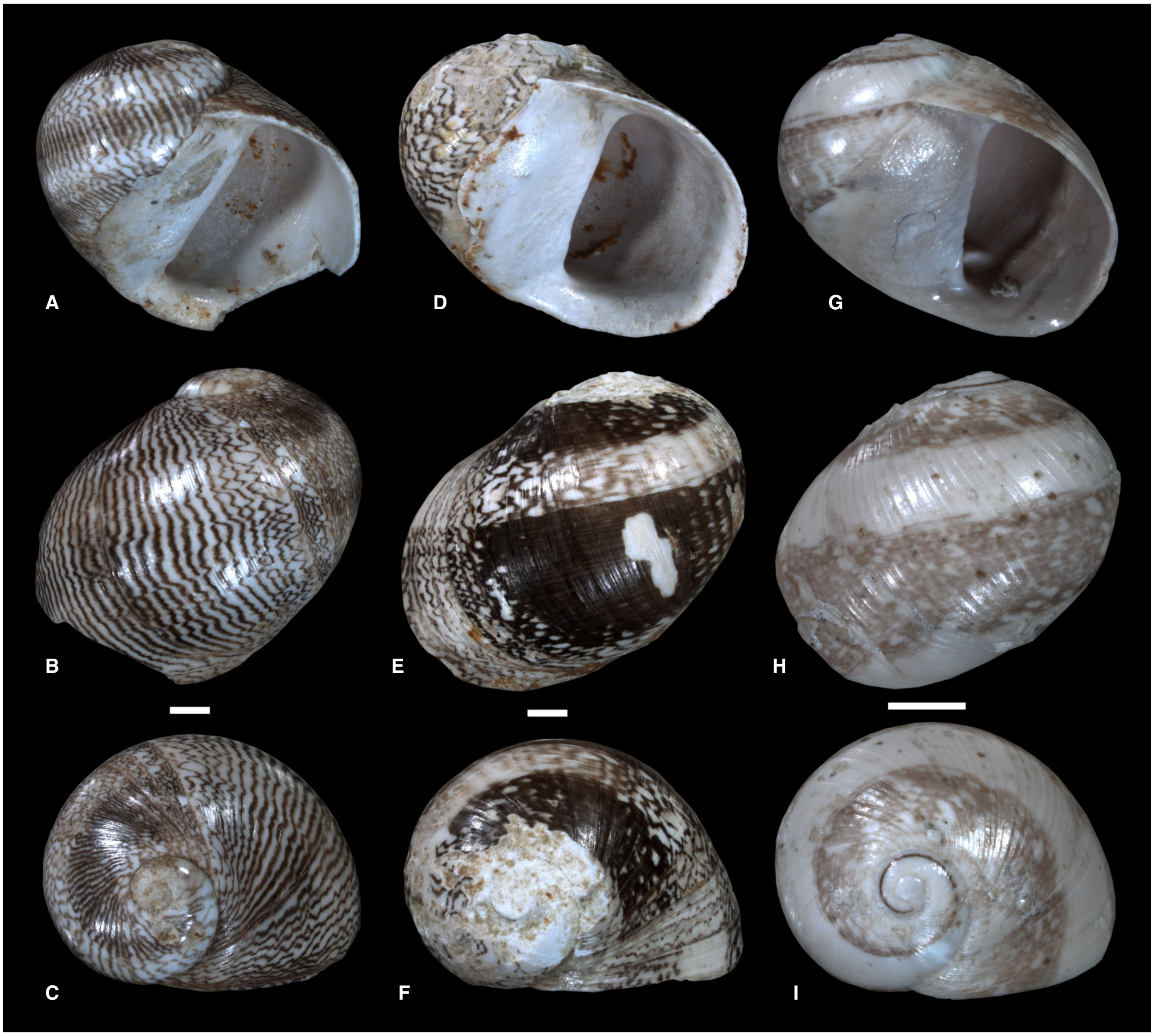

FIG. 2. Neritidae. *Theodoxus zivkovici* (Pavlović, 1903*b*). A–C, NHMB 7121. D–F, NHMB 7120. G–I, juvenile specimen, NHMB 7119. All from Mađere. Scale bars represent 1 mm. Colour online.

Shells from Vrmdža identified as *Neritodonta* cf. *xanthozona* by Pavlović (1931) perfectly match juvenile specimens of the present species in terms of shape and the presence of thin dark spiral bands. *Theodoxus xanthozona* (Brusina, 1884) from the latest Miocene to early Pliocene of Grgeteg near Novi Sad, northern Serbia, differs in its more elongate shell.

A similar species is *T. suskalovici* (Pavlović, 1903*a*) from the middle Miocene of the Skopje Basin. The type material of Pavlović (1903*a*) stored in the NHMB collection shows a hemispherical shell, a low spire, which lies almost in one plane with the last whorl, a dentate callus pad, and variable colouration, including narrow parallel, discontinuous belts, zigzag lines or irregular patterns. A major difference to *T. zivkovici* is the wider shell and the apically expanded aperture. Specimens of *T. zivkovici* with prominent spiral bands also resemble *T. veljetinensis* (Pavlović, 1903*a*) from the late Miocene of the Veljetin Hills in the Kosovo Basin (see also Milošević 1962, pl. 20, fig. 8). That species, however, lacks the callus pad dentation. *Theodoxus brusinai* (Pavlović, 1931) from Bresnica has a more spherical shell and a colour pattern that typically shows broad zigzag bands (see also Milošević 1962, pl. 20, fig. 6; misspelt as '*brusinae*' in figure captions). The subspecies *T. brusinai rugosa* (Pavlović, 1931) from the same locality, treated as distinct species by Milošević (1983, pl. 2, figs 9–12), differs in the ribbed surface and the often more elevated spire. The widespread middle Miocene species *Theodoxus crenulatus* (Klein, 1853) differs in its strongly dentate callus pad and the more elongate shell (Harzhauser *et al.* 2012*b*). Juvenile specimens of *T. zivkovici* resemble *Theodoxus miljkovici* (Brusina, 1902) from the Sarmatian of the Visoka Hills at the Dacian Basin margin in eastern Serbia. That species differs by its more elongate shell and the slightly higher spire. Moreover, the type specimens available at CNHM (lectotype, CNHM 2734-380/1, designated by Jurišić-Polšak 1973, and paralectotypes, CNHM 2734-380/2–6) show a mottled pattern that is not found in *T. zivkovici*.

Occurrence. Endemic to the SLS, known from Zvezdan (Pavlović 1903*b*), Vrmdža (Pavlović 1931), and Mađere and Medoševac (this study).

Subclass CAENOGASTROPODA Cox, 1960
Superfamily CERITHIOIDEA Fleming, 1822
Family MELANOPSIDAE H. Adams & A. Adams, 1854
Subfamily MELANOPSINAE H. Adams & A. Adams, 1854

Genus MELANOPSIS J. Férrusac *in* Férrusac & Férrusac, 1807

Type species. Melania costata Olivier, 1804; by subsequent designation by Neubauer *et al.* (2014*b*). Recent, Middle East.

Melanopsis petkovici Pavlović, 1931
Figure 3A–I

*1931 *Melanopsis Petkovići* Pavlović, p. 19, pl. 10, figs 19–20.
1931 *Melanopsis* cf. *Šoštarići* Brus.; Pavlović, p. 19, pl. 10, figs 21–24 [non *Melanopsis sostarici* Brusina, 1897].
1952 *Melanopsis decollata* Stol.; Veselinović-Čičulić, pl. 1, fig. 5 [non *Melanopsis decollata* Stoliczka, 1862].
1952 *Melanopsis pterochila* Brus.; Veselinović-Čičulić, pl. 1, fig. 5 [non *Melanopsis pterochila* Brusina, 1874].
1962 *Melanopsis petkovići* Pavl.; Milošević, p. 24, pl. 29, fig. 5.

Types. To fix a name-bearing type, we designate the specimen from Vrmdža illustrated in Pavlović (1931, pl. 10, figs 19–20) as lectotype (NHMB 1294, formerly NHMB 2888) (note that Milošević 1962 erroneously gave Skopje as type locality).

Material. 716 specimens from Mađere (NHMB 2502, 7126–7129, 7131–7136), 122 juvenile specimens from Medoševac (NHMB 7130).

Description. Slender, elongate, conical to weakly ovoid shell with at least seven teleoconch whorls (exact number unknown given that apex never preserved in adult specimens). Whorls weakly convex to straight sided, sometimes forming slightly stepped spire. Suture thin, not incised. Last whorl about ton-shaped with weakly flattened flanks and weakly convex base; attains two-thirds to three-quarters of total shell height. Aperture broad lanceolate, marked by prominent, glossy callus pad, which is strongest in its posterior part. Very faint columellar swelling occurs in some specimens. Outer lip thin, sharp, rarely preserved. Anterior canal short, narrow. Weak, thin, sharp fasciole present on neck. In a single specimen, colour pattern is preserved on last whorl, consisting of yellow, irregular, occasionally interrupted zigzag lines, which disintegrate on upper part of whorl into shapeless blotches.

Dimensions. H 15.64 mm, W 7.86 mm (NHMB 7126; Fig. 3A, B); H 13.75 mm, W 6.49 mm (NHMB 7127; Fig. 3C–E); H 9.59 mm, W 4.76 mm (NHMB 7128; Fig. 3F, G); H 13.83 mm, W 6.49 mm (NHMB 7129; Fig. 3H, I); largest specimen found: H 19.37 mm, W 8.49 mm.

Remarks. Pavlović (1931) identified some of the specimens from Mađere as '*Melanopsis* cf. *sostarici*'. That species, originally described by Brusina (1897) from the late early Miocene of Dugoselo in central Croatia (*c.* 16 Ma; Mandic *et al.* 2012), has a more deltoid shape with marked but blunt angulation on the last whorl. In contrast, the specimens clearly range within the morphological spectrum of *M. petkovici*.

A probably closely related species is *Melanopsis arsinovi* Brusina, 1902 from the approximately coeval and geographically close locality Zvezdan in the Timok Basin. Comparison with the type material of that species stored at CNHM and topotypic material stored at NHMB shows that *M. arsinovi* is on average bigger, has a relatively shorter spire and a more elongate aperture and neck, as well as a more massive callus pad. To bring stability to the taxonomy of that species, we designate the syntype CNHM 2503-149/2 (3N–O) as lectotype; specimens CNHM 2503-149/1 and 2503-149/3 (Fig. 3P–Q) are paralectotypes.

Melanopsis suskalovici (Pavlović, 1903*a*) from the middle Miocene (?) of the Skopje Basin is more slender and has a larger last whorl and a very distinct fasciole. *Melanopsis petkovici* closely resembles *M. mojsisovicsi* (Neumayr, 1880) from the early middle Miocene of Džepi, which is smaller and more slender (see also Neubauer *et al.* 2016*c*). *Melanopsis filifera* Neumayr, 1880 from the early middle Miocene of the vicinity of Drvar differs in the strongly flattened profile. The species *M. decollata* Stoliczka, 1862, described from the Pannonian of Zalaapáti in Hungary, has a stouter shape and a boarder last whorl.

Occurrence. Endemic to the SLS, reported from Vrmdža (Pavlović 1931) and Mađere (this study). The juvenile specimens from Medoševac could not be identified with certainty but are tentatively attributed to *M. petkovici*.

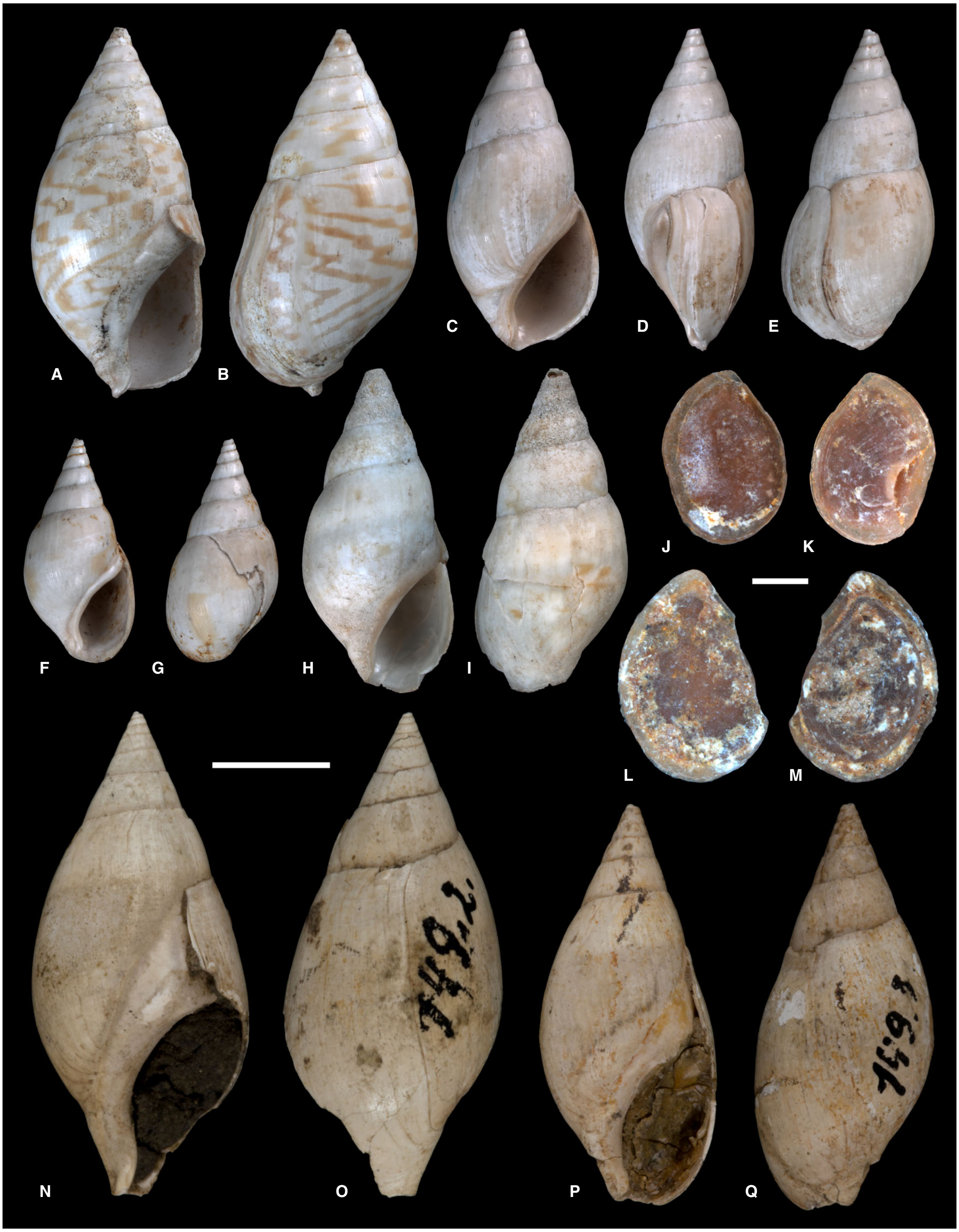

FIG. 3. Melanopsidae and Bithyniidae. A–B, *Melanopsis petkovici* Pavlović, 1931, specimen with colour pattern preserved, NHMB 7126, from Mađere. C–E, *M. petkovici*, NHMB 7127, from Mađere. F–G, *M. petkovici*, juvenile specimen, NHMB 7128, from Mađere. H–I, *M. petkovici*, NHMB 7129, from Mađere. J–K, *Bithynia* sp., NHMB 7137, from Mađere. L–M, *Bithynia* sp., NHMB 7138, from Mađere. N–O, *Melanopsis arsinovi* Brusina, 1902, lectotype, CNHM 2503-149/2, from Zvezdan. P–Q, *M. arsinovi*, paralectotype, CNHM 2503-149/3, from Zvezdan. Each of the photos of *Melanopsis* and *Bithynia* are given at the same scale, respectively. Scale bars represent: 5 mm (A–I, N–Q); 1 mm (J–M). Colour online.

Order LITTORINIMORPHA Golikov & Starobogatov, 1975
Superfamily TRUNCATELLOIDEA Gray, 1840
Family BITHYNIIDAE Gray, 1857

Genus BITHYNIA Leach *in* Abel, 1818

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

Bithynia sp.
Figure 3J–M

Material. Four opercula from Medoševac (NHMB 7139), two from Mađere (NHMB 7137, 7138).

Remarks. The calcareous opercula with posterior notch and concentric growth lines are characteristic of the genus *Bithynia*. The largest operculum measures 3.8 mm in height (Fig. 3L, M). Determination at species level is, however, not possible.

Family HYDROBIIDAE Stimpson, 1865
Subfamily PYRGULINAE Brusina, 1882*b*

Genus PROSOSTHENIA Neumayr, 1869

Type species. Prososthenia schwartzi Neumayr, 1869; by subsequent designation (Herbich & Neumayr 1875). Middle Miocene, Dalmatia.

Remarks. The generic affiliation of the species listed here is based on overall shell shape, shell size, protoconch features, shape of the aperture, and the sinuate outer lip typical of *Prososthenia* (compare Neumayr 1869; Neubauer *et al.* 2011, 2013*a*, *b*, 2016*b*).

Prososthenia milosevici sp. nov.
Figure 4A–M

LSID. urn:lsid:zoobank.org:act:C2E2ABEC-36ED-4D26-AA2D-03882BAB3927

Derivation of name. In honour of Velimir M. Milošević, who substantially contributed to our knowledge of Miocene mollusc faunas of the Balkan Peninsula.

Types. Holotype: NHMB 7140, H 2.39 mm, W 1.22 mm (Fig. 4A–C, L); paratypes: NHMB 7141, H 2.51 mm, W 1.20 mm (Fig. 4D, E, M); NHMB 7143, H 2.40 mm, W 1.24 mm (Fig. 4F–H, K); NHMB 7144, H 2.24 mm, W 1.07 mm (Fig. 4I, J).

Type locality and stratum. Early middle Miocene lacustrine deposits of Mađere, Serbia.

Material. 26 specimens from Mađere (NHMB 7140–7146).

Diagnosis. Slender, ovoid shell with five low convex and laterally slightly flattened whorls, producing weakly stepped spire; protoconch low domical, with malleate surface, and distinct growth stop at transition to teleoconch; aperture ovoid, often detached in late ontogeny.

Description. Gracile, slender, ovoid shell with up to 5.5 whorls. Protoconch poorly preserved in all studied specimens; consists of about one whorl with traces of formerly malleate sculpture; P/T transition marked by distinct, bulgy growth rim. Teleoconch whorls low convex and laterally slightly flattened, often producing slightly stepped spire. Last whorl ton-shaped, attains 59–63% of total shell height, grades into convex or rarely straight-sided base. Aperture ovoid, inclined, thickened, often expanded; often markedly detached in late ontogeny, forming irregular, broad last whorl. External bulge occurs on last whorl closely behind aperture in about half of the specimens. Umbilicus narrow, slit-like, always open. Outer lip weakly sinuate, with weak posterior and basal indentations.

Remarks. The uneven shape of *Prososthenia milosevici* facilitates distinction from most other species. Given the abundance of this morphology we consider it unlikely that it is a mere growth aberration; also, it can be well distinguished from co-occurring or coeval species. A morphologically very similar species is *P. eburnea* Brusina, 1897 from the Drniš Basin. That species can be distinguished by its larger size and its low convex but not flattened whorls (Neubauer *et al.* 2016*b*). Morphotypes with strongly detached aperture (Fig. 4A, F) are reminiscent of *Cyclothyrella candidula* (Neumayr, 1869) from the Drniš Basin, which has stronger convex whorls and a larger and more inclined aperture. See below for comparison with co-occurring *P. rundici* sp. nov.

Occurrence. Endemic to the SLS, known only from Mađere.

Prososthenia? *naissensis* sp. nov.
Figure 5A–P

LSID. urn:lsid:zoobank.org:act:78F010A5-8678-4DC5-BBCF-CD9B87D0FFCD

Derivation of name. After the town of Niš (*Lat.* Naissus), a large city near the type locality.

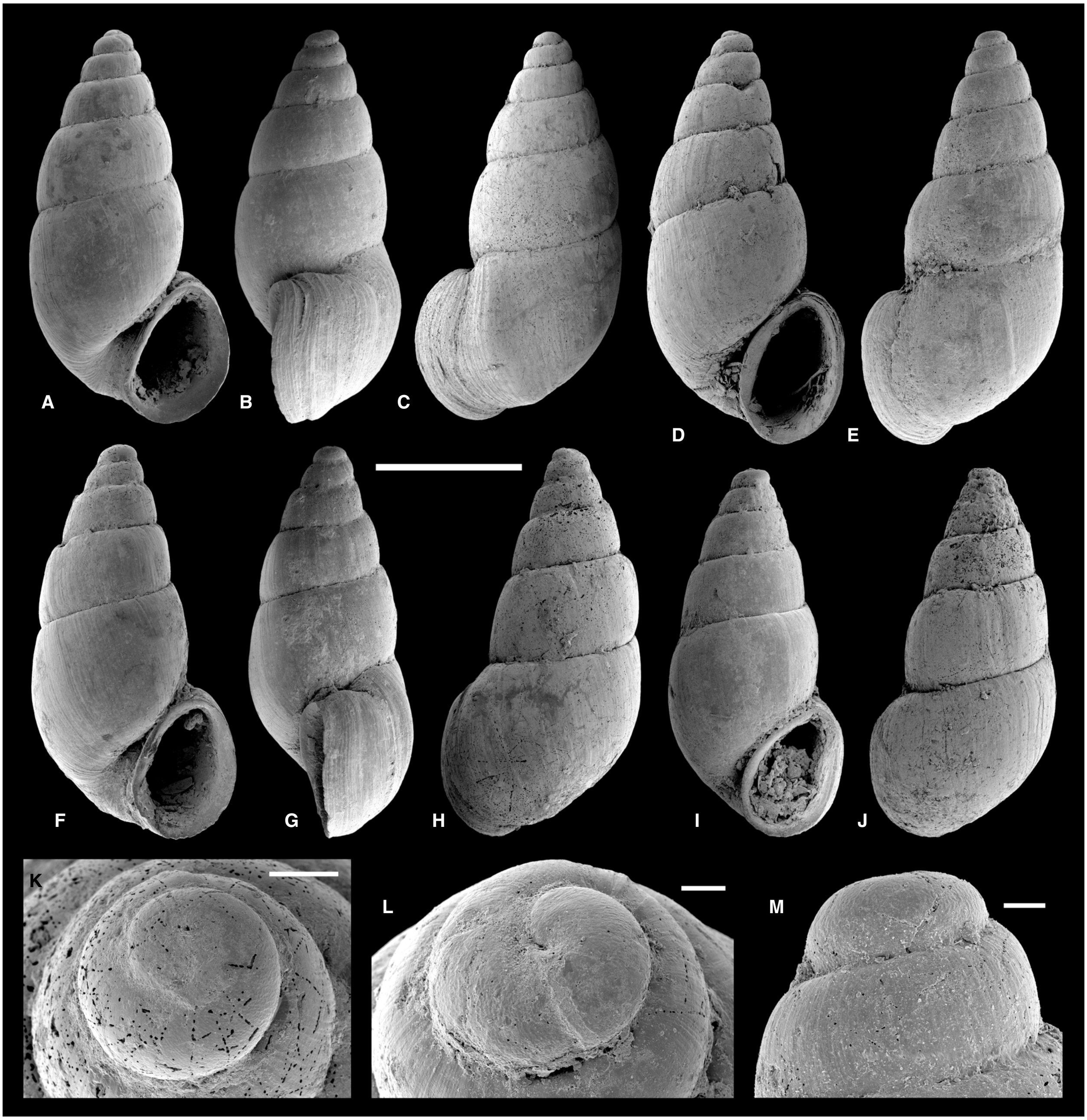

FIG. 4. Hydrobiidae. *Prososthenia milosevici* sp. nov. A–C, L, holotype, NHMB 7140. D, E, M, paratype, NHMB 7141. F–H, K, paratype, NHMB 7143. I–J, paratype, NHMB 7144. All from Mađere. Scale bars represent: 1 mm (A–J); 100 μm (K); 50 μm (L, M).

Types. Holotype: NHMB 7147, H 3.04 mm, W 1.47 mm (Fig. 5A–C, K); paratypes: NHMB 7148, H 2.84 mm, W 1.43 mm (Fig. 5D, E, L); NHMB 7149, H 2.58 mm, W 1.30 mm (Fig. 5F–H, N); NHMB 7150, H 3.16 mm, W 1.41 mm (Fig. 5I, M); NHMB 7151, H 2.85 mm, W 1.33 mm (Fig. 5J, O, P).

Type locality and stratum. Early middle Miocene lacustrine deposits of Medoševac near Niš, Serbia.

Material. 205 specimens from Medoševac (NHMB 7147–7152).

Diagnosis. Fragile, shiny, slender, ovoid to near-conical shell with six highly and regularly convex whorls; protoconch low domical, with granulate surface; P/T boundary marked by shallow furrow followed by distinct orthocline rim; aperture ovoid, leaving narrow umbilicus; outer lip weakly sinuate in lateral view; teleoconch bears numerous spiral furrows of irregular strength and spacing.

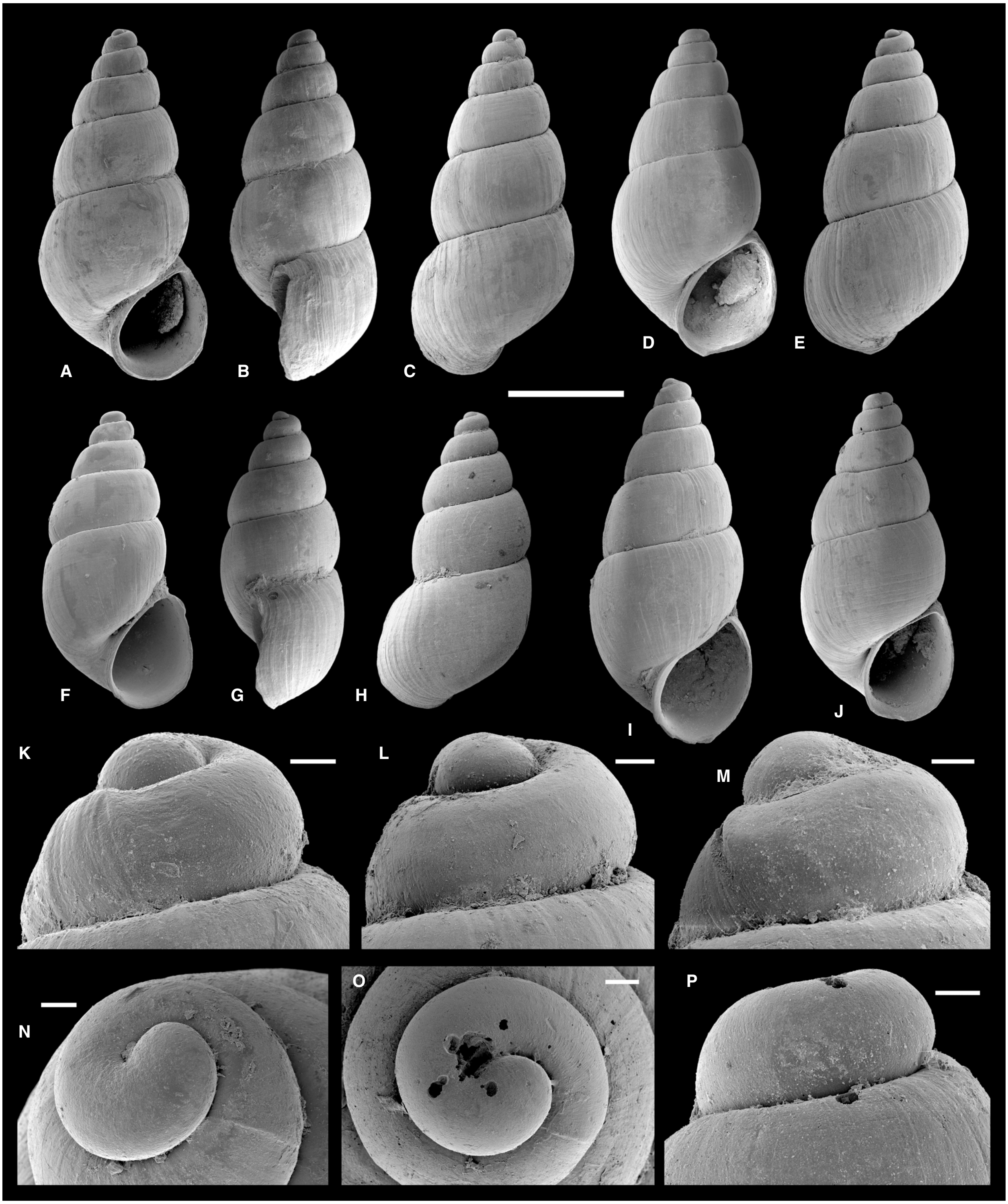

FIG. 5. Hydrobiidae. *Prososthenia*? *naissensis* sp. nov. A–C, K, holotype, NHMB 7147. D, E, L, paratype, NHMB 7148. F–H, N, paratype, NHMB 7149. I, M, paratype, NHMB 7150. J, O, P, paratype, NHMB 7151. All from Medoševac. Scale bars represent: 1 mm (A–J); 50 μm (K–P).

Description. Fragile, shiny, slender shell with up to six highly and regularly convex whorls. Shape variable, depending on expansion rate of whorl height vs width and thus size of last whorl; ranging from ovoid to almost conical. Protoconch consists of 1.0 whorls, with long nucleus and granular surface; sometimes it bears traces of faint spiral sculpture; diameter

325 µm; P/T transition very distinct, formed by shallow furrow followed by orthocline axial rim. Suture narrow, moderately incised. Last whorl attains 55–65% of total shell height; slightly inflated in some individuals. Base steep, weakly convex to straight-sided. Aperture regularly ovoid, with not or poorly thickened peristome; sometimes slightly detached. Outer lip weakly sigmoidal in lateral view, showing weak posterior indentation and broad basal indentation. Umbilicus narrow to almost closed. Growth lines moderately distinct, weakly sigmoidal, with opisthocyrt upper half and prosocyrt lower half. Additionally, spiral grooves of variable strength and irregular spacing cover shell or parts of it.

Remarks. The attribution of this species to *Prososthenia* is questionable. The species differs from other members in having a more gracile shell with more rounded whorls and a less thickened aperture. The protoconch and course of the growth lines, in turn, are very similar to those observed in *Prososthenia*. We thus only tentatively attribute the new species to the genus.

Prososthenia? *naissensis* differs from co-occurring *P. milosevici* sp. nov. by the highly convex whorls, deeper suture, the broader last whorl, and the pointed aperture. *Prososthenia rundici* sp. nov. is smaller and stouter, has less rounded whorls but a relatively larger last whorl.

A similar species is *Nematurella*? *nikolajevici* Brusina, 1902 from Zvezdan. The type series stored at CNHM 2590-236/1–5 is variable and might contain more than one species. To bring stability to the name, we designate the specimen illustrated by Brusina (1902, pl. 9, fig. 6) (CNHM 2590-236/1) as the lectotype. The species differs from *P.*? *naissensis* in the regular conical shape with slowly growing whorls, the blunt apex, the straight-sided aperture with thin peristome, and the lack of an umbilicus.

Prososthenia? *bythinelloides* (Milošević, 1980) comb. nov. from the middle Miocene Peć series in Kosovo has similarly convex whorls but a broader shell and detached aperture. *Prososthenia*? *naissensis* resembles the DLS species *P. eburnea* Brusina, 1897 regarding shape and size, but that taxon differs in the low convex whorls (see also Neubauer *et al.* 2016*b*). *Romania fastigata* Neubauer & Harzhauser in Harzhauser *et al.*, 2012*b* from the early middle Miocene of the Aflenz Basin in Austria is of similar size and shape and shares the high whorls convexity but can be distinguished based on its straight-sided outer lip and the presence of an internal groove for the operculum. '*Hydrobia*' *pseudocornea* Brusina, 1902 from the Sarmatian of the Visoka Hills in north-eastern Serbia is larger while having the same number of whorls, has a more conical shell, and whorls gain less rapidly in height; also, whorls are more convex (CNHM 2617-263/1–4). The smaller variety '*H.*' *pseudocornea minor* Brusina, 1902 from the same locality is much more similar to *P.*? *naissensis*, but it is more slender and has a deeper suture and a nearly elliptical aperture with thin peristome (CNHM 2618-264/1–6).

Occurrence. Endemic to the SLS, known only from Medoševac.

Prososthenia rundici sp. nov.
Figure 6A–R

LSID. urn:lsid:zoobank.org:act:83DB84C0-118C-40FF-92D2-BEDA550C57CF

Derivation of name. In honour of Ljupko Rundić (University of Belgrade) for his contributions to palaeontology in Serbia.

Types. Holotype: NHMB 7153, H 2.84 mm, W 1.57 mm (Fig. 6A, B, M); paratypes: NHMB 7154, H 2.77 mm, W 1.48 mm (Fig. 6C, D); NHMB 7155, H 2.78 mm, W 1.46 mm (Fig. 6E, F, N); NHMB 7156, H 2.57 mm, W 1.39 mm (Fig. 6G, H, P); NHMB 7157, H 2.44 mm, W 1.38 mm (Fig. 6I, J, Q); NHMB 7158, H 2.79 mm, W 1.49 mm (Fig. 6K, L); NHMB 7159, H 2.73 mm, W 1.47 mm (Fig. 6O, R).

Type locality and stratum. Early middle Miocene lacustrine deposits of Medoševac near Niš, Serbia.

Material. 176 specimens from Mađere (NHMB 2498, 2499, 7156–7160), 42 from Medoševac (NHMB 7153–7155, 7161, 7162).

Diagnosis. Small, broadly ovoid shell with five low to moderately convex whorls and large last whorl; protoconch low domical, with weakly granulate surface with traces of spiral threads; P/T transition marked by growth rim; aperture ovoid, upper half of inner lip adnate, outer lip weakly sinuate in lateral view; teleoconch surface bears spiral furrows.

Description. Small, broadly ovoid shell consisting of up to five whorls. Protoconch comprises one whorl that measures 300 µm in diameter; surface weakly granulate, sometimes showing traces of spiral threads in about the last third, where they cross with beginning growth lines; transition into teleoconch marked by weak orthocline growth rim. Teleoconch whorls weakly to moderately convex, separated by distinct, incised suture. Last whorl ton-shaped (in specimens with low-convex whorls) or regularly convex, attains 62–72% of total shell height, passes into straight-sided or weakly convex base. Aperture ovoid, inclined, occasionally slightly thickened and/or expanded; inner lip adnate in upper half. Outer lip weakly sinuate in profile,

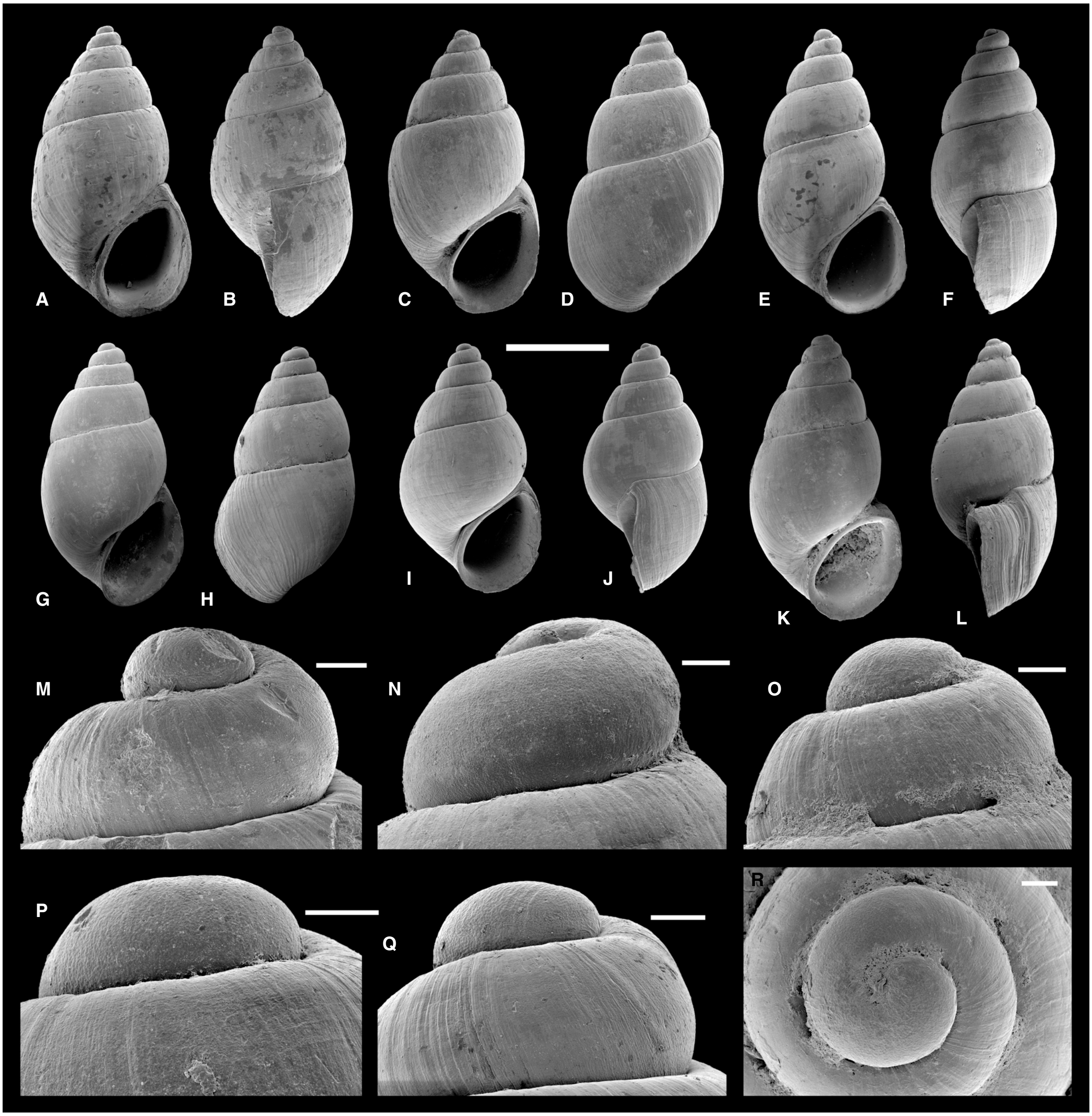

FIG. 6. Hydrobiidae. *Prososthenia rundici* sp. nov. A–B, M, holotype, NHMB 7153, from Medoševac. C–D, paratype, NHMB 7154, from Medoševac. E–F, N, paratype, NHMB 7155, from Medoševac. G, H, P, paratype, NHMB 7156, from Mađere. I–J, Q, paratype, NHMB 7157, from Mađere. K–L, paratype, NHMB 7158, from Mađere. O, R, paratype, NHMB 7159, from Mađere. Scale bars represent: 1 mm (A–L); 50 μm (M–R).

with broad, shallow posterior indentation. Umbilicus usually very narrow, slit-like; sometimes fully covered by inner lip. Growth lines mostly indistinct, near orthocline in lower half and weakly opisthocyrt in upper half. Additionally, spiral grooves of variable strength and irregular spacing cover shell or parts of it.

Remarks. This species is highly polymorphic and sometimes difficult to delimitate from some of the co-occurring species. Co-occurring *P. milosevici* sp. nov. is more slender and has less convex, often slightly stepped whorls. *Prososthenia zuzorici* (Brusina, 1902) is larger and has almost straight-sided whorls.

Prososthenia? *bythinelloides* (Milošević, 1980) and *Bythinella cvijici* Pavlović, 1933, the latter of which probably also belongs in the genus *Prososthenia*, both from the middle Miocene Peć series in Kosovo, are more conical with broader last whorl and detached aperture (for *B. cvijici* see also Milošević 1962, pl. 11, fig. 3). *Nematurella vrabaci* Neubauer *et al.*, 2013*a* from the middle Miocene of the Kupres Basin is larger and exposes a strongly detached last whorl. *Illyricella dzepiensis* Neubauer *et al.*, 2016*c*, from the middle Miocene of the Prozor Basin resembles *P. rundici* in terms of shell shape, size, number of whorls, and whorl convexity; marked differences are the presence of a columellar swelling and the malleate protoconch surface in *I. dzepiensis*. The similarly shaped *Tournouerina turiecensis* Neubauer & Harzhauser *in* Neubauer *et al.* (2015*c*) from the late Miocene of the Turiec Basin is of similar size and shares the convex whorls but differs in the extremely bulbous last whorl and well discernible umbilicus.

Neubauer *et al.* (2013*a*, *b*) misidentified some small and stout hydrobiid specimens of the Gacko and Kupres assemblages as *P. eburnea* Brusina, 1897 and *P. neutra* Brusina, 1897, respectively (see discussion in Neubauer *et al.* 2016*b*). Those specimens closely resemble the present material but differ in their lower whorl convexity and narrower last whorl, which is tightly coiled and leaves the umbilicus covered.

Occurrence. Endemic to the SLS, known only from Mađere and Medoševac.

Prososthenia serbica Brusina, 1893
Figure 7A–M

*1893 *Prososthenia serbica* Brusina, pp. 66–68.
1893 *Prososthenia serbica* Brusina; Brusina, pp. 194–196.
? 1902 [*Hydrobia*]? *Valtrovići* [Brus.]; Brusina, p. vi, pl. 9, figs 4–5.
1902 [*Prososthenia*] *Radičevići* [Brus.]; Brusina, p. ix, pl. 8, figs 15–18.
1902 [*Prososthenia*] *serbica* [Brus.]; Brusina, p. ix, pl. 8, figs 21–23.
1903*b* *Prososthenia Fuchsi* Pavlović, p. 324, pl. 9, figs 11–14.
? 1926 *Hydrobia valtrovići* Brusina; Wenz, p. 1952.
1926 *Prososthenia fuchsi* Pavlović; Wenz, p. 1992.
1926 *Prososthenia radičevići* Brusina; Wenz, p. 1995.
1926 *Prososthenia serbica* Brusina; Wenz, p. 2001.
1931 *Prososthenia Fuchsi* Pavl.; Pavlović, p. 23, pl. 11, figs 21–22.
1931 *Prososthenia Fuchsi* var. *gracilis* Pavlović, p. 23 [as '*glacilis*'], pl. 11, figs 23–24.
1931 *Prososthenia Radičevići* Brus.; Pavlović, p. 25.
1931 *Prososthenia Valtrovići* Brus.; Pavlović, p. 25.
1952 *Prosostenia* [sic] *serbica* Brus.; Veselinović-Čičulić, pl. 1, figs 10–11.
1952 *Prosostenia* [sic] *fuchi* [sic] Pavl.; Veselinović-Čičulić, pl. 1, figs 12–13.
1952 *Prosostenia* [sic] sp.; Veselinović-Čičulić, pl. 1, figs 14–15.
1962 *Prososthenia fuchsi* Pavl.; Milošević, p. 17, pl. 10, fig. 2.
1962 *Prososthenia fuchsi gracilis* [sic] Pavl.; Milošević, p. 17, pl. 10, fig. 4.
2018 *Prososthenia fuchsi* Pavlović; Sant *et al.*, pp. 125, 127, fig. 5 (5).

Types. The syntype series from the middle Miocene (?) deposits of Zvezdan, Zaječar, Serbia, is stored in the CNHM collection (CNHM 2568-214/1–3), along with the types of *P. radicevici* from Bresnica (CNHM 2566-212/1–4) (Milan *et al.* 1974). To bring stability to those names, we designate as lectotypes the specimens CNHM 2568-214/1 for *P. serbica* and CNHM 2566-212/2 for *P. radicevici*. The syntypes of *P. fuchsi* from Mađere are unfortunately missing; the specimens indicated as types in the NHMB collection (NHMB 1254, formerly NHMB 3318) do not belong to that species; probably the labels were mixed up.

Material. 3568 specimens from Mađere (NHMB 7163–7176).

Description. Slender conical shell with up to eight whorls. Protoconch bulbous, low domical, covered with weak, irregular to distinct wrinkles; size and transition to teleoconch unknown. Early teleoconch has high convexity in upper half, producing weakly stepped early spire. Suture thin, poorly incised. Ribs appear on second to third teleoconch whorl. Ribs intensify gradually, starting as weak opisthocline swellings at whorl centre that do not span whole flank. In early stage, ribs have straight to weakly concave profile in upper half and weakly convex in lower half. On following whorl, ribs become more prominent, thin, sharply edged, spiky in profile. Ribs soon become more elongate, less opisthocline, and span entire whorl flank but remain sharp and thin, while formerly prominent convexity (in lateral view) near whorl centre decreases in strength. Weak, slightly protruding bulges are formed where ribs touch upper suture. Penultimate whorl usually broadest, given that ribs are more convex than on last whorl. Ribs are more elongate on last whorl, without pronounced convexity in centre; ribs are straight in upper half, but fade out and become sigmoidal towards base. Throughout ontogeny, width of interspaces approximately doubles width of ribs. In some specimens, gradually intensifying ribs produce weakly coeloconoid outline. Rarely, ribs are strongly reduced, creating irregular, 'bumpy' shell surface (variety *gracilis* of Pavlović 1931). In addition to ribs, whole teleoconch is covered with numerous small but distinct, thin, sharply edged spiral ridges, which slightly intensify during ontogeny. Ridges are visible to naked eye, creating impression of fine striation on entire shell. Ridges are less prominent in central whorl portion. Last whorl attains 45–50% of total shell height. Aperture ovoid, thickened all around, with strongly sinuate outer lip, forming distinct posterior indentation and prominent basal emargination. Sinuate

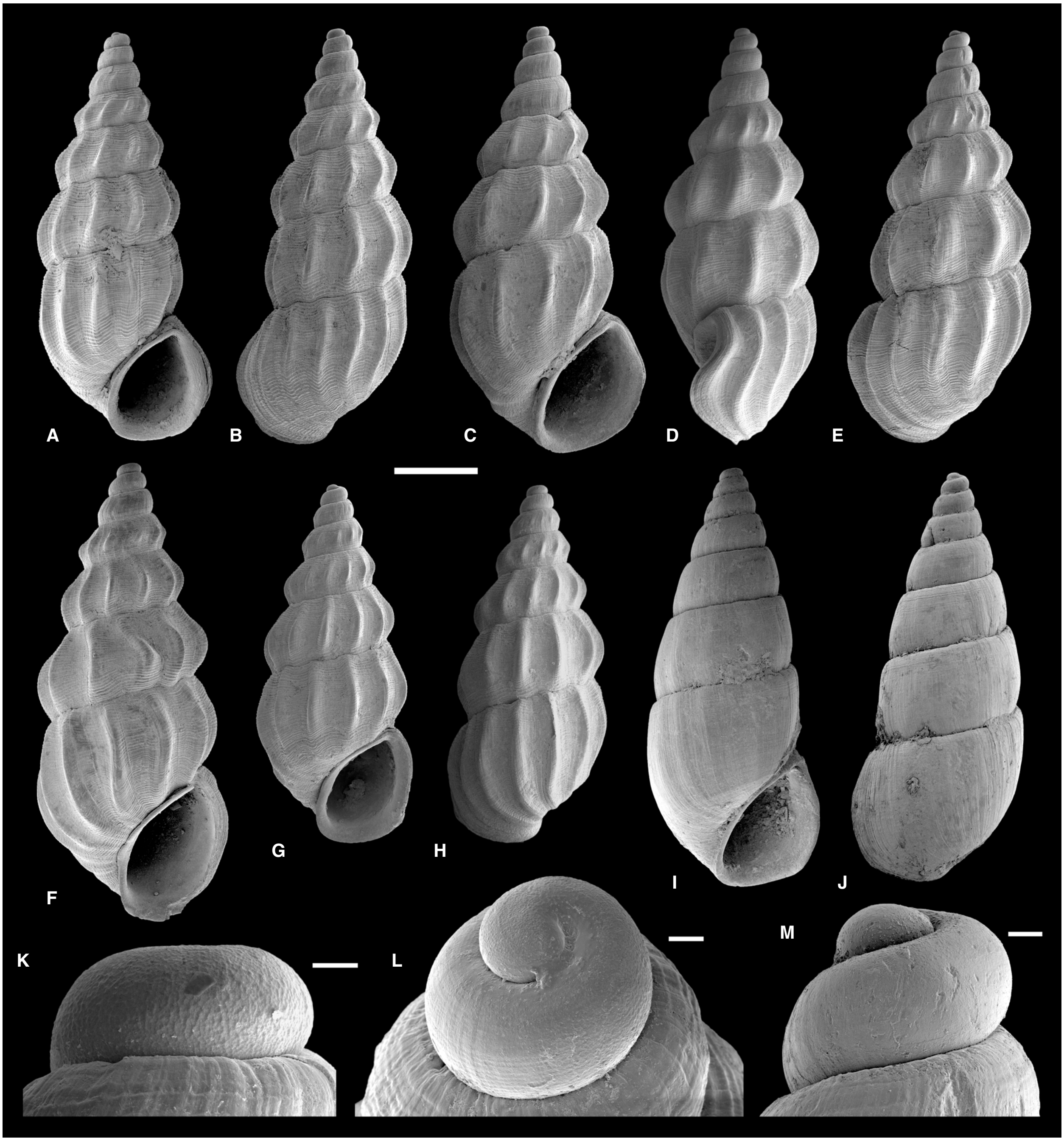

FIG. 7. Hydrobiidae. *Prososthenia serbica* Brusina, 1893. A–B, NHMB 7163. C–E, M, NHMB 7164. F, NHMB 7165. G–H, K–L, subadult specimen, NHMB 7166. I–J, specimen with reduced sculpture (variety *gracilis* of Pavlović 1931), NHMB 7167. All from Mađere. Scale bars represent: 1 mm (A–J); 50 μm (K–M).

form also present and equally strong in specimens with ribs reduced. Umbilicus usually fully covered, but occasionally visible as very narrow, slit-like opening.

Dimensions. H 4.91 mm, W 2.11 mm (NHMB 7163; Fig. 7A, B); H 5.13 mm, W 2.36 mm (NHMB 7164; Fig. 8C–E, M); H 5.51 mm, W 2.30 mm (NHMB 7165; Fig. 7F); H 4.31 mm, W 1.88 mm (NHMB 7166; Fig. 7G, H, K, L); H 5.03 mm, W 2.08 mm (*gracilis*-type; NHMB 7167; Fig. 7I, J).

Remarks. Our specimens perfectly match the description and illustrations of *P. serbica* provided by Brusina (1893, 1902), concerning the anterior emargination of aperture, the curved ribs that fade out towards base, the fine striation, and the weak subsutural groove (which is present in some of our specimens). Pavlović (1903*b*) did not detect the subsutural groove in his specimens from Mađere. Moreover, he apparently overlooked the respective part of the description by Brusina (1893) and wrongly claimed that *P. serbica* lacks striation. Based on these differences, he found it necessary to introduce the new species *P. fuchsi*. Later, Pavlović (1931) found further differences between *P. serbica* and *P. fuchsi* and claimed that 'the Zvezdan species is more slender and has more ribs with narrower interspaces' (translated from Pavlović 1931, p. 24). However, none of the differences noted by Pavlović can be confirmed based on our material from Mađere, and we consider both synonymous.

The reduction of ribs in a few specimens led Pavlović (1931) to the introduction of a new subspecies (*gracilis*), based on seven individuals (compared with numerous *P. fuchsi*; see Pavlović 1931, p. 24). However, given its co-occurrence with the ribbed morphotype in the same environment and their limited number, we consider this form a morphological variety and not a biologically distinct unit. (Note that Pavlović 1931 used multiple spellings of his new variety: *glacilis* in description header but *gracilis* in the caption to plate 11. Following the description, however, referring to a slender variety with weak ribs, the name is unambiguously *gracilis*.)

Prososthenia radicevici Brusina, 1902 from Bresnica has a very similar morphology and shares both the ribs and the spiral striation. The only difference is the larger size of the shell, which attains up to 9 mm in height. Given the overall similarity and the SLS provenance, we consider *P. radicevici* a junior synonym of *P. serbica*. Perhaps, *Hydrobia valtrovici* Brusina, 1902 from Bresnica forms the rib-less counterpart, same as the variety *gracilis* discussed above. *Hydrobia valtrovici* resembles the specimens detected herein regarding the distinct striation and the high ovoid shell. Like *P. radicevici*, however, *H. valtrovici* is larger than the present shells. In addition, it has a more stepped spire. Therefore, we only tentatively list it as a synonym of *P. serbica*.

Prososthenia zujovici Brusina, 1902, also from Bresnica, also shows strong axial ribs and spiral striation, but the shell is regularly conical, the whorls are weakly convex or straight-sided, the ribs are more inclined, more numerous, and start later in ontogeny, and a prominent bulge is formed below the suture. *Micromelania proni* Milošević, 1971 from Serbia and Kosovo superficially resembles *P. serbica* and should be classified as a *Prososthenia* species as well. It differs from the present species in being

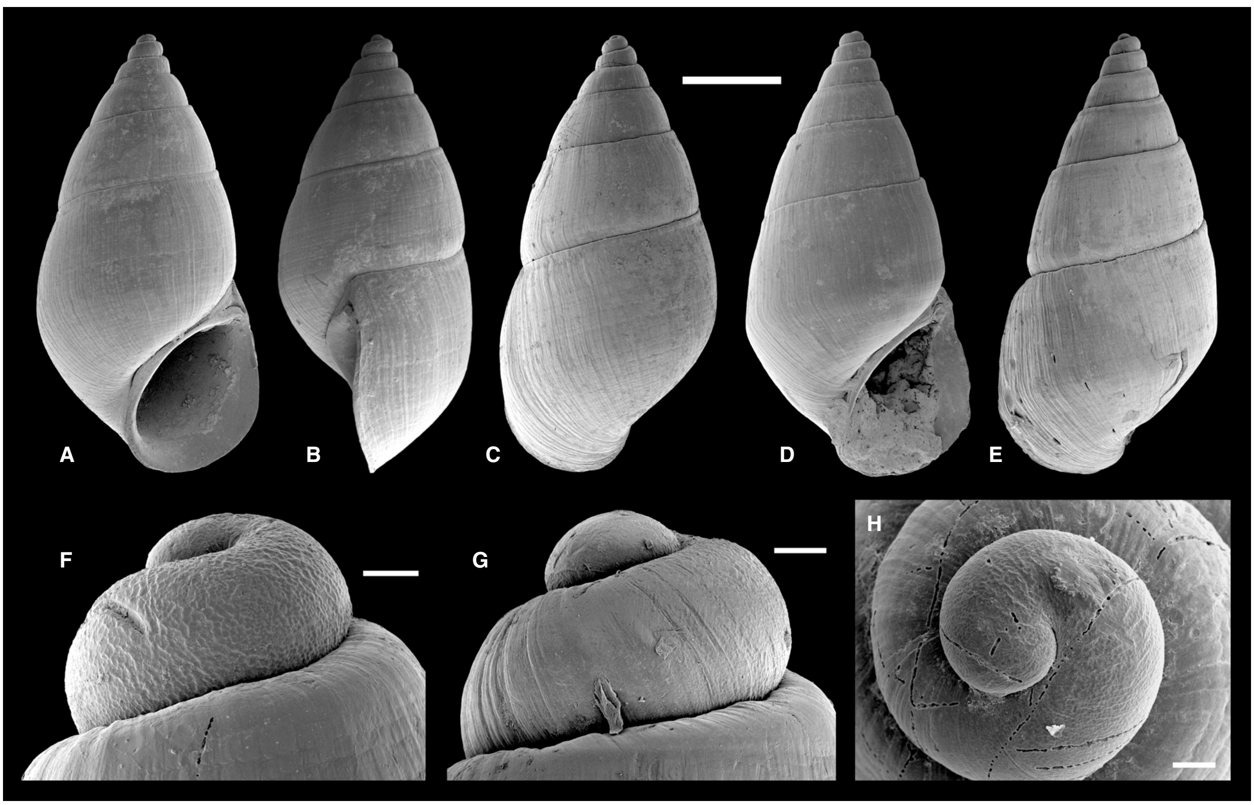

FIG. 8. Hydrobiidae. *Prososthenia zuzorici* (Brusina, 1902). A–C, F, NHMB 7177. D–E, G, NHMB 7178. H, NHMB 7179. All from Mađere. Scale bars represent: 1 mm (A–E); 50 μm (F–H).

more slender, with narrower and higher last whorl, and having a near straight-sided outer lip.

The present species furthermore resembles the type species of *Prososthenia*, *P. schwartzi* Neumayr, 1869, which shares the ribbed and striate shell and the sinuate aperture. That species can be distinguished based on its stouter appearance and the bulbous penultimate whorl (see also Neubauer *et al.* 2011). The likewise ribbed and striate *Prososthenia suessi* Burgerstein, 1877 from the Skopje Basin differs from *P. fuchsi* in its slightly larger size and more slender shape, the higher number and more delicate expression of ribs, which are about equally strong across the whole whorl flank, and the course of the outer lip, showing a very weak posterior indentation and a prominent anterior emargination (pers. obs. based on type material of *P. suessi*). *Prososthenia diaphoros* Neubauer *et al.*, 2013*a* from the middle Miocene of the Kupres Basin is smaller and has more delicate ribs. *Cyclothyrella tryoniopsis* (Brusina, 1874), which also shares ribs and striation, differs in its round, everted aperture with straight-sided outer lip, as well as the malleate protoconch (Neubauer *et al.* 2013*a*, 2016*b*). *Prososthenia cubrilovici* Pavlović, 1933 from the middle Miocene Peć series in Kosovo appears to be broader but shares the prominent ribs. Further similarities or differences cannot be explored, because that species was poorly described and illustrated in the original publication and the whereabouts of the type material are unknown.

Occurrence. Endemic to the SLS, known from Mađere (Pavlović 1931; this study), Velika Lomnica (Krstić *et al.* 1996), and Zvezdan (Brusina 1902). Note that Wenz (1923–1930) erroneously gave Zvezdan as the type locality of *P. fuchsi*.

Prososthenia zuzorici (Brusina, 1902) comb. nov.
Figure 8A–H

*1902 *Nematurella*? *Zuzorići* Brusina, p. viii, pl. 9, figs 16–19.
1926 *Nematurella zuzorići* Brusina; Wenz, pp. 2014–2015.
1931 *Nematurella Zuzorići* Brus.; Pavlović, p. 25.
1933 *Hydrobia šantrići* Pavlović, p. 81, pl. 1, fig. 8.
1935 *Hydrobia šantrići* nov. spec.; Pavlović, p. 47, pl. 1, fig. 8.
1962 *Hydrobia šantrići* Pavl.; Milošević, p. 15, pl. 5, fig. 3.
1980 *Hydrobia šantrići* p.s. Pavlović, 1933; Milošević, p. 70, pl. 1, figs 1–4.
1980 *Hydrobia šantrići oblonga* Milošević, p. 72, pl. 1, figs 5–6.

Types. The syntype series derives from SLS locality Bresnica and is stored at CNHM 2593-239/1–4. We designate the specimen illustrated by Brusina (1902, pl. 9, fig. 17; CNHM 2593-239/1) as the lectotype. The syntypes of *H. santrici* originate from the middle Miocene Peć series at Peć, Kosovo (NHMB 1240, formerly NHMB 1214).

Material. 492 specimens from Mađere (NHMB 2498, 2500, 7177–7180).

Description. Broad conical shell with up to six whorls. Protoconch bulbous, low dome-shaped, consists of *c.* 0.8 whorls; covered with weak, irregular wrinkles that gradually fade out towards indistinct transition to teleoconch. Suture thin, poorly incised. Whorl convexity declines steadily, with first teleoconch whorl highly convex and low convex to straight-sided penultimate and last whorl. Base low convex to straight. In some specimens with near straight-sided last whorl, marked but blunt angulation is formed between flank and base. Last whorl attains about two-thirds of total shell height. Aperture ovoid, weakly expanded, with slightly thickened outer and inner lip and markedly thickened posterior notch. Outer lip sigmoidal in profile, with weak to prominent posterior indentation and basal emargination. Umbilicus usually fully covered by inner lip, but occasionally visible as a very narrow, slit-like opening. In addition to weakly sigmoidal growth lines, numerous spiral grooves appear on early teleoconch and become constantly stronger. Some specimens exhibit thin, barely visible subsutural band.

Dimensions. H 4.45 mm, W 2.27 mm (NHMB 7177; Fig. 8A–C, F); H 4.53 mm, W 2.29 mm (NHMB 7178; Fig. 8D, E, G); H 4.98 mm, W 2.42 mm (NHMB 2500); H 4.11 mm, W 2.08 mm (NHMB 2500); H 4.45 mm, W 2.31 mm (NHMB 2500).

Remarks. The conical shape and near straight-sided last and penultimate whorls allow an easy discrimination of *P. zuzorici* from other *Prososthenia* species from Mađere and Medoševac. The species was introduced as a *Nematurella*, but the overall habitus, the shape of the aperture and the lateral course of the outer lip suggest placement in the genus *Prososthenia*. Species of *Nematurella* typically have a straight-sided outer lip with bulge behind the aperture (Schlickum 1960).

Hydrobia santrici Pavlović, 1933 from the middle Miocene Peć series in Kosovo almost perfectly matches the type series of *P. zuzorici* in terms of shell size, overall shape, characteristics of the aperture, and spiral striation and is considered to be a junior synonym accordingly. At Peć, larger and slightly more elongated specimens of *H. santrici* co-occur with the typical morphotype. They were distinguished as new subspecies *Hydrobia santrici oblonga* by Milošević (1980). Given the morphological plasticity of *P. santrici* (and all other co-occurring hydrobiids), the taxonomic separation seems unjustified. The smaller form with fewer and more convex whorls, which was described as *Hydrobia santrici bythinelloides* by Milošević (1980), appears to be a different species and is tentatively re-combined as *Prososthenia bythinelloides* (Milošević, 1980) comb. nov.

Prososthenia? *cvijici* (Pavlović, 1933) comb. nov., also from Peć, has a similar conical shape with basal angulation but it is smaller and broader, has a detached aperture, and lacks the subsutural band (see also Milošević 1962, pl. 11, fig. 3). *Prososthenia neutra* Brusina, 1897 from the early middle Miocene of the Sinj, Drniš, and Gacko basins is similar in shape but differs in its smaller size and more convex whorls (Neubauer *et al.* 2011, 2013*b*, 2016*b*). *Prososthenia*? *bosnensis* (Brusina, 1902) and *Prososthenia*? *stenostoma* (Brusina, 1902) from the middle Miocene of the Prozor Basin (Neubauer *et al.* 2016*c*) differ in their markedly thickened peristomes and convex bases. *Nematurella zuschini* Neubauer & Harzhauser in Harzhauser *et al.*, 2012*b* from the early middle Miocene of the Aflenz Basin in Austria shares the conical shape and near straight-sided last and penultimate whorls; it differs in the smaller size and the almost straight-sided outer lip. *Tournouerina turiecensis* from the Turiec Basin has whorls that are more convex and a well discernible umbilicus.

Occurrence. The species has been reported from numerous localities in Serbia and Kosovo. In Serbia, it occurs at Bresnica, Ramaća-Bare/Gruža, Donja Mutnica, Mađere, and Pardik (Brusina 1902; Milošević 1980; this study), and Velika Lomnica (Krstić *et al.* 1996).

HYDROBIIDAE incertae sedis

Genus BANIA Brusina, 1896

Type species. Stalioa prototypica Brusina, 1872; by monotypy. Miocene, Balkan Peninsula.

Bania urosevici (Pavlović, 1931) comb. nov.
Figure 9A–M

1922 *Pseudoamnicola* [sic] *Uroševići* n. sp.; Pavlović, p. 50 [nomen nudum].
*1931 *Pseudoamnicola* [sic] *Uroševići* Pavlović, p. 25, pl. 11, figs 25–28.
1962 *Pseudoamnicola* [sic] *uroševići* Pavl.; Milošević, p. 18, pl. 14, fig. 3.

Types. The syntypes from the SLS locality Vrmdža are stored at NHMB. We designate the specimen illustrated by Pavlović (1931, pl. 11, fig. 25) and Milošević (1962) as the lectotype (NHMB 1260, formerly NHMB 2890).

Material. 161 specimens from Medoševac (NHMB 7181–7185).

Description. Small, stout, ovoid or conical shell with up to four whorls. Protoconch consists of about one low whorl; surface finely and densely malleate; transition into teleoconch unclear. Teleoconch whorls low convex, often slightly flattened at mid-height; suture narrow. Last whorl attains 70–80% of total height; passes over marked but blunt angulation into rather shallow, straight-sided base, often producing near-deltoid shell shape. Aperture drop-shaped with weak anterior notch and massively thickened anterior tip; upper half of parietal margin adnate, leaving narrow umbilicus; in some specimens, lower half of parietal margins passes over weak angulation into columellar margin; outer lip thin, straight, inclined with *c.* 15° in lateral view. Growth lines prosocline, moderately distinct.

Dimensions. H 1.82 mm, W 1.39 mm (NHMB 7181; Figure 9A–C, K); H 1.67 mm, W 1.22 mm (NHMB 7182; Figure 9D, I, L); H 1.64 mm, W 1.21 mm (NHMB 7183; Figure 9E, F); H 1.83 mm, W 1.18 mm (NHMB 7184; Figure 9G, H, J, M).

Remarks. The present specimens fit well to '*Pseudoamnicola*' *urosevici* from Vrmdža as described by Pavlović (1931) and illustrated by Milošević (1962) in terms of size and the conical shape with basal angulation. The small stout shell with the malleate protoconch surface suggests a placement in the genus *Bania* (cf. Neubauer *et al.* 2016*b*, *c*). *Bania torbariana* (Brusina, 1874) from the Sinj and Drniš basins (Croatia) and *Bania*? *pachychila* (Brusina, 1902) from Džepi (Bosnia and Herzegovina) match the present species in size and number of whorls, but they are both broader and have regularly rounded body whorls and wider apertures.

Occurrence. Endemic to the SLS, known from localities Vrmdža (Pavlović 1931) and Medoševac (this study).

Subcohort PANPULMONATA Jörger *et al.*, 2010
Superorder HYGROPHILA Férussac, 1822
Superfamily LYMNAEOIDEA Rafinesque, 1815
Family BULINIDAE Fischer & Crosse, 1880

Genus BULINUS Müller, 1781

Type species. Bulinus senegalensis Müller, 1781; by Linnaean tautonomy (see ICZN 1999, Art. 68.5). Recent, Senegal.

Bulinus matejici (Pavlović, 1931)
Figure 10A–I

*1931 *Kosovia Matejići* Pavlović, p. 22, pl. 11, figs 14–16.
2017 *Bulinus matejici* (Pavlović, 1931); Neubauer *et al.*, pp. 296–299, fig. 1 [cum syn.]

Types. Lectotype designated by Neubauer *et al.* (2017) is the specimen illustrated by Pavlović (1931, pl. 11, fig. 16) stored in the type collection of the NHMB 1339 (formerly

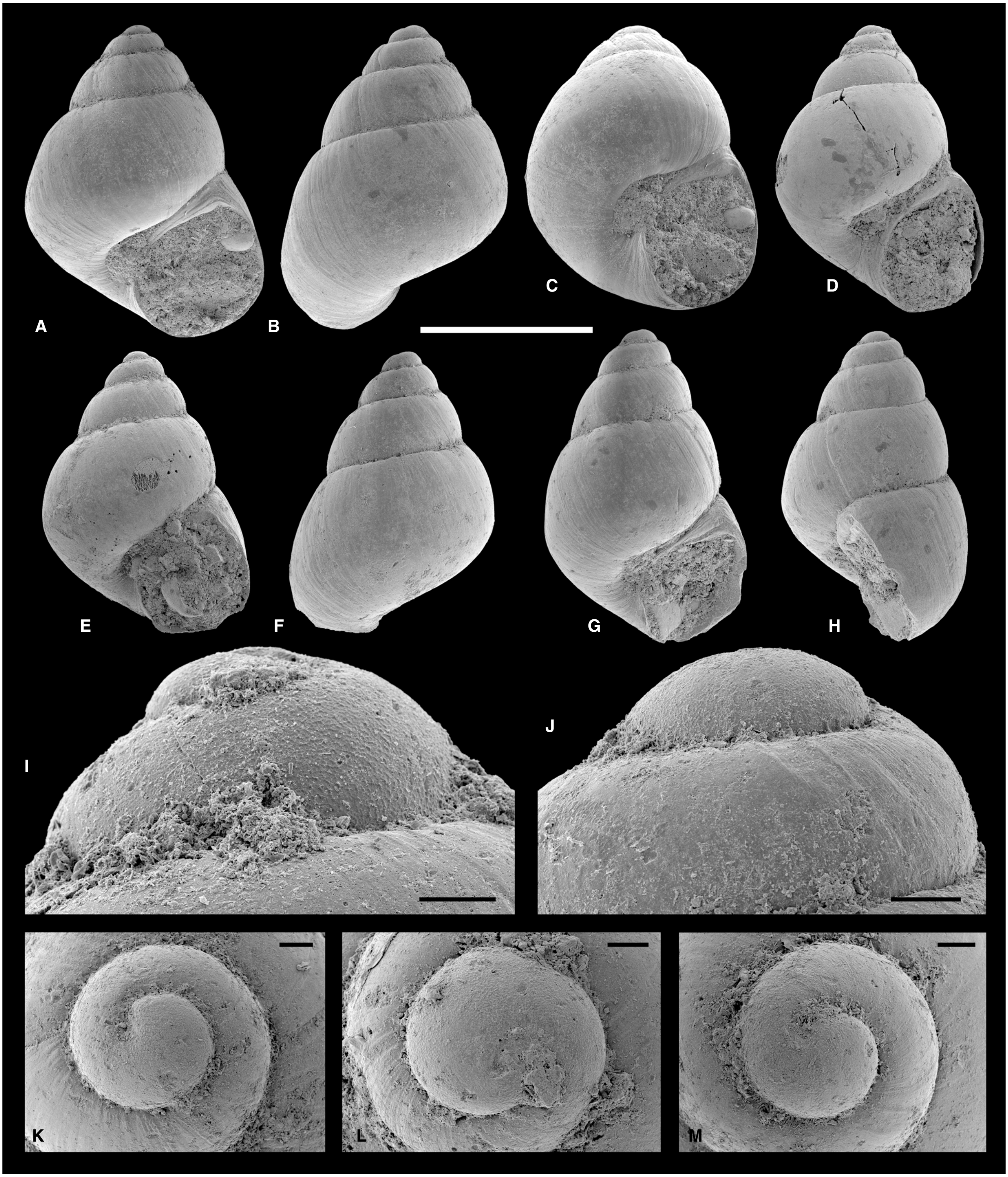

FIG. 9. Hydrobiidae. *Bania urosevici* (Pavlović, 1931). A–C, K, NHMB 7181. D, I, L, NHMB 7182. E–F, NHMB 7183. G–H, J, M, NHMB 7184. All from Medoševac. Scale bars represent: 1 mm (A–H); 50 μm (I–M).

NHMB 2870) (Milošević 1962). Paralectotypes: four juvenile and fragmentary shells (NHMB 2496, formerly NHMB 2871), one juvenile specimen (NHMB 7186, formerly NHMB 2521/2495).

Material. Type material (six specimens) from Mađere.

Remarks. A detailed description and discussion of the systematic classification, as well as notes on the synonymization of the genus *Kosovia* Atanacković, 1959 with *Bulinus*, was recently provided by Neubauer *et al.* (2017).

Occurrence. Endemic to the SLS, reported from localities Mađere, Ćerane near Kaona, Gornja Mutnica, and Pardik (Pavlović 1931; Veselinović-Čičulić 1952; Milošević 1967).

Family PLANORBIDAE Rafinesque, 1815
Subfamily PLANORBINAE Rafinesque, 1815

Genus GYRAULUS Charpentier, 1837

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

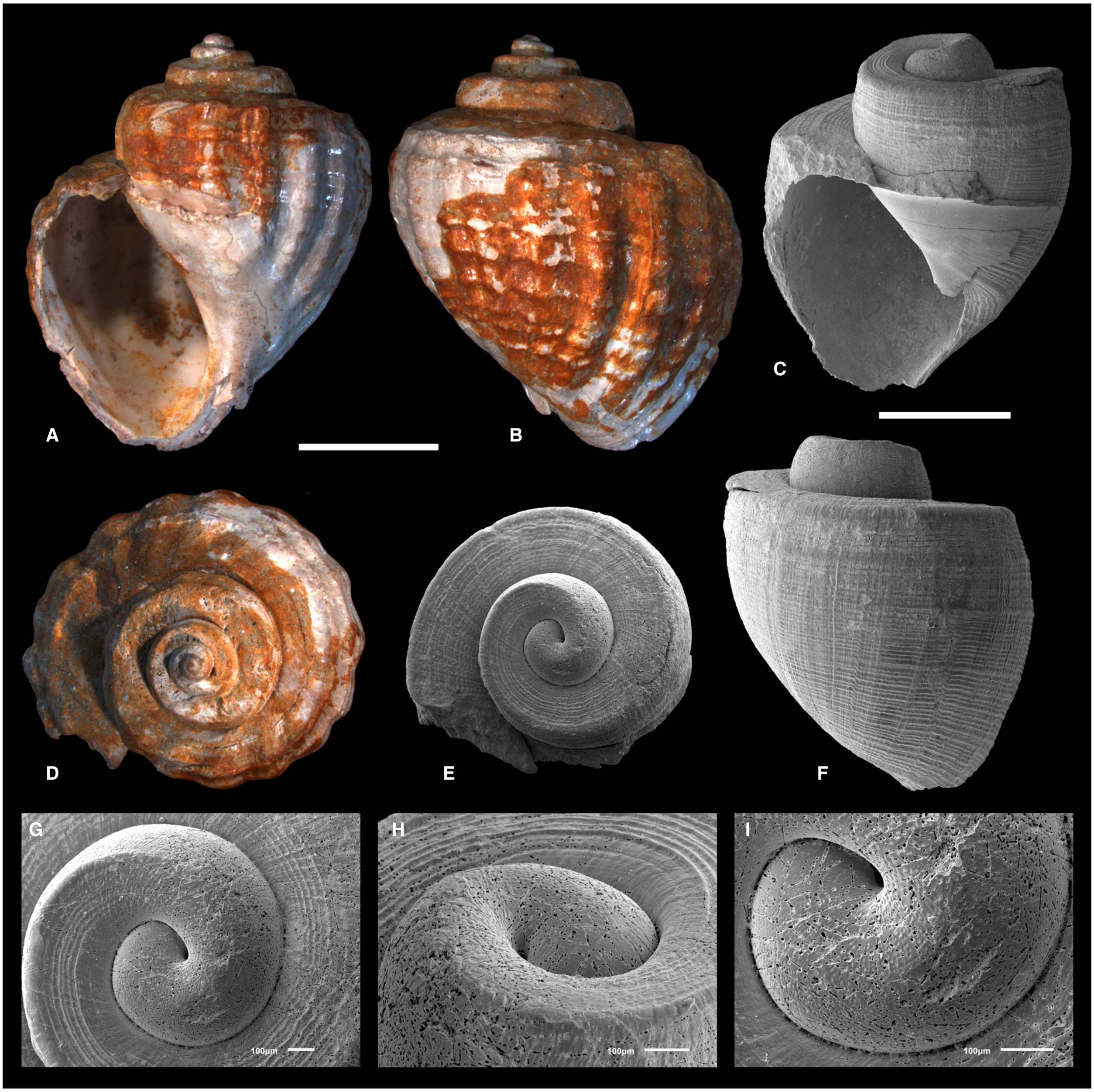

FIG. 10. Bulinidae. *Bulinus matejici* (Pavlović, 1931). A–B, D, lectotype, NHMB 1339. C, E–I, paralectotype, juvenile specimen, showing details of the protoconch, NHMB 7186. All from Mađere. Scale bars represent: 5 mm (A, B, D); 1 mm (C, E, F); 100 µm (G–I). Colour online.

Gyraulus nisseanus (Pavlović, 1931) comb. nov. Figure 11A–K

*1931 *Planorbis nisseanus* Pavlović, p. 18, pl. 10, figs 11–12.
1931 *Planorbis truncatocarinatus* Pavlović, p. 19, pl. 10, figs 15–18.
1931 *Planorbis Živkovići* Pavlović, p. 18, pl. 10, figs 13–14.
1962 *Planorbis nisseanus* Pavl.; Milošević, p. 28.
1962 *Planorbis truncatocarinatus* Pavl.; Milošević, p. 28, pl. 20, fig. 3.
1962 *Planorbis živkovići* Pavl.; Milošević, p. 28.

Types. The syntype series stored at NHMB contains 91 specimens from Medoševac near Niš. We choose as lectotype the specimen illustrated here on Fig. 11A–D (NHMB 7187). The type material of the synonym *P. truncatocarinatus* derives from Vrmdža (NHMB 1316, formerly NHMB 2886), that of *P. zivkovici* from Ramaća (NHMB 1315, formerly NHMB 2325).

Material. Syntype series from Medoševac containing 91 specimens (NHMB 1314, 7187, 7189, 7192, 7193) and four poorly preserved specimens from Mađere (NHMB 7191). Also, one of the paralectotypes of *Planorbis verticilloides* Pavlović, 1931 from Mađere (Fig. 11I–K) is referred to *G. nisseanus* herein (NHMB 7190).

Description. Shell small, asymmetric-discoid, massively keeled, with up to 2.8 whorls. Protoconch consists of 1.1 whorl, marked by distinct spiral threads (nine in specimen shown in Fig. 11H); interspaces between threads slightly uneven; protoconch diameter: 330 μm (measured on umbilical side); P/T transition formed by thin axial line, coinciding with termination of threads and onset of growth lines. In juveniles, a near centrally placed angulation appears that quickly passes into offset keel. Additionally, blunt crests form at transitions between whorl flank and apical and umbilical regions, respectively. This results in funnel-shaped apical and umbilical regions; apical one is deep and narrow, umbilical one is broad and shallow. During ontogeny, blunt crests bordering whorl flank develop into strong keels. Keels (including central one) may be thin and sharp or broad and blunt but are always strong. In some specimens, position of central keel shifts during ontogeny towards apical side, even above level of (formerly) upper keel, producing trapezoid shell profile (Fig. 11F). Irrespective of position and strength of keels, flank portion above central angulation/keel is weakly concave, portion below weakly convex; only weak concavities may be formed directly at keels on otherwise convex lower flank portion, resulting in weakly sinuate flank profile (Fig. 11B, F). In some of those specimens, this convex lower flank portion may form a weak central bulge. Whorls grow fast in diameter, covering about two-thirds of preceding whorls (in apical view). Suture coincides with keels on upper side and in early ontogeny on lower side; in late ontogeny, suture on lower side is closer to periphery. Aperture unevenly heart-shaped, with very thin peristome. Shell surface marked by very distinct growth lines and, in well-preserved specimens, thin spiral grooves (Fig. 11I–K).

Dimensions. H 1.10 mm, W 2.51 mm (NHMB 7187; Fig. 11A–D); H 1.05 mm, W 2.31 mm (NHMB 7189; Fig. 11E–H); H 0.82 mm, W 2.40 mm (NHMB 7192); H 0.86 mm, W 2.22 mm (NHMB 7192).

Remarks. The species' variability as to coiling and the position and strength of the middle keel led Pavlović (1931) to split it into three distinct species: *Planorbis nisseanus* from Medoševac, *P. truncatocarinatus* from Vrmdža, and *P. zivkovici* from Ramaća. Comparison of the type material of all three species suggests, however, that these differences are due to local intraspecific variability. The same range of morphological variation as spanned by the type material of the three species is found in the material of *G. nisseanus* from Medoševac. A reliable distinction of morphotypes is not possible, and we consider the three species synonymous. As first reviser, we choose *G. nisseanus* as the valid name of the species.

Several other species of keeled planorbids have been described from Serbia and Kosovo, some of which closely resemble *G. nisseanus*. Juvenile specimens of *G. nisseanus* resemble co-occurring *G. verticilloides*, which, however, lacks the marked keel. In fact, one of the paralectotypes of *G. verticilloides* (NHMB 7190, Fig. 11I–K) is a juvenile specimen with a distinct keel and is thus referred here to *G. nisseanus*.

Gyraulus kosovensis (Pavlović, 1903*a*) from the late Miocene of the Kosovo Basin is similarly keeled, but the keels are placed near the periphery and the shell is much flatter (see also Milošević 1962, pl. 20, fig. 5). *Gyraulus nusici* (Pavlović, 1903*a*), which co-occurs with the former species, bears less pronounced keels, and the keels are likewise near the periphery; also, the shell is flatter than in *G. nisseanus* and regularly discoid (Milošević 1962, pl. 20, fig. 4). Similarly, the Pliocene Metohia Basin species *G. orahovacensis* (Pavlović, 1903*a*) differs in the flatter, regularly discoid shell with keels close to the periphery. *Gyraulus tetracarinatus* (Pavlović, 1903*a*), also from the Pliocene of the Metohia Basin, can be distinguished based on the presence of an additional keel. The late Miocene *G. bouei* (Pavlović, 1932) from the Metohia Basin differs in the organization of the keels: one along the periphery and a central one on the apical side.

Gyraulus sachsenhoferi Harzhauser & Neubauer *in* Harzhauser *et al.*, 2012*b* from the middle Miocene Aflenz Basin (Austria) shares with *G. nisseanus* the keel at the periphery and the strong growth lines. It lacks the keels on the umbilical and apical sides and has a slightly lower whorl expansion rate.

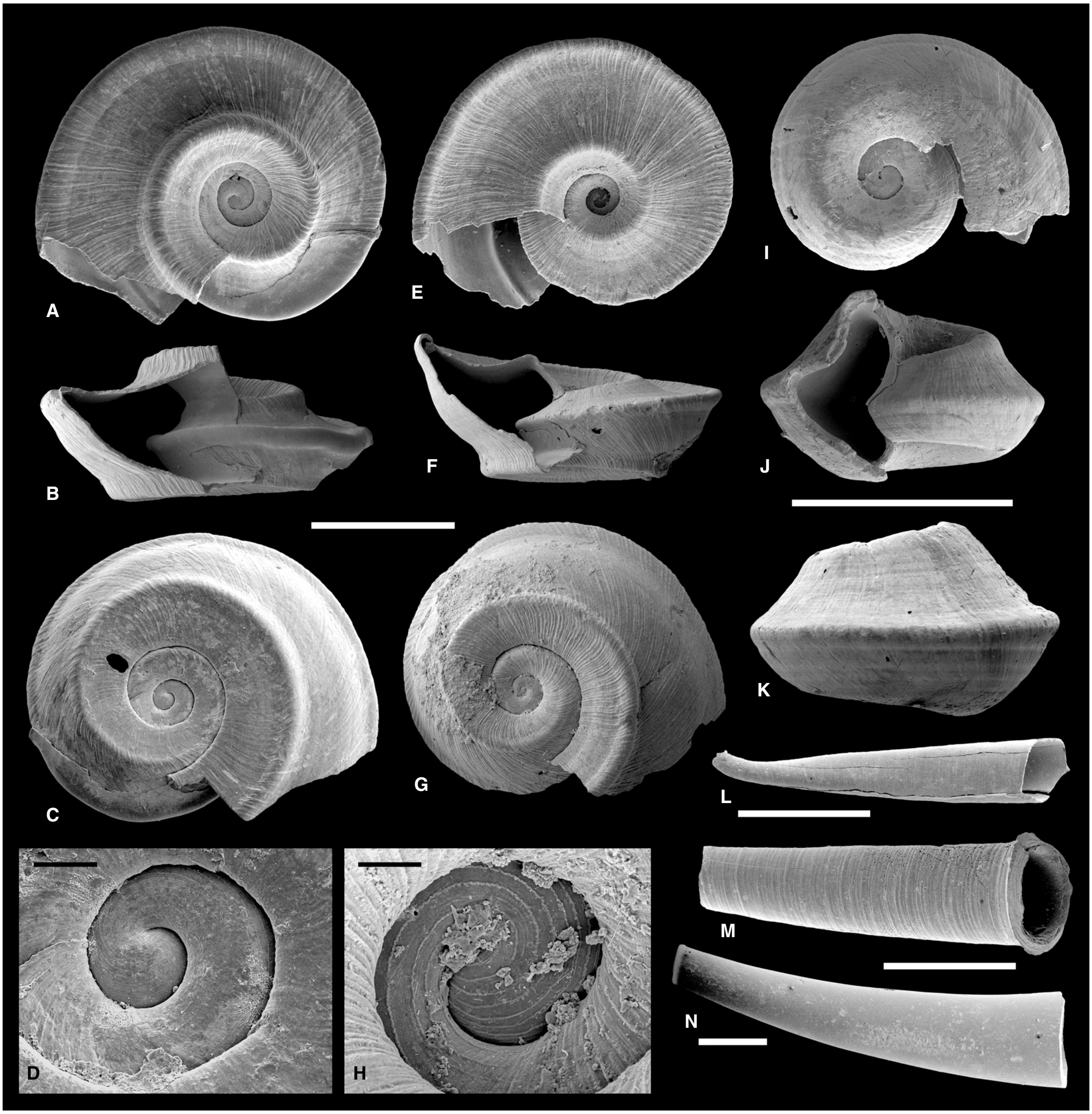

FIG. 11. Planorbidae. A–D, *Gyraulus nisseanus* (Pavlović, 1931), lectotype designated herein, NHMB 7187, from Medoševac. E–H, *G. nisseanus*, paralectotype, NHMB 7189, from Medoševac. I–K, *G. nisseanus*, paralectotype of *G. verticilloides*, juvenile, NHMB 7190, from Mađere. L, *Orygoceras dentaliforme* Brusina, 1882*a*, NHMB 7199, from Medoševac. M, *O. dentaliforme*, NHMB 7200, from Medoševac. N, *O. dentaliforme*, NHMB 7201, from Mađere. Scale bars represent: 1 mm (A–C, E–G, I–N); 100 μm (D); 50 μm (H).

Pavlović originally classified all the planorbids he described in the genus *Planorbis*. We consider all of his species that bear keels and are discussed here (including *G. nisseanus*) to belong in *Gyraulus*. The classification is based on their resemblance with the Recent congeners *G. stankovici* Hadžišče, 1955 and *G. trapezoides* Poliński, 1929 from Lake Ohrid, showing similarly asymmetric and massively keeled shells (Welter-Schultes 2012).

Occurrence. Endemic to the SLS, known only from Medoševac, Mađere, Ramaća, and Vrmdža.

Gyraulus pavlovici (Brusina, 1893)
Figure 12A–H

1886 *Planorbis Hoernesi* Rolle; Žujović, p. 114 [non *Planorbis Hoernesi* Rolle, 1860].

*1893 *Planorbis Pavlovići* Brusina, pp. 68–69.
1893 *Planorbis Pavlovići* Brusina; Brusina, pp. 196–197.
1902 *Planorbis Pavlovići* Brus.; Brusina, p. viii, pl. 3, figs 13–15.
1923 *Gyraulus* (*Gyraulus*) *pavlovići* (Brusina); Wenz, p. 1566 [cum syn.].
1931 *Planorbis Petrovići* Pavlović, pp. 17–18, pl. 10, figs 6–7.
non 1955 *Gyraulus* (*Gyraulus*) *pavlovici* (Brusina); Bartha, p. 305, pl. 2, figs 23–25.
1962 *Planorbis petrovići* Pavl.; Milošević, p. 27.

Types. The syntype series from the middle Miocene (?) deposits of Zvezdan, Zaječar, Serbia, is stored in the CNHM collection (CNHM 2437-197/1–3) (Milan *et al.* 1974). Although we consider *Planorbis petrovici* Pavlović, 1931 as a junior synonym of *Gyraulus pavlovici* (Brusina, 1893), we designate a lectotype from Pavlović's syntypes to bring stability to the species name. We choose as lectotype the specimen from Medoševac near Niš illustrated here in Fig. 12A–D (NHMB 7197; note that Milošević 1962 erroneously indicated the type locality as 'environment of Peć').

Material. 412 specimens from Medoševac (NHMB 1312, 2909, 7142, 7194–7197).

Description. Small discoid shell with up to *c.* 2.8 whorls. Protoconch consisting of about one whorl of *c.* 270 μm diameter (measured on umbilical side); surface covered by weakly raised, broad spiral threads (seven were counted in specimen shown in Fig. 12D); transition into teleoconch indistinct, marked by fading of threads and onset of growth lines. Whorls expand rapidly in diameter, covering between one-third and half of preceding whorl. Maximum convexity above whorl centre; strength of convexity varies along with shell height: shapes range from low discoid with marked convexity at transition to apical plane and narrow aperture to relatively higher shells with blunter and more centrally placed convexity and wider aperture; these extremes are linked via intermediate morphotypes. Discoid morphotypes are more asymmetric, with almost flattened apical side and almost straight-sided whorl flank below convexity. In both types, apical and umbilical sides are sunken, yet slightly deeper on apical side. Aperture heart-shaped, with very thin peristome. Growth lines moderately distinct.

Dimensions. H 0.80 mm, W 1.89 mm (NHMB 7194; Fig. 12A–D); H 0.65 mm, W 1.87 mm (NHMB 7195; Fig. 12E, F); H 0.80 mm, W 2.85 mm (NHMB 2909); H 0.72 mm, W 2.59 mm (NHMB 2909); H 0.73 mm, W 2.63 mm (NHMB 2909).

Remarks. The type material of *Planorbis petrovici* Pavlović, 1931 matches almost perfectly the illustrations of *Gyraulus pavlovici* (Brusina, 1893) in Brusina (1902) regarding shell profile and whorl expansion rate. Only shell size seems to differ slightly, but this is hard to evaluate from the illustrations alone (neither Pavlović nor Brusina provided measurements, and Brusina's type material is unavailable to us). We consider both species synonymous. Brusina (1893) described *Planorbis pavlovici* from deposits at Zvezdan in the Timok Basin, which also belonged to the SLS, for shells previously misidentified as *Planorbis hoernesi* Rolle, 1860.

Gyraulus pulici (Brusina, 1897) from early middle Miocene deposits of the Gacko Basin, *G. geminus* (Brusina, 1897) from the coeval Sinj and Drniš basins, and the widespread middle Miocene *G. kleini* (Gottschick & Wenz, 1916) have a similar shape and profile but are less involute (Neubauer *et al.* 2011, 2013*b*, 2016*b*; Harzhauser *et al.* 2014). *Gyraulus dalmaticus* (Brusina, 1897) reported from the Sinj and Drniš basins is flatter and develops a marked keel (see also Neubauer *et al.* 2016*b*). *Gyraulus gladilini* (Pavlović, 1931) comb. nov. from the late Miocene of the Kosovo Basin is larger (diameter up to 3.9 mm after Pavlović 1931) and more involute (Milošević 1962). Bulbous juveniles of *G. pavlovici* resemble *Gyraulus austroalpinus* (Harzhauser & Neubauer in Harzhauser *et al.*, 2012*b*) comb. nov. from middle Miocene strata of the Aflenz Basin (Austria). That species differs in the even more involute shell with an extremely narrow and deeply sunken spire.

The record of *G. pavlovici* from the Pannonian of Várpalota in Hungary by Bartha (1955) is based on a misidentification. The specimen illustrated in that work differs from *G. pavlovici* in the presence of a distinct keel.

Occurrence. Endemic to the SLS, known from Zvezdan (Brusina 1893) and Medoševac (Pavlović 1931; this study).

Gyraulus verticilloides (Pavlović, 1931) comb. nov.
Figure 12I–L

*1931 *Planorbis verticilloides* Pavlović, p. 18, pl. 10, figs 8–10.
1962 *Planorbis verticiloides* [sic] Pavl.; Milošević, p. 27.

Types. The syntype series of this species also contains a juvenile specimen of *G. nisseanus* (Fig. 11I–K, NHMB 7190). To fix the identity of *G. verticilloides*, we designate the syntype from Mađere illustrated here on Fig. 12I–L as the lectotype (NHMB 7198).

Material. Five specimens from Mađere (NHMB 1313, 2494, 7198).

Description. Shell small, bulbous, with narrow and about equally deep apical and umbilical sides, with up to 2.6 whorls. Protoconch has 1.2 whorls covered by distinct but unevenly

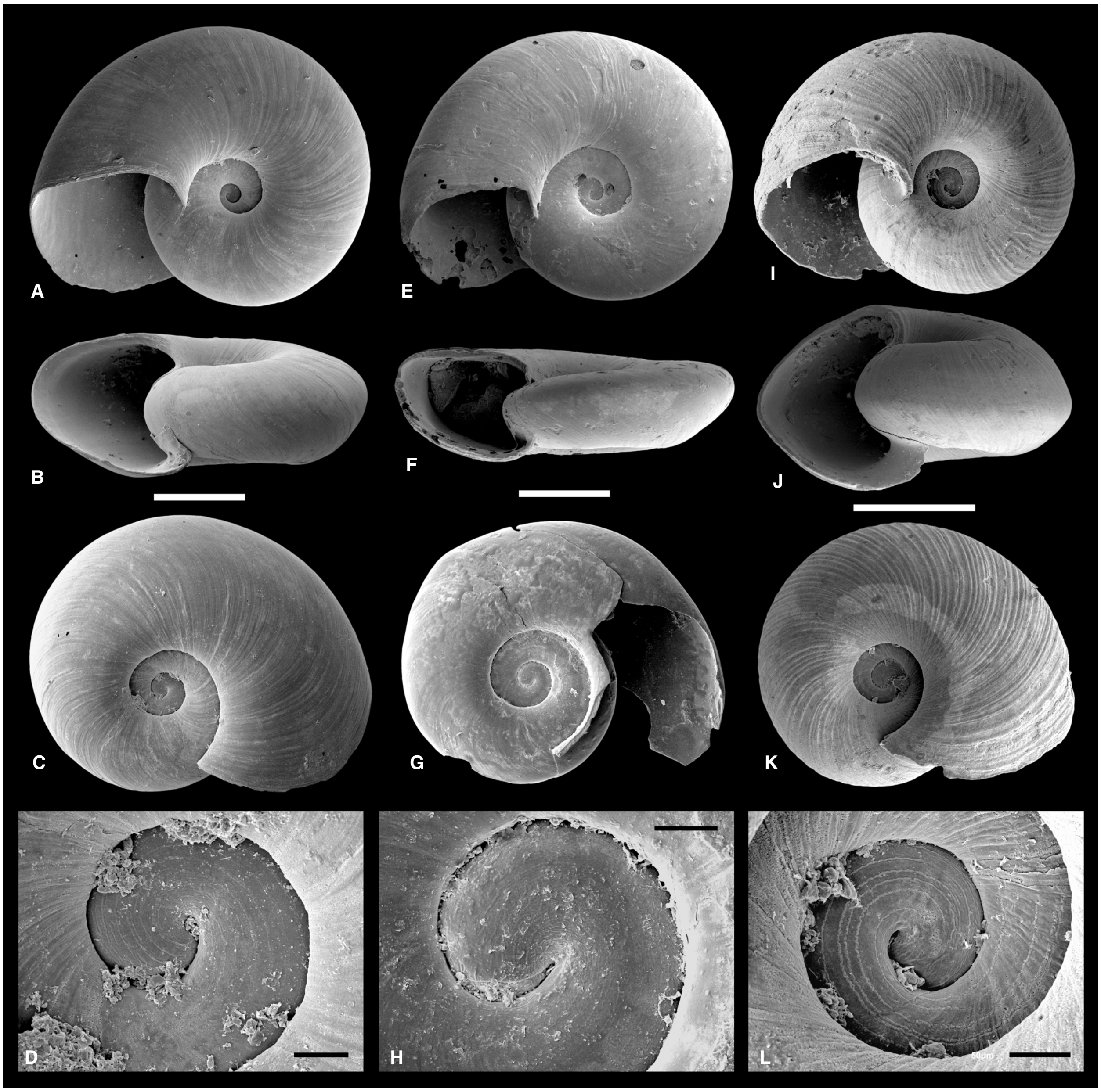

FIG. 12. Planorbidae. A–D, *Gyraulus pavlovici* (Brusina, 1893), lectotype of *Planorbis petrovici* Pavlović, 1931, designated herein, NHMB 7194, from Medoševac. E–F, *G. pavlovici*, paralectotype of *P. petrovici*, NHMB 7195, from Medoševac. G–H, *G. pavlovici*, paralectotype of *P. petrovici*, NHMB 7142, from Medoševac. I–L, *Gyraulus verticilloides* (Pavlović, 1931), lectotype, NHMB 7198, from Ma*đ*ere. Scale bars represent: 500 μm (A–C, E–G, I–K); 50 μm (D, H, L).

spaced spiral striae (seven were counted on specimen shown in Fig. 12L); nucleus devoid of striae, bears irregular wrinkles; protoconch diameter: *c.* 230 μm (measured on umbilical side); P/T transition marked by thin axial line, coinciding with termination of threads and onset of growth lines. Teleoconch whorls expand slowly in diameter, covering about three-quarters of preceding whorls (apical view). Blunt angulation appears slightly below whorl centre. Aperture symmetric, evenly heart-shaped; peristome thin. Evenly spaced and strong growth lines cover shell.

Dimensions. H 0.79 mm, W 1.33 mm (NHMB 7198; Fig. 12I–L); H 0.87 mm, W 1.54 mm (NHMB 2494).

Remarks. Gyraulus verticilloides differs from co-occurring *G. petrovici* in its more involute shell at about the same size, an angulation that is placed below the centre (instead of above) and the stronger growth lines. It also resembles juveniles of *G. nisseanus*, which can be distinguished based on the presence of distinct keels and the larger protoconch. The DLS species *G. oncostomus* (Brusina, 1902) from Dugoselo is more bulbous and lacks the peripheral angulation and the distinct growth lines. *Gyraulus austroalpinus* (Harzhauser & Neubauer in Harzhauser *et al.*, 2012*b*) comb. nov. from the Aflenz Basin is even more bulbous and involute, with very narrow umbilical and apical regions. In addition, the growth lines are less pronounced in that species.

Occurrence. Endemic to the SLS, known only from Mađere.

Genus ORYGOCERAS Brusina, 1882*a*

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

Orygoceras dentaliforme Brusina, 1882*a*
Figure 11L–N

*1882*a* *Orygoceras dentaliforme* Brusina, p. 42, pl. 11, figs 9–15.
1931 *Orygoceras* spec.; Pavlović, p. 16, pl. 4, figs 8–9.
1931 *Orygoceras* cf. *corniculum* Brus.; Pavlović, p. 16, pl. 4, figs 10–11 [non *Orygoceras corniculum* Brusina, 1902].
2016*b* *Orygoceras dentaliforme* Brusina; Neubauer *et al.*, pp. 45–46, figs 8N–O, R [cum syn.]

Material. 15 fragmented specimens from Medoševac (NHMB 7199, 7200, 7202), 6 from Mađere (NHMB 2507, 7201, 7203).

Remarks. The available fragments fully correspond to the early middle Miocene representatives from the DLS (Neubauer *et al.* 2016*b*; see there for a detailed description and synonymy list of this polymorphic species). *Orygoceras corniculum* Brusina, 1902 has been described from much younger, middle Pannonian strata of Markuševec in Croatia and differs in the strongly curved shell.

Dimensions. The largest fragment measures H 5.86 mm, W 1.43 mm (NHMB 7201; Fig. 11N).

Occurrence. Widespread species in the middle Miocene of the DLS and SLS, known from the Drniš, Gacko, Glina, Prozor, Udbina, Kupres, and Sinj basins (Brusina 1882*a*, 1884, 1897, 1902; Bittner 1887; Jurišić-Polšak *et al.* 1993, 2000; Neubauer *et al.* 2013*a*, *b*, 2016*b*, *c*), as well as from Medoševac and Mađere (this study). Its presence in the late Miocene of Tomislavgrad Basin (Šuica gaz) and Livno Basin (Čelebić-Jaruga) indicated by Jurišić-Polšak & Slišković (1988) needs verification.

Class BIVALVIA Linnaeus, 1758
Infraclass EUHETERODONTA Giribet & Distel, 2003
Superorder IMPARIDENTIA Bieler, Mikkelsen & Giribet *in* Bieler *et al.*, 2014
Order MYIDA Stoliczka, 1870
Superfamily DREISSENOIDEA Gray, 1840
Family DREISSENIDAE Gray, 1840
Subfamily CONGERIINAE Mandic & Harzhauser *in* Neubauer *et al.*, 2016*b*

Genus TRIGONIPRAXIS Starobogatov, 1970

Type species. *Congeria triangularis* Partsch, 1835; by original designation. Late Miocene, Hungary.

Trigonipraxis madjerensis sp. nov.
Figure 13A–J

? 1952 *Congeria ornithopsis* Brus.; Veselinović-Čičulić, pl. 1, figs 18–19 [non *Congeria ornithopsis* Brusina, 1892].
1952 *Congeria* cf. *ungula caprae* [sic] Brus.; Veselinović-Čičulić, pl. 1, figs 20–23 [non *Mytilus ungulacaprae* Münster *in* Goldfuss, 1838].
2012 *Mytilopsis cvitanovici servica*; Jovanović, p. 28, fig. 21 [non *Congeria cvitanovici servica* Knežević, 1996].
? 2018 *Trigonipraxis zoici* (Andrusov); Sant *et al.*, pp. 125, 127, fig. 5 (1–2) [non *Congeria zoici* Andrusov, 1897].

LSID. urn:lsid:zoobank.org:act:55302619-266C-4A12-8204-4DD313DC1F6D

Derivation of name. After the type locality.

Types. Holotype: NHMB 7228, L 21.3 mm, H 26.8 mm, Ld 28.6 mm, Hd 21.3 mm, C 15.2 mm (LV, incomplete; Fig. 13A–C); paratypes: NHMB 2508, L 30.4 mm, H 23.6 mm, Ld 27.3 mm, Hd 28.6 mm, C 8.6 mm (LV, incomplete; Fig. 13D); NHMB 7229, L 17.0 mm, H 17.5 mm, Ld 22.0 mm, Hd 16.3 mm, C 15.1 mm (LV, incomplete; Fig. 13E–G); NHMB 7230, L 20.8 mm, H 19.4 mm, Ld 20.5 mm, Hd 22.4 mm, C 12.5 mm (RV, incomplete; Fig. 13H–J).

Type locality and stratum. Early middle Miocene lacustrine deposits of Mađere near Ražanj, on the road next to the cemetery.

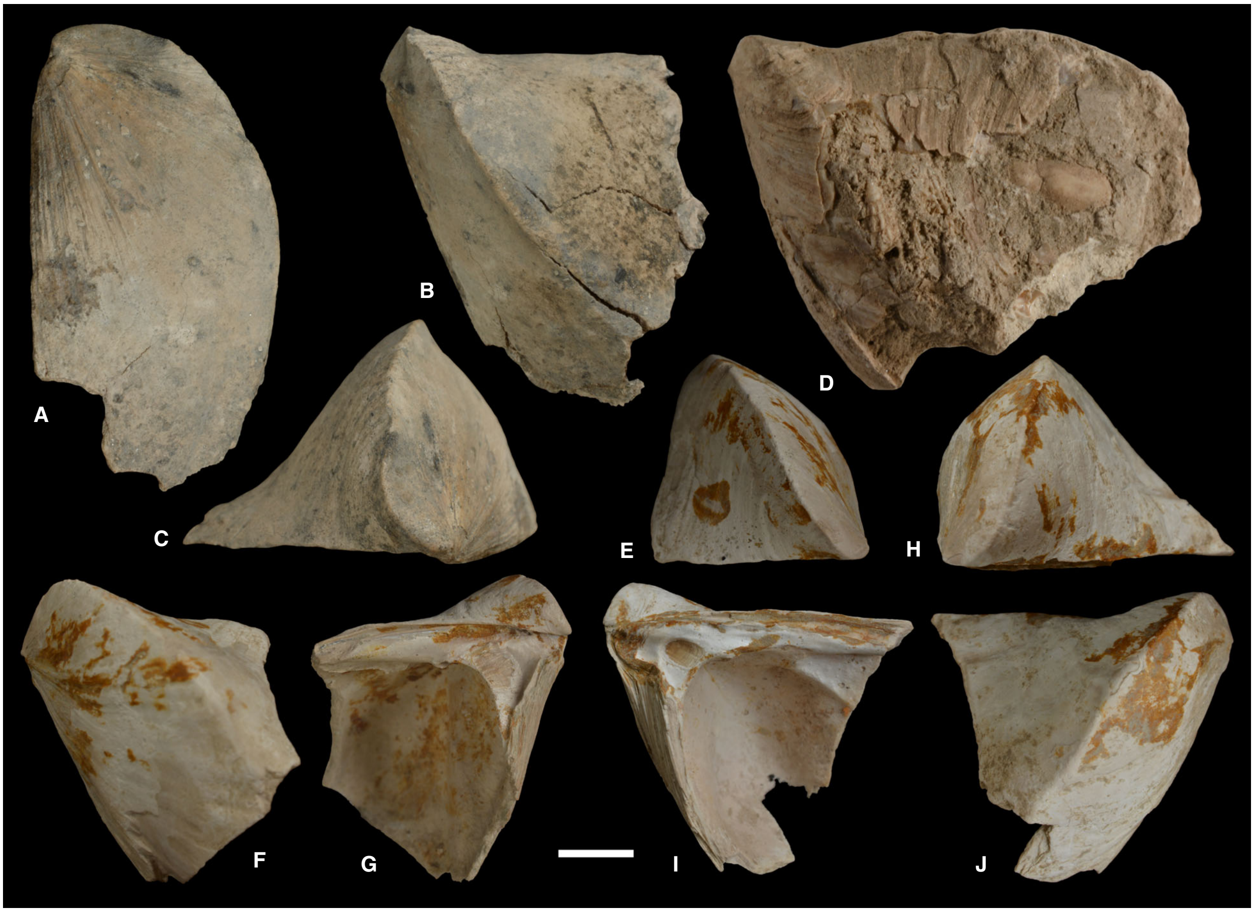

FIG. 13. Dreissenidae. *Trigonipraxis madjerensis* sp. nov. A–C, holotype, LV fragment, NHMB 7228. D, paratype, LV fragment, NHMB 2508. E–G, paratype, LV fragment, NHMB 7229. H–J, paratype, RV fragment, NHMB 7230. All from Mađere. Scale bar represents 5 mm. Colour online.

Material. 197 specimens from Mađere (NHMB 2508, 2492, 2493, 7188, 7228–7232).

Description. Shell trigonal in outline, with twisted, anteriorly pointed umbo and distally pointing posterodorsal and posteroventral tips; highly convex, with arched umbonal area projecting over dorsal margin, with flattened, steep, and high anteroventral area, and with radially depressed, wing-like pointed posterodorsal area. The two latter areas are bounded by a ledge-like, sigmoidal bended, radial ridge, being sharp proximally and solid distally. Outline shows straightened to slightly convex margins. Shell surface smooth, with distally coarsening comarginal lirae. Shell strongly thickened proximally, getting much thinner distally. Shell interior bears massive hinge-plate and nymph only slightly projecting over the umbonal cavity, which is shallow due to infill with shell material. Due to the thickened shell wall, anterior adductor muscle scar appears relatively small and shallow. Ligament suture is deep, apophysis small, less projecting, and hidden beneath the hinge plate.

Remarks. The present species is characterized by the projecting transversal ledge throughout ontogeny, a feature absent in *T. nisseana* (Pavlović, 1931). Previously, it was erroneously reported from the present region by Veselinović-Čičulić (1952) as *Congeria* cf. *ungulacaprae* (Münster *in* Goldfuss, 1838). While our material consists only of incomplete specimens, Veselinović-Čičulić (1952, pl. 1, fig. 21) illustrated a complete shell, showing a deltoid shape with an Ld of *c.* 3.5 cm. Specimens identified there as *Congeria ornithopsis* (Brusina, 1892) are somewhat larger (Ld *c.* 4.0 cm) and the keel is less sharp, but this might be only a secondary preservation effect, and the specimens probably belong to the same species. The specimens from Popovac illustrated by Sant *et al.* (2018) as *Trigonipraxis zoici* are in an even worse state of preservation and are only tentatively attributed to the present species.

Another ledge-bearing species previously described from the SLS is *Trigonipraxis*? *servica* (Knežević, 1996), which appears to be much smaller and less arched. Besides, the original material of Knežević (1996) also includes specimens with supressed ledge. The holotype drawing in Knežević (1996) suggests a close relationship to the present specimens, but they are distinctly smaller. The low documentation quality in the original publication calls for a restudy of the type material of *T.*? *servica* to clarify this relationship. The type material derives from Donja Sabanta near Kragujevac in Central Serbia, originating from middle Miocene deposits of the Kruševica-Pčelice Formation.

Specimens from Laznica in the Žagubica Basin (NE Serbia) illustrated by Popović (1960) as '*Congeria ungula-caprae* Münst.' have the same common morphological features as our specimens, i.e. a ledge-like keel throughout ontogeny, twisted and arched umbo, high convexity, and acute apical angle. Still, with an up to 82 mm diagonal length (measured from illustrations) they are apparently much larger. Specimens from the same deposits identified as '*Congeria croatica* Brus.', with a similar ledge-like keel, differ by a rectangular apical angle and somewhat smaller size. Both forms have a broadly impressed anteroventral margin adjacent to the umbo differing clearly from the straightened margin of our specimens.

Popović (1960) attributed the respective deposits in the Žagubica Basin to the late Pannonian ('Pontian' therein; see Mandic *et al.* 2015). Marović *et al.* (1984) resampled the fauna and concluded that it mostly consists of dreissenids closely related to *Trigonipraxis antecroatica* (Katzer, 1921) (which is at present considered a synonym of *T. kucici* (Brusina, 1907)) from the early Miocene of the DLS. Pointing to the absence of lymnocardiids typically present in Pannonian lacustrine assemblages, they associated the Žagubica Basin deposits with the SLS series. *Trigonipraxis kucici* indeed has a solid and sharp keel throughout ontogeny, reaching a maximum diagonal length of 51 mm (Kochansky-Devidé & Slišković, 1978, p. 50). It differs from the present species by a stronger wing-like posterodorsal elongation and the greater diagonal length and thus less slender shape.

Occurrence. Endemic to the SLS, known from Mađere, Pardik, and Setka (= Šetke) near Ražanj and tentatively from Popovac (Veselinović-Čičulić 1952; Jovanović 2012; Sant *et al.* 2018; this study).

Trigonipraxis nisseana (Pavlović, 1931) comb. nov.
Figure 14A–V

1889 *Congeria triangularis* Part.; Žujović, p. 111 [non *Congeria triangularis* Partsch, 1835].
1893 *Congeria triangularis* Partsch; Brusina, p. 62 [non Partsch, 1835].
*1931 *Congeria nisseana* Pavlović, p. 6, pl. 1, figs 10–11.
1931 *Congeria dactyloides* Pavlović, p. 6, pl. 1, figs 8–9.
1931 *Congeria* spec. aff. *Zoići* Brus.; Pavlović, p. 5, pl. 4–7.
? 1967 *Congeria neumayri* Andr.; Popović & Novković, p. 322, pl. 1, figs 5–9.
? 1967 *Congeria ornithopsis* Brus.; Popović & Novković, p. 322, pl. 1, fig. 1.
2012 *Mytilopsis* sp.; Jovanović, p. 28, fig. 23.

Types. The syntype series of *Congeria nisseana* Pavlović, 1931 originates from riverbanks of the river Nišava at Medoševac and Jagodan Mali, which are northern and western districts of the town Niš in south-eastern Serbia. We designate here the LV from the steep riverbank of the Nišava near Medoševac illustrated by Pavlović (1931, pl. 1, fig. 11; NHMB 1212, formerly NHMB 2895) as the lectotype of *Trigonipraxis nisseana*. The paralectotype illustrated by Pavlović (1931, pl. 1, fig. 10) is a single RV from the same locality as the lectotype (NHMB 1212). The only illustrated syntype of *C. dactyloides* is a single LV from the same locality (NHMB 1211, formerly NHMB 2898).

Unfortunately, the remaining parts of the type series at NHMB seem to be mislabelled. The original labels were obviously not revised after publication of Pavlović (1931) to be in accordance with those results. In particular, from the box labelled as '*Congeria dactyloides* Pavl.' we found four tubes containing 25 instead of the seven specimens mentioned by Pavlović (1931). Furthermore, a box with 12 juvenile valves is labelled as '*Congeria zoisi* Brus.', while the illustrated specimens of '*Congeria* spec. aff. *Zoići* Brus.' are labelled as '*Congeria* ex. gr. *triangularis* Partsch'. Hence, a full reconstruction of Pavlović's type series is impossible.

Material. 2138 specimens from Medoševac including syntypes illustrated by Pavlović (1931) (NHMB 1211, 1212, 2505, 2520, 2521, 2524, 2525, 7204–7227).

Description. Shell solid, slightly inequivalve with only LV showing byssal notch, higher than long, elongated posteriorly and posteroventrally, showing anterodorsally and terminally positioned, strongly twisted beak. Outline trigonal, with anteriorly pointed beak and narrowly convex posterodorsal and posteroventral edges, and with horizontal, straightened to slightly convexly bended dorsal margin, subvertical to steeply posteriorly inclined, narrowly concave to convex posterior margin, and straightened sigmoidal anteroventral margin. Shell moderately convex with the convexity axis running from beak to posteroventral shell edge, followed dorsally by flattened to slightly concave, posterodorsal area, showing wing-like, posterodorsally pointed margin; anteroventral area is narrow, subplane, slightly convex or concave, steep, inclined anteroventrally or sometimes orthogonal to commissure plane; byssal notch is present in anterior half of LV. Diagonal axis of maximum convexity more or less sigmoidal, beginning at beak, usually narrowly convex, sometimes trigonal in cross-section, developed as a keel that might be solid umbonally, but never as sharp to form a ledge. Exterior surface smooth, shiny, showing irregular comarginal

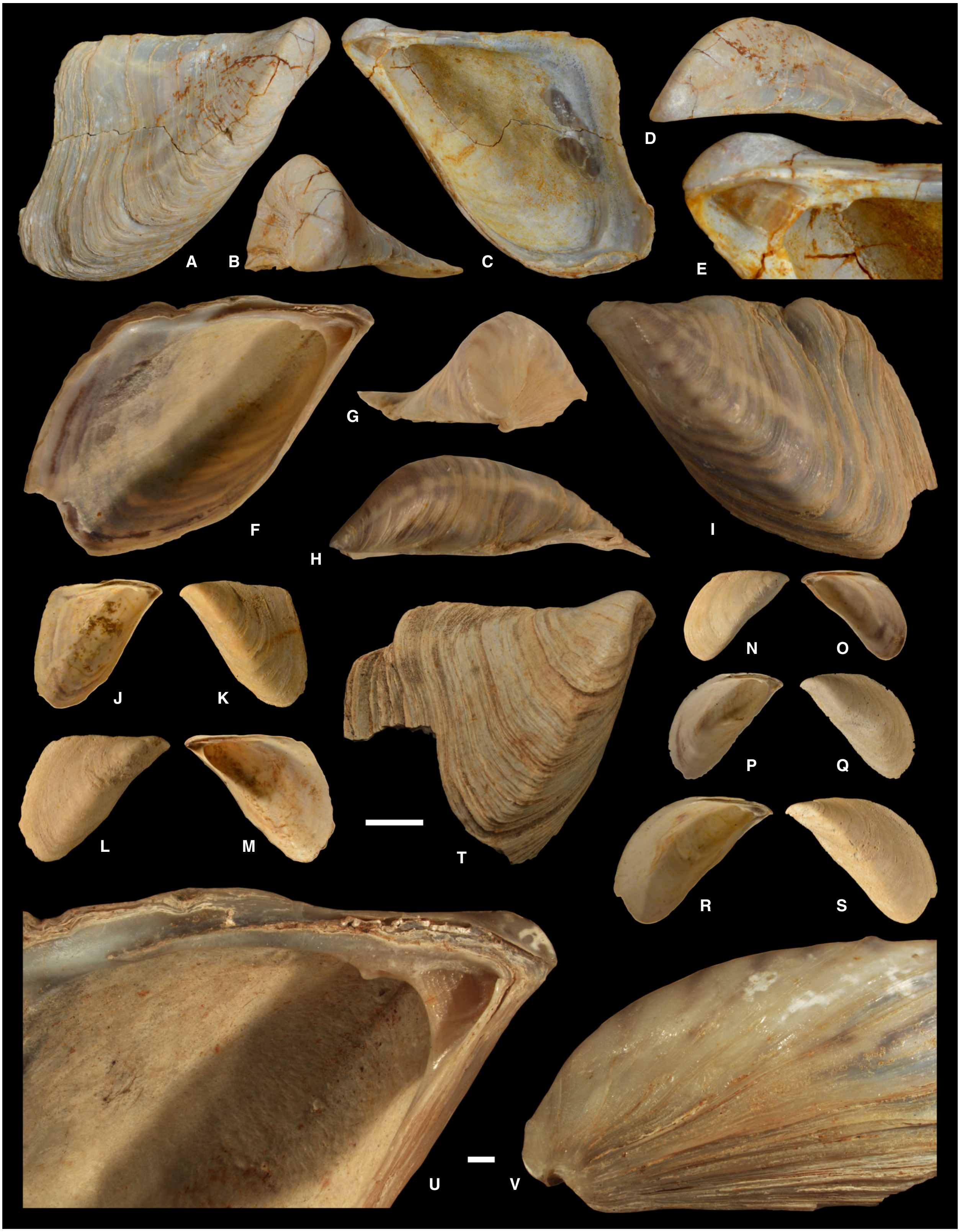

FIG. 14. Dreissenidae. *Trigonipraxis nisseana* (Pavlović, 1931). A–E, RV, NHMB 2520. F–I, U, V, LV, NHMB 7204. J–K, LV, NHMB 7205. L–M, RV, NHMB 7206. N, O, RV, NHMB 7207. P–Q, LV, NHMB 7208. R–S, LV, NHMB 7209. T, RV illustrated by Pavlović (1931, pl. 1, fig. 7, as '*Congeria* spec. aff. *Zoići* Brus.'), NHMB 7210. All from Medoševac. Scale bars represent: 5 mm (A–S); 1 mm (U, V). Colour online.

lirae and growth constrictions, more commonly on distal shell portion. Interior shell shows straightened ledge-like nymph starting at umbo and reaching half-way to posterior margin; ligament suture above it is deep; ventrally, near distal end of the hinge plate, small apophysis with elongated anterior byssal/pedal retractor muscle scar is attached to it. Hinge plate fully occupied by anterior adductor muscle scar, which is moderate in size, deeply depressed, flattened, posteriorly elongated, trigonal, well-projecting above the deep umbonal cavity. Pallial line without sinus, adjoined posterodorsally by rounded posterior adductor muscle scar, followed by narrower vertically elongated posterior byssal retractor scar.

Dimensions. L 27.7 mm, H 23.2 mm, Ld 34.5 mm, Hd 20.6 mm, C 9.6 mm (RV; Fig. 14A–E; NHMB 2520); L 35.0 mm, H 23.2 mm, Ld 33.3 mm, Hd 20.0 mm, C 8.8 mm (LV; Fig. 14F–I, U, V; NHMB 7204); L 12.7 mm, H 11.2 mm, Ld 15.1 mm, Hd 7.9 mm, C 3.9 mm (RV; Fig. 14L, M; NHMB 7206).

Remarks. The collection from Medoševac represents a unique opportunity to study Congeriinae specimens from the SLS in aragonite preservation. Congeriinae shells are usually strongly leached, available only as external or internal moulds (Mandic *et al.* 2019*a*). The material is dominated by young and juvenile individuals and shell fragments, yet contains a number of fully preserved adult valves. While demonstrating a high phenotypic plasticity typical for this subfamily, the specimens maintain a trigonal, convex, and carinate general shape. This feature is also typical for the type species of *Trigonipraxis*, i.e. *T. triangularis*, with which Žujović (1889) and Brusina (1893) confused the present specimens. Based on this misidentification the series was erroneously attributed to the Pliocene. *Trigonipraxis triangularis* differs from *T. nisseana* in being more highly inflated, having a more robust shell with prominent growth rugae, a more prominent keel and commonly a secondary keel in the dorsal shell region.

Pavlović (1931) originally distinguished three species: two new to science (*Congeria nisseana* and *Congeria dactyloides*) and one potentially related to *Trigonipraxis zoici* ('*Congeria* spec. aff. *Zoići* Brus.'). He referred almost all the material to *T. nisseana*, while only seven specimens were considered to belong to *T. dactyloides* and 'few' others to *T.* aff. *zoici* (but see section 'Types' above).

Trigonipraxis dactyloides is much smaller than *T. nisseana* and exceptionally narrow, having a reduced dorsal wing. A detailed comparison of the material proved, however, that such morphs are very rare and represent a variation of the same species, showing high plasticity of the outline. The adult Serbian shells are slightly larger than *T. zoici*, with a maximum transversal length of 35 mm, compared with the 28 mm length measured on Croatian specimens (Kochansky-Devidé & Slišković 1978). They are more slender, with a stronger acute umbonal angle and a narrower radial convexity zone. The latter is shifted anteroventrally due to broader posterodorsal and narrower anteroventral areas. *Trigonipraxis zoici* is unknown from Dalmatia as erroneously indicated by Pavlović (1931). Originally described from central Croatia (Lovča and Dugo Selo Lasinjsko) from deposits Ar/Ar dated to *c.* 16.0 Ma (Mandic *et al.* 2012), its spatial distribution is restricted to the northern Dinarides and the southern Pannonian Basin in Croatia and Bosnia and Herzegovina (Kochansky-Devidé & Slišković 1978).

Specimens illustrated from the Kraljevo Basin by Popović & Novković (1967) as *Congeria ornithopsis* and *C. neumayri* are apparently misidentifications and might be related to *T. nisseana*. Their specimens lack the ledge-like keel, but the material is either poorly preserved (*C. ornithopsis*) or contains only young adult specimens (*C. neumayri*) and does not allow a more detailed assessment. *Trigonipraxis sumadica* (Knežević, 1996) from the Levač Basin is probably closely related to *T. nisseana*, but has a less steep and broader posteroventral margin and a more rounded outline. It was originally described as a subspecies of the DLS species *T. antecroatica*, which is presently considered a synonym of *T. kucici* and differs markedly in the presence of a sharp keel.

The difference to *Trigonipraxis* sp. found at Mađere is the lack of a sharp projecting transversal keel (see below). Such a keel, if present in *T. nisseana*, is neither ledge-like nor sharp and solid.

Note on the spelling of Trigonipraxis zoici*.* The prevailing spelling of the species in the literature is *Trigonipraxis* (or sometimes *Congeria*) *zoisi*. Andrusov (1897) based his description on an unpublished manuscript of Brusina (who had used the spelling '*Zoisi*'). However, Andrusov (1897) used in both the text and plate volume the spelling '*Zoići*' without exception or providing an etymology. The shorter German summary, where he used both '*Zoisi*' and '*Zoići*' (p. 33), appeared not before 1898. Both the original Russian and the German versions are featured in volume 25 of the *Travaux de la Société des Naturalistes de St. Pétersbourg, Section de la Géologie et de Minéralogie*, but the Separatum of the German text contains an extra preface, where Andrusov clearly stated that the German text was finished in January 1898. Brusina (1897) also mentioned the taxon as '*Congeria Zoisi*' in the introduction to his monograph on the Balkanese mollusc faunas, but as a *nomen nudum*. Katzer (1918) listed both names and selected '*zoisi*' as the valid one, which is an unjustified emendation. Kochansky-Devidé & Slišković (1978) suggested that Andrusov had named the species after Sigmund Zois (also known as Žiga Zois), but given that the etymology was not provided in the original work, there is no evidence for this intention. According to ICZN Art.

32.5.1 the correct spelling of the species is '*zoici*'. Given that the original spelling *zoici* has been used as a valid name after 1899 (e.g. Pavlović 1931, Taktakishvili 1973, Sant *et al.* 2018), the conditions for maintaining an incorrect subsequent spelling because of prevailing usage (Art. 23.9.1.) are not fulfilled. Still, given that '*zoisi*' is, at more than 80%, the prevailing spelling in the literature, maintaining its senior synonym would cause too much confusion. Thus, the matter should be referred to the ICZN Commission for a ruling under the plenary power (Art. 23.9.3).

Occurrence. Endemic to the SLS, known only from Medoševac.

RESULTS

Altogether, 16 species were identified from the two studied localities (Table 1). The fauna is dominated by Hydrobiidae (6 species) and Planorbidae (4 species), along with two species of Dreissenidae and one species of each Neritidae, Melanopsidae, Bithyniidae and Bulinidae. Taking into account the new species descriptions and synonymizations made herein, 28 gastropod species are known for the SLS, with 20 (71.4%) of them being endemic. With regard to the herein studied fauna, 10 of the 13 gastropod species identified to species level (76.9%) are endemic to the SLS and so are both bivalve species. The overall bivalve fauna of the SLS is by far less well documented than the gastropods and so far only three dreissenid and one unionid species are ascertained to occur in the SLS; further investigations are required to provide a more detailed picture; the Discussion chapter below is therefore mainly based on the gastropod fauna.

The statistical analyses indicate a high similarity of the gastropod fauna presented here with that of the neighbouring Timok Basin (Fig. 1), regarding species-level data as well as type of fauna (Fig. 15A, B). The composition at the genus level confirms a close relationship of the SLS fauna with both DLS and Lake Pannon faunas (Figs 1, 15B). Except for the erratic occurrence of *Bulinus* in the SLS, all genera are also found in the DLS and Lake Pannon assemblages. Most notable is the presence of the enigmatic planorbid genus *Orygoceras*, which occurs only in those three systems. *Orygoceras dentaliforme* is the only species shared between the SLS and DLS; *Prososthenia radicevici*, which is herein considered a synonym of *P. serbica*, is the only SLS species mentioned also from Lake Pannon.

Only three gastropod species (10.7%) are shared between the SLS and the presumably coeval Lake Metohia in Kosovo, i.e. *Micromelania metochiana* Milošević, 1971, *M. proni*, and *P. zuzorici*. Two SLS gastropod species (7.1%) have been claimed from presumably late Miocene strata of Lake Skopje, but at least one of these matches is questionable: the mention of *Prososthenia suessi* Burgerstein, 1877 from Zvezdan by Živković (1893) is probably based on a misidentification of the similar *P. serbica*. The faunas of Soceni in Romania as well as those from Austria and Germany (lakes Groisenbach, Rein, and Steinheim) have very little similarity, at both a species and genus level.

DISCUSSION

The present study is only a first step towards revising the SLS fauna. Nonetheless, our comparisons with material from nearby SLS localities, such as the diverse assemblage from Zvezdan in the Timok Basin studied by Brusina (1893, 1902), Živković (1893), and Pavlović (1903*a*), settled the taxonomic identities of a number of species. The high similarity between the Timok assemblages and those of central and southern Serbia suggest that they belong to the SLS as well. It is likely that at least a temporary hydrological connection existed between the Timok Basin and the southern extent of the SLS (Fig. 1). There is still some uncertainty as to age of the Timok deposits. Rundić *et al.* (2018) recently suggested a late early Miocene age (*c.* 16.9 Ma) for the lacustrine deposits there based on radiometric dating, but it is not clear if all the mollusc species recorded from the basin actually derive from that dated layer. If so, this would set back the onset of the SLS by at least 2 myr.

The assemblages from Mađere and Medoševac are somewhat different, and there is a number of possible hypotheses to explain that. On the one hand, the differences may be rooted in varying local environmental conditions. Some of the species might have been adapted to specific conditions that limited their dispersal capability. On the other hand, the differences might be the effect of selective transport, preservation or sampling techniques. The sample from Medoševac contains only small species or small specimens of larger species, such as the juveniles of *Theodoxus* and *Melanopsis*. Given the lack of information about the sedimentology of the deposits from which the fossils were collected, these considerations remain speculative. Fieldwork and a detailed palaeoenvironmental reconstruction are required to address this issue. Alternatively, the presumed connection between the southern and northern parts of the SLS (Fig. 1) might have been only temporarily available, and dispersal was merely a matter of chance.

TABLE 1. Freshwater mollusc species occurring at Mađere and Medoševac.

Species	Authority	Family	No. specimens	Mađere	Medoševac	SLS endemic
Theodoxus zivkovici	(Pavlović, 1903*b*)	Neritidae	84	x	x	x
Melanopsis petkovici	Pavlović, 1931	Melanopsidae	838	x	x	x
Bithynia sp.		Bithyniidae	6		x	
Prososthenia milosevici	sp. nov.	Hydrobiidae	26	x		x
Prososthenia? *naissensis*	sp. nov.	Hydrobiidae	205		x	x
Prososthenia rundici	sp. nov.	Hydrobiidae	218	x	x	x
Prososthenia serbica	Brusina, 1893	Hydrobiidae	3568	x		x
Prososthenia zuzorici	(Brusina, 1902)	Hydrobiidae	492	x		
Bania urosevici	(Pavlović, 1931)	Hydrobiidae	161		x	x
Bulinus matejici	(Pavlović, 1931)	Bulinidae	6	x		x
Gyraulus nisseanus	(Pavlović, 1931)	Planorbidae	95	x	x	x
Gyraulus pavlovici	(Brusina, 1893)	Planorbidae	412		x	x
Gyraulus verticilloides	(Pavlović, 1931)	Planorbidae	5	x		x
Orygoceras dentaliforme	Brusina, 1882*a*	Planorbidae	21	x	x	
Trigonipraxis madjerensis	sp. nov.	Dreissenidae	197	x		x
Trigonipraxis nisseana	(Pavlović, 1931)	Dreissenidae	2138		x	x

SLS, Serbian Lake System.

Regional gastropod palaeobiogeography

Krstić *et al.* (2012) considered the middle Miocene lacustrine systems of central to southern Serbia, Kosovo, Macedonia, Bulgaria and northern Greece to belong to a single, huge 'Serbian Lake', but this is not reliably supported by data and conflicts with regional tectonics (Sant *et al.* 2018). The mollusc faunas indicate little similarity at a species level between Serbian and Kosovan (Pavlović 1903*a*, 1931, 1932, 1933, 1935; Milošević 1962; present study) and Macedonian systems (Burgerstein 1877), respectively (Figs 1, 15A). The connection to Bulgaria and Greece presumed by Krstić *et al.* (2012), in turn, is based on outdated stratigraphic concepts (Neubauer *et al.* 2015*a*). The differences at a species level between the SLS, DLS, and Lake Pannon is most probably rooted in their different stratigraphical ages, environmental conditions (brackish Lake Pannon vs freshwater DLS and SLS), as well as the isolated evolution in those long-lived lakes. Because of this, the three systems have been classified into different palaeobiogeographical regions (Neubauer *et al.* 2015*a*).

Given the large faunal overlaps at the genus level and the intermediate stratigraphical position, we hypothesize that the SLS fauna (*c.* 16.9 or 14.6–14.2 Ma; Sant *et al.* 2018; Rundić *et al.* 2018) is a stepping stone between the faunas of the DLS (*c.* 18.2–14.8 Ma; De Leeuw *et al.* 2012) and the late Miocene Lake Pannon (*c.* 11.6–4.5 Ma; Neubauer *et al.* 2016*d*). However, there is still a considerable stratigraphic gap between the SLS and Lake Pannon. Taking into account the late Badenian marine transgression in the southern Morava Basin near Popovac, which flooded the SLS at *c.* 13.8 Ma (Sant *et al.* 2018; Mandic *et al.* 2019*b*), this still leaves a gap of more than 2 myr, which coincides with the Serravallian stage (corresponding to the late Badenian to Sarmatian). A major problem in tracking the biogeographical affinities for that interval is the lack (or lack of knowledge) of diverse and well-studied faunas. As representatives of a typical long-lived lake fauna, the majority of the SLS taxa are expected to require stable conditions and are unlikely to be found in assemblages of temporary character. The only long-lived lake fauna known for the interval in question is that of Lake Steinheim, which shares with the SLS the genera *Bania* and *Gyraulus* (Rasser 2013). Other potential stepping stones involve the Sarmatian/late Serravallian fauna of Soceni in Romania (including the only record for the genus *Prososthenia* for the entire 2 myr gap; Jekelius 1944), as well as several unnamed freshwater systems fringing the Central Paratethys in Austria, Slovenia, Hungary, Croatia, Romania and Serbia (variably containing *Theodoxus*, *Melanopsis*, *Bania* and *Gyraulus*) (see Neubauer *et al.* 2015*a*, *b* for details and geographical distribution). None of the faunas known for the late Langhian and Serravallian, however, contains species of *Orygoceras*. It is unlikely that its peculiar and unique uncoiled shell developed twice independently. Consequently, we expect that *Orygoceras*, as well as some of the other SLS species lineages, survived in yet unknown and potentially long-lived environments on the Balkan Peninsula.

Another similar type of fauna has been found in Lake Groisenbach in the Aflenz Basin in the Austrian Alps (Harzhauser *et al.* 2012*b*). It also contains a species of *Bulinus*, which only rarely occurred in Europe during the Miocene (Neubauer *et al.* 2017), as well as similar and presumably related species of planorbids (see also Systematic Palaeontology section above). The deposits there are considered to be of early middle Miocene (Langhian,

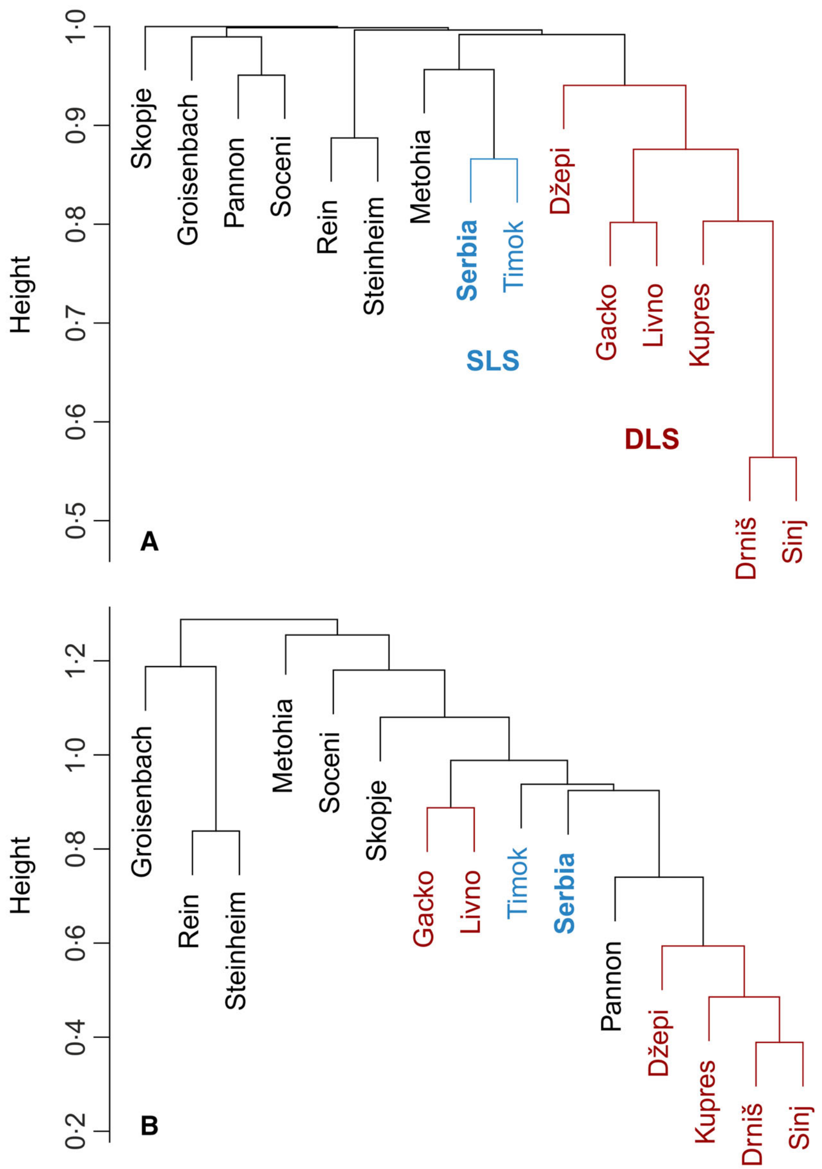

FIG. 15. Dendrograms of the cluster analyses. A, species-level relationships of gastropod faunas discussed in the text, based on a Dice distance matrix of species presence–absence data. B, type of gastropod fauna, based on a Euclidean distance matrix of the number of species per genus. Note the clear dissimilarities at species level between faunas of the selected lakes and lake groups compared with the higher similarity at genus level. *Abbreviations*: DLS, Dinaride Lake System; SLS, Serbian Lake System. Colour online.

early Badenian; Harzhauser *et al.* 2012*b*) age and thus coeval with those of the SLS. Neubauer *et al.* (2017) hypothesized a waterfowl-mediated transport to explain the similarity of the faunas deriving from hydrologically unconnected ecosystems.

CONCLUSION

1. We provide the first revision of the freshwater mollusc assemblages derived from the two localities Mađere and Medoševac in central and southern Serbia. The fauna is part of the Serbian Lake System (SLS) and consists of 14 species of gastropods and two species of bivalves.
2. The fauna is dominated by the gastropod family Hydrobiidae, consisting of six species of which three are new to science: *Prososthenia milosevici* sp. nov., *Prososthenia*? *naissensis* sp. nov. and *Prososthenia rundici* sp. nov. The Planorbidae are, with four species, the second-most diverse, followed by Dreissenidae with two species, including the new species *Trigonipraxis madjerensis* sp. nov. Neritidae, Melanopsidae, Bithyniidae, and Bulinidae are represented by one species each.
3. At *c.* 55% the hydrobiids also dominate in terms of relative abundance, followed by Dreissenidae (28%), Melanopsidae (10%) and Planorbidae (6%). The remaining taxa account for less than 1%. Relative abundance varies considerably between the two

localities, perhaps owing to varying local environmental conditions.

4. On the species, genus and family level, the composition is typical of a long-lived lacustrine fauna and is similar to the stratigraphically slightly older faunas of the Dinaride Lake System in Croatia and Bosnia and Herzegovina, as well as that of the late Miocene Lake Pannon. Although more than 80% of the species found at Mađere and Medoševac are endemic to the SLS, most genera are also known from those two other systems. In particular, the presence of the enigmatic, uncoiled planorbid genus *Orygoceras*, which is known only from these three systems, indicates a close evolutionary relationship of these faunas. In addition to its stratigraphically intermediate position as well as the geographical vicinity, this similarity suggests that the SLS was a stepping stone for mollusc lineages from the DLS to Lake Pannon.
5. Despite the importance of the SLS as a centre of evolution on the Balkan Peninsula and its biogeographic significance, it is still a fairly understudied freshwater lacustrine system, and we have only begun to understand its role in the shaping of European biodiversity in the middle Miocene.

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DATA ARCHIVING STATEMENT

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REFERENCES

ABEL, C. 1818. *Narrative of a journey in the interior of China, and of a voyage to and from that country, in the years 1816 and 1817; containing an account of the most interesting transactions of Lord Amherst's embassy to the court of Pekin, and observations on the countries which it visited. Illustrated by maps and other engravings*. Longman, Hurst, Rees, Orme, and Brown, London, xvi + 420 pp.

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.

ALABURIĆ, S. and MARKOVIĆ, Z. 2010. New records of mammal remains from the Miocene sediments of the cement mine in Popovac (Serbia). *Bulletin of the Natural History Museum, Serbia*, **3**, 95–103.

ANĐELKOVIĆ, M., EREMIJA, M., PAVLOVIĆ, M., ANĐELKOVIĆ, J. and MITROVIĆ-PETROVIĆ, J. 1991. *Paleogeography of Serbia. The Tertiary*. Institute for Regional Geology and Palaeontology, Faculty of Mining and Geology, University of Belgrade, 236 pp. [in Serbian with English summary]

ANDRUSOV, N. 1897. *Iskopayemyya i zhivushchiya Dreissensidae Yevrazii*. M. Merkusheva, St Petersburg, text (683 pp) + atlas (20 pls).

ATANACKOVIĆ, M. 1959. Pliocène du Bassin de Kosovo (Serbie méridionale). *Geološki Glasnik*, **3**, 257–377. [in Serbian]

BARTHA, F. 1955. A várpalotai pliocén puhatestü fauna biosztratigrafiai vizsgálata. *A Magyar Állami Földtani Intézet Évkönyve*, **43**, 275–359.

BIELER, R., MIKKELSEN, P. M., COLLINS, T. M., GLOVER, E. A., GONZÁLEZ, V. L., GRAF, D. L., HARPER, E. M., HEALY, J., KAWAUCHI, G. Y., SHARMA, P. P., STAUBACH, S., STRONG, E. E., TAYLOR, J. D., TËMKIN, I., ZARDUS, J. D., CLARK, S., GUZMÁN, A., MCINTYRE, E., SHARP, P. and GIRIBET, G. 2014. Investigating the Bivalve Tree of Life: an exemplar-based approach combining molecular and novel morphological characters. *Invertebrate Systematics*, **28**, 32–115.

BITTNER, A. 1887. Zur Kenntniss der Melanopsidenmergel von Džepe bei Konjica in der Hercegovina. *Verhandlungen der k. k. Geologischen Reichsanstalt*, **1887** (16), 298–300.

BORCARD, D., GILLET, F. and LEGENDRE, P. 2011. *Numerical ecology with R*. Springer, 306 pp.

BOUCHET, P., ROCROI, J.-P., HAUSDORF, B., KAIM, A., KANO, Y., NÜTZEL, A., PARKHAEV, P., SCHRÖDL, M. and STRONG, E. E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia*, **61** (1–2), 1–526.

BRUSINA, S. 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.

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

—— 1882*b*. Le Pyrgulinae dell'Europa orientale. *Bollettino della Società Malacologica Italiana*, **7** (13–19), 229–292.

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

—— 1892. Ueber die Gruppe der *Congeria triangularis*. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **44**, 488–497.

—— 1893. Frammenti di Malacologia terziaria Serba. *Annales Géologiques de la Péninsule Balkanique*, **4** (2), 25–74.

—— 1896. Neogenska zbirka iz Ugarske, Hrvatske, Slavonije i Dalmacije na Budimpestanskoj izlozbi. *Glasnik Hrvatskoga Naravoslovnoga Društva*, **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.

—— 1907. Naravoslovne crtice sa sjevero-istočne obale Jadranskoga mora. Dio cetvrti i posljednji. Specijalni. *Rad Jugoslavenske akademije znanosti i umjetnosti*, **169**, 195–251.

BURGERSTEIN, L. 1877. Beitrag zur Kenntniss des Jungtertiären Süsswasser-Depôts bei Ueskueb. *Jahrbuch der k. k. Geologischen Reichsanstalt*, **27**, 243–250.

CHARPENTIER, J. D. 1837. Catalogue des mollusques terrestres et fluviatiles de la Suisse. Formant la seconde partie de la faune Helvétique. *Nouveaux Mémoires de la Société Helvétique des Sciences Naturelles*, **1**, 1–28.

ČIČULIĆ, M. 1977. Jezerski neogen Moravskog rova. 74–82. *In* PETKOVIĆ, K. (ed.) *Geologija Srbije, II-3. Stratigrafija – Kenozoik*. University of Belgrade.

COSSMANN, M. 1921. *Essais de Paléoconchologie Comparée*. Privately published, Paris, Douzième Livraison, 348 pp.

COX, L. R. 1960. Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London*, **33**, 239–261.

CUVIER, G. 1795. Second Mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième. *Magasin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts*, **2**, 433–449.

DALL, W. H. 1870. On the genus *Pompholyx* and its allies, with a revision of the Limnaeidae of authors. *Annals of the Lyceum of Natural History of New York*, **9**, 333–361.

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** (1–2), 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**, 29–43.

—— —— —— —— —— 2012. Paleomagnetic and geochronologic constraints on the geodynamic evolution of the Central Dinarides. *Tectonophysics* **530–531**, 286–298.

DRAY, S. and DUFOUR, A.-B. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, **22** (4), 1–20.

—— —— and THIOULOUSE J. 2018. *ade4: Analysis of ecological data: exploratory and Euclidean methods in environmental sciences. Version 1.7–11*. http://CRAN.R-project.org/package=ade4

DUMURDZANOV, N., SERAFIMOVSKI, T. and BURCHFIEL, B. C. 2005. Cenozoic tectonics of Macedonia and its relation to the South Balkan extensional regime. *Geosphere*, **1**, 1–22.

FÉRUSSAC, A. E. J. P. J. F. D'. A. DE [and continued by DESHAYES, G. P. P.] 1819–1851. *Histoire naturelle générale et particulière des mollusques terrestres et fluviatiles tant des espèces que l'on trouve aujourd'hui vivantes, que des dépouilles fossiles de celles qui n'existent plus; classés d'après les caractères essentiels que présentent ces animaux et leurs coquilles*. J.-B. Bailliere, Paris.

FÉRUSSAC, J. B. L. D'. A. DE and 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.

FISCHER, P. and CROSSE, H. 1870–1878. Etudes sur les mollusques terrestres et fluviatales du Mexique et du Guatemala. 1–702. *In* MILNE EDWARDS, H. (ed.) *Recherches zoologiques pour servir à l'histoire de la faune de l'Amérique Centrale et du Mexique. Septième partie. Tome second*. Imprimerie Nationale, Paris.

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

FRÝDA, J. 1998. Higher classification of the Paleozoic gastropods inferred from their early shell ontogeny. 108. *In* BIELER, R. and MIKKELSEN, P. M. (eds). *13th International Malacological Congress, Abstracts*. Unitas Malacologica, Washington DC, 376 pp.

GIRIBET, G. and DISTEL, D. L. 2003. Bivalve phylogeny and molecular data. 45–90. *In* LYDEARD, C. and LINDBERG, D. R. (eds). *Molecular systematics and phylogeography of mollusks*. Smithsonian Institution, Washington DC, 312 pp.

GLÖER, P. and PEŠIĆ, V. 2015. The morphological plasticity of *Theodoxus fluviatilis* (Linnaeus, 1758) (Mollusca: Gastropoda: Neritidae). *Ecologica Montenegrina*, **2** (2), 88–92.

GOLDFUSS, A. 1834–1840. *Petrefacta Germaniae tam ea, quae in Museo Universitatis Regiae Borussicae Fridericiae Wilhelmiae rhenanae servantur quam alia quaecunque in Museis Hoeninghusiano Muensteriano aliisque extant, iconibus et descriptionibus illustrata. Zweiter Theil*. Arnz & Co., Düsseldorf, i, 1–312, pls 72–165.

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

GOTTSCHICK, F. and WENZ, W. 1916. Die Sylvanaschichten von Hohenmemmingen und ihre Fauna. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft*, **48** (1–3), 17–31, 55–74, 97–113.

GRAY, J. E. 1840. Shells of molluscous animals. 105–152. *In Synopsis of the contents of the British Museum*, 42nd edition. G. Woodfall, London, 370 pp.

—— 1857. *Guide to the systematic distribution of Mollusca in the British Museum. Part I*. Taylor & Francis, London, xii + 230 pp.

HADŽIŠČE, S. 1955. Prilog poznavanju Gastropoda Prespanskog i Ohridskog Jezera. *Glasnik Bioloske Sekcije [Periodicum*

Biologorum], Hrvatsko Prirodoslovno Drustvo (II/B), **7**, 174–177.

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

—— —— LATAL, C. and KERN, A. 2012*a*. Stable isotope composition of the Miocene Dinaride Lake System deduced from its endemic mollusc fauna. *Hydrobiologia*, **682**, 27–46.

—— NEUBAUER, T. A., MANDIC, O., ZUSCHIN, M. and ĆORIĆ, S. 2012*b*. A Middle Miocene endemic freshwater mollusc assemblage from an intramontane Alpine lake (Aflenz Basin, Eastern Alps, Austria). *Paläontologische Zeitschrift*, **86**, 23–41.

—— —— GROSS, M. and BINDER, H. 2014. The early Middle Miocene mollusc fauna of Lake Rein (Eastern Alps, Austria). *Palaeontographica, Abt. A: Palaeozoology – Stratigraphy*, **302**, 1–71.

HERBICH, F. and NEUMAYR, M. 1875. Beiträge zur Kenntnis fossiler Binnenfaunen. VII. Die Süsswasserablagerungen im südöstlichen Siebenbürgen. *Jahrbuch der k. k. geologischen Reichsanstalt*, **25**, 401–431.

HERRMANNSEN, A. N. 1846–1847. *Indicis generum malacozoorum primordia. Nomina subgenerum, generum, familiarum, tribuum, ordinum, classium; adjectis auctoribus, temporibus, locis systematicis atque literariis, etymis, synonymis. Praetermittuntur Cirripedia, Tunicata et Rhizopoda. Vol. I.* Fischer, Cassellis, xxvii + 637 pp.

ICZN. 1999. *International Code of Zoological Nomenclature*. 4th edn. International Trust for Zoological Nomenclature. 306 pp.

JEKELIUS, E. 1944. Sarmat und Pont von Soceni (Banat). *Memoriile Institutului Geologic al României*, **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 & 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.

JOVANOVIĆ, G. 2012. *Srpsko jezero*. Narodni muzej Kruševac, Prirodnjački muzej Beograd, Kruševac, 59 pp.

JURIŠIĆ-POLŠAK, Z. 1973. Opis nekih fosilnih vrsta roda *Theodoxus* iz zbirke S. Brusine s nalazišta u Srbiji. *Geološki vjesnik*, **25**, 299–309.

—— and SLIŠKOVIĆ, T. 1988. Slatkovodni gastropodi neogenskih naslaga jugozapadne Bosne. 167–174. *In Zbornik referata naučnog skupa "Minerali, stijene, izumrli i živi svijet BIH"*, Zemaljski Muzej Bosne i Hercegovine, Sarajevo, 7.–8. Oktobar 1988.

—— KRIZMANIĆ, K. and HAJEK-TADESSE, V. 1993. Freshwater Miocene of Krbavsko Polje in Lika (Croatia). *Geologia Croatica*, **46**, 213–228.

—— BULIĆ, J. and POSILOVIĆ, H. 2000. Pojava visokospecijaliziranih oblika nekih gastropoda u miocenskim slatkovodnim naslagama Crvenog Klanca, Sinjsko polje, Hrvatska. 231–237. *In* VLAHOVIĆ, I. and BIONDIĆ, R. (eds). *Proceedings Second Croatian Geological Congress, Cavtat-Dubrovnik*. Institut za geološka istraživanja, Zagreb, 862 pp.

KATZER, F. 1918. *Die fossilen Kohlen Bosniens und der Hercegovina*. Selbstverlag, Wien, Erster Band, 403 pp.

—— 1921. *Die fossilen Kohlen Bosniens und der Hercegovina. Zweiter Band*. Bosn.-Herc. Geologischen Landesanstalt, Sarajevo, 271 pp.

KLEIN, A. 1853. Conchylien der Süsswasserkalkformation Württembergs. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, **9**, 203–223.

KNEŽEVIĆ, S. 1996. New *Congeria* from Šumadija and Pomoravlje. *In* KRSTIĆ, N. (ed.) *Neogene of Central Serbia*. Special Publication of Geoinstitute, **19**, 27–31.

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

KRSTIĆ, N., VULETOVIĆ, V., BOJIĆ, Z. and STOJADINOVIĆ, D. 1996. Neogena jezerska fauna Lomnice kod Kruševaca (Srbija). *Annales Géologiques de la Péninsule Balkanique*, **60**, 247–263.

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

—— KNEŽEVIĆ, S. and PAVIĆ, S. 2007. Fauna of a large early middle Miocene lake of Serbia. *Joannea, Geologie und Paläontologie*, **9**, 51–54.

—— SAVIĆ, L. and JOVANOVIĆ, G. 2012. The Neogene lakes of the Balkan land. *Annales Géologiques de la Péninsule Balkanique*, **73**, 37–60.

—— JOVANOVIĆ, G. and SAVIĆ, L. 2013. Jezerski ostrakodi i prateci mekušci iz kupreškog polja, donji deo dinaridskog sistema jezera (Otnang) na visini od 1,150 m. *Zapisnici Srpskog Geološkog Društva*, **2011**, 1–25.

LINNAEUS, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. Laurentius Salvius, Holmiae, iv + 824 pp.

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.

—— —— BULIĆ, J., KUIPER, K. F., KRIJGSMAN, W. and JURIŠIĆ-POLŠAK, Z. 2012. Paleogeographic evolution of the Southern Pannonian Basin: ^{40}Ar/^{39}Ar age constraints on the Miocene continental series of northern Croatia. *International Journal of Earth Sciences*, **101**, 1033–1046.

—— KUREČIĆ, T., NEUBAUER, T. A. and HARZHAUSER, M. 2015. Stratigraphic and paleogeographic significance of lacustrine mollusks from the Pliocene *Viviparus* beds in central Croatia. *Geologia Croatica*, **68**, 179–207.

—— HAJEK-TADESSE, V., BAKRAČ, K., REICHENBACHER, B., GRIZELJ, A. and MIKNIĆ, M. 2019*a*. Multiproxy reconstruction of the middle Miocene Požega palaeolake in the Southern Pannonian Basin (NE Croatia) prior to the Badenian transgression of the Central Paratethys Sea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **516**, 203–219.

—— RUNDIĆ, L., ĆORIĆ, S., PEZELJ, Đ., THEOBALT, D., SANT, K. and KRIJGSMAN, W. 2019*b*. Age and model of the middle Miocene marine flooding of the Pannonian Basin: constraints from Central Serbia. *Palaios*, **34**, 71–95.

—— SANT, K., KALLANXHI, M.-E., ĆORIĆ, S., THEOBALT, D., GRUNERT, P., DE LEEUW, A. and KRIJGSMAN, W. 2019*c*. Integrated bio-magnetostratigraphy of the Badenian reference section Ugljevik in southern Pannonian Basin: implications for the Paratethys history (middle Miocene, Central Europe). *Global & Planetary Change*, **172**, 374–395.

MAROVIĆ, M., MIHAJLOVIĆ, Đ. and KNEŽEVIĆ, S. 1984. Prilog poznavanju starosti sedimenata Žagubičkog neogenskog basena. *Zapisnici Srpskog Geološkog Društva*, **1983**, 53–61.

—— DJOKOVIĆ, I., PEŠIĆ, L., RADOVANOVIĆ, S., TOLJIĆ, M. and GERZINA, N. 2002. Neotectonics and seismicity of the southern margin of the Pannonian Basin in Serbia. *EGU Stephan Mueller Special Publication Series*, **3**, 277–295.

—— TOLJIĆ, M., RUNDIĆ, L. and MILIVOJEVIĆ, J. 2007. *Neoalpine tectonics of Serbia*. Serbian Geological Society, series monographs, Belgrade, pp. 87.

MATENCO, L. and RADIVOJEVIĆ, D. 2012. On the formation and evolution of the Pannonian Basin: constraints derived from the structure of the junction area between the Carpathians and Dinarides. *Tectonics*, **31**, TC6007.

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.

MILOŠEVIĆ, V. M. 1962. Sistematski pregled primeraka-originala iz paleontološke zbirke Prirodnjackog muzeja u Beogradu. *Bulletin du Museum d'Histoire Naturelle de Belgrade, Série A*, **16–17**, 3–44.

—— 1967. O sistematskom položaju Gastropodske vrste *Kosovia compressa* P. Pavlović. *Bulletin du Museum d'Histoire Naturelle de Belgrade, Série A*, **22**, 3–15.

—— 1971. Nazalak novih Hidrobija u jezerskim sedimentima gornjeg Miocena okoline Peći, Paraćina i Stalaća. *Bulletin du Museum d'Histoire Naturelle de Belgrade, Série A*, **26**, 117–127.

—— 1980. Prilog poznavanju hidrobijske fosilne faune iz Pećke serije Metohije. *Bulletin du Museum d'Histoire Naturelle de Belgrade, Série A*, **35**, 69–80.

—— 1981. Novi fosilni barski poževi iz roda Limnaea iz Sedimenata Pećke serije Metohije. *Bulletin du Museum d'Histoire Naturelle de Belgrade, Série A*, **36**, 57–69.

—— 1983. Metohijska neogena slatkovodna fauna mekušaca i rod *Theodoxus* (Gastropoda). *Bulletin du Museum d'Histoire Naturelle de Belgrade, Série A*, **38**, 135–150.

—— 1984. Prilog poznavanju foslinih Gastropoda iz familije *Valvatidae* iz slatkovodnih sedimenata metohijske kotline (Neogen). *Bulletin du Museum d'Histoire Naturelle de Belgrade, Série A*, **39**, 167–184.

MONTFORT, P. D. DE 1810. *Conchyliologie systématique et classification méthodique de 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. Tome second*. Schoell, Paris, 676 pp.

MÜLLER, O. F. 1773–1774. *Vermium terrestrium et fluviatilium historia, seu animalium Infusoriorum, Helminthicorum et Testaceorum non marinorum succincta historia*. Heineck & Faber, Havniae et Lipsiae, xxxiii + 135, xxxvi + 214.

—— 1781. Geschichte der Perlen-Blasen. *Der Naturforscher*, **15**, 1–20.

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**, 201–237.

—— —— —— and HRVATOVIĆ, H. 2013*a*. A new Miocene lacustrine mollusc fauna of the Dinaride Lake System and its palaeobiogeographic, palaeoecologic, and taxonomic implications. *Palaeontology*, **56**, 129–156.

—— —— —— 2013*b*. The middle Miocene freshwater mollusk fauna of Lake Gacko (SE Bosnia and Herzegovina): taxonomic revision and paleoenvironmental analysis. *Fossil Record*, **16**, 77–96.

—— —— —— 2014*a*. A new melanopsid species from the Middle Miocene Kupres Basin (Bosnia and Herzegovina). *The Nautilus*, **128**, 51–54.

—— HARZHAUSER, M., GEORGOPOULOU, E., MANDIC, O. and KROH, A. 2014*b*. Replacement names and nomenclatural comments for problematic species-group names in Europe's Neogene freshwater Gastropoda. *Zootaxa*, **3785**, 453–468.

—— —— KROH, A., GEORGOPOULOU, E. and MANDIC, O. 2015*a*. A gastropod-based biogeographic scheme for the European Neogene freshwater systems. *Earth-Science Reviews*, **143**, 98–116.

—— —— GEORGOPOULOU, E., KROH, A. and MANDIC, O. 2015*b*. Tectonics, climate, and the rise and demise of continental aquatic species richness hotspots. *Proceedings of the National Academy of Sciences*, **112**, 11478–11483.

—— —— and PIPÍK R. 2015*c*. Upper Miocene endemic lacustrine gastropod fauna of the Turiec Basin: addressing taxonomic, paleobiogeographic and stratigraphic issues. *Geologica Carpathica*, **66**, 139–156.

—— —— MANDIC, O., GEORGOPOULOU, E. and KROH, A. 2016*a*. Paleobiogeography and historical biogeography of the non-marine caenogastropod family

Melanopsidae. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **444**, 124–143.

—— MANDIC, O. and HARZHAUSER, M. 2016*b*. The freshwater mollusk fauna of the Middle Miocene Lake Drniš (Dinaride Lake System, Croatia): a taxonomic and systematic revision. *Austrian Journal of Earth Sciences*, **108** (2), 15–67.

—— —— —— 2016*c*. The early middle Miocene lacustrine gastropod fauna of Džepi Bosnia and Herzegovina (Dinaride Lake System): high endemism in a small space. *Bulletin of Geosciences*, **91**, 271–296.

—— —— MANDIC, O., KROH, A. and GEORGOPOULOU, E. 2016*d*. Evolution, turnovers and spatial variation of the gastropod fauna of the late Miocene biodiversity hotspot Lake Pannon. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **442**, 84–95.

—— —— —— and JOVANOVIĆ G. 2017. The discovery of *Bulinus* (Pulmonata: Planorbidae) in a Miocene palaeolake in the Balkan Peninsula. *Journal of Molluscan Studies*, **83**, 295–303.

—— —— JOVANOVIĆ, G. and HARZHAUSER, M. 2020. Gastropod species occurrence data for Serbian Lake System and selected Miocene faunas. *Pangaea*, https://doi.org/10.1594/pangaea.909449

NEUMAYR, M. 1869. Beiträge zur Kenntniss fossiler Binnenfaunen. *Jahrbuch der k. k. Geologischen Reichsanstalt*, **19**, 355–382.

—— 1880. Tertiäre Binnenmollusken aus Bosnien und der Hercegovina. *Jahrbuch der k. k. Geologischen Reichsanstalt*, **30**, 463–486.

OKSANEN, J., BLANCHET, F. G., FRIENDLY, M., KINDT, R., LEGENDRE, P., McGLINN, D., MINCHIN, P. R., O'HARA, R. B., SIMPSON, G. L., SOLYMOS, P., STEVENS, M. H. H., SZOECS, E. and WAGNER, H. 2018. *vegan: Community Ecology Package. version 2.5–2*. http://CRAN.R-project.org/package=vegan

OLIVIER, G. A. 1804. *Voyage dans l'Empire Othoman, l'Égypte et la Perse, fait par ordre du gouvernement, pendant les six premières années de la République. Tome second*. Agasse, Paris, 466 pp.

PANTIĆ, N. 1956. Biostratigraphy of Tertiary flora in Serbia. *Geološki anali Balkanskoga Poluostrva*, **24**, 199–322.

PARTSCH, P. 1835. Über die sogenannten versteinerten Ziegenklauen aus dem Plattensee in Ungarn, und ein neues, urweltliches Geschlecht zweischaliger Conchylien. *Annalen des Wiener Museums der Naturgeschichte*, **1**, 93–102.

PAVLOVIĆ, P. S. 1903*a*. Građa za poznavanje tercijara u Staroj Srbiji. *Annales Géologiques de la Péninsule Balkanique*, **6**, 155–189.

—— 1903*b*. Prinove Geologškog Zavoda. *Annales Géologiques de la Péninsule Balkanique*, **6**, 293–325.

—— 1922. Prilozi za poznavanje Tercijara u Srbiji. *Annales Géologiques de la Péninsule Balkanique*, **7**, 42–50.

—— 1930. O tercijarnoj fauni skopske kotline i njenom odnosu prema nekolikim srodnim u Severnoj Srbiji. *Glas Srpske Kraljevske Akademije*, **140**, 3–9.

—— 1931. O fosilnoj fauni mekušaca iz Skopske Kotline. *Glasnik Skopskog naučnog društva, Odeljenje prirodnih Nauka*, **9**, 1–28.

—— 1932. Novi prilošci za poznavanje fosilne faune iz Kosovske i Metohiskopodrimske Kotline. *Bulletin du Service Géologique du Royaume de Yougoslavie*, **1**, 231–253.

—— 1933. O fosilnoj fauni mekušaca iz okoline Peci. *Glas Srpske Kraljevske Akademije*, **158** (78), 75–91.

—— 1935. Sur la faune fossile de Mollusques des environs de Pec (Serbie du Sud). *Bulletin de l'Académie serbe des sciences mathématiques et naturelles, B. Sciences naturelles*, **2**, 43–50.

PEZELJ, Đ., MANDIC, O. and ĆORIĆ, S. 2013. Paleoenvironmental dynamics in the southern Pannonian Basin during initial middle Miocene marine flooding. *Geologica Carpathica*, **64**, 81–100.

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 la isla de Cuba*, **1** (8), 77–96.

POLIŃSKI, W. 1929. Limnoloshka ispitivanja Balkanskog Poluostrva. I. Reliktna fauna gasteropoda Ochridskog Jezera. *Glas Srpske Kraljevske Akademije*, **137** (65), 129–182.

POPOVIĆ, R. 1960. O starosti sedimenata Žagubičke kotline. *Vesnik (Geologija). Zavod za Geološka i Geofizička Istraživanja, Beograd, A*, **18**, 85–92.

—— and NOVKOVIĆ, M. 1967. Donjokongerijske naslage slatkovodnih base na Zapadne Morave i Gruže sa osvrtom na starost ugljenih slojeva. *Vesnik Zavoda za Geološka i Geofizička Istraživanja N.R. Srbije, Serija A*, **24–25**, 317–332.

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

RAKIĆ, M., DIMITRIJEVIĆ, M., CVETKOVIĆ, D., TERZIN, V., BODIĆ, D., PETROVIĆ, V. and HADŽIVUKOVIĆ, M. 1965. *Basic geological map of SFRY 1:100000, Niš sheet*. Savezni geološki zavod, Beograd. [in Serbian]

—— —— TERZIN, V., CVETKOVIĆ, D. and PETROVIĆ, V. 1973. *Explanatory booklet of the Basic Geological Map of the SFR Yugoslavia, Sheet Niš 1:100000. K 34–32*. Savezni geološki zavod, Beograd, 52 pp. [in Serbian with English summary]

RASSER, M. W. 2013. Evolution in isolation: the *Gyraulus* species flock from Miocene Lake Steinheim revisited. *In* VON RINTELEN, T., MARWOTO, R. M., HAFFNER, G. D. and HERDER, F. (eds). *Speciation in ancient lakes: Classic concepts and new approaches*. Hydrobiologia, **739**, 7–24.

R CORE TEAM. 2016. R: A language and environment for statistical computing. Version 3.3.2. R Foundation for Statistical Computing, Vienna. https://www.R-project.org

ROLLE, F. 1860. Die Lignit-Ablagerung des Beckens von Schönstein in Unter-Steiermark und ihre Fossilien. *Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, **41**, 7–46.

RUNDIĆ, L., VASIĆ, N., BANJEŠEVIĆ, M., PRELEVIĆ, D., GAJIĆ, V., JOVANOVIĆ, M., PANTELIĆ, N. and STEFANOVIĆ, J. 2018. New biostratigraphic, sedimentological, and radiometric data from the Lower-Middle Miocene of the Zajecar area (westernmost part of the Dacian Basin, eastern Serbia). 99. *In* NEUBAUER, F., BRENDEL, U. and FRIEDL, G. (eds). XXI International Congress of the CBGA, Salzburg, Austria, September 10–13, 2018, Abstracts. *Geologica Balcanica*, 399 pp.

SANT, K., MANDIC, O., RUNDIĆ, L., KUIPER, K. F. and KRIJGSMAN, W. 2018. Age and evolution of the

Serbian Lake System: integrated results from Middle Miocene Lake Popovac. *Newsletter on Stratigraphy*, **51**, 117–143.

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

STAROBOGATOV, Y. I. 1970. *Fauna mollyuskov i zoogeographicheskoye rayonirovaniye kontinental'nykh vo do emov zemnogo shara*. Nauka, Leningrad, 372 pp.

STEVANOVIĆ, P., PAVLOVIĆ, M. B. and EREMIJA, M. 1977*a*. Jezerski neogen. 185–213. *In* PETKOVIĆ, K. (ed.) *Geologija Srbije, II-3. Stratigrafija: Kenozoik*. University of Belgrade, Belgrade.

—— —— —— 1977*b*. Stratigrafski položaj kosovijskih horizonata u slatkovodnom neogenu Srbije (Šumadija i Pomoravlje). *Zapisnici Srpskog Geološkog Društva za***1975 i 1976**, 77–81.

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.

STOJADINOVIĆ, U., MATENCO, L., ANDRIESSEN, P. A. M., TOLJIĆ, M. and FOEKEN, J. P. T. 2013. The balance between orogenic building and subsequent extension during the Tertiary evolution of the NE Dinarides: constraints from low-temperature thermochronology. *Global & Planetary Change*, **103**, 19–38.

STOLICZKA, F. 1862. Beitrag zur Kenntnis der Molluskenfauna der Cerithien- und Inzersdorfer Schichten des ungarischen Tertiärbeckens. *Verhandlungen der kaiserlichen und königlichen zoologisch-botanischen Gesellschaft in Wien*, **12**, 529–538.

—— 1870–1871. Cretaceous fauna of southern India. The Pelycopoda, with a review of all known Genera of this class, fossil and recent. *Memoirs of the Geological Survey of India*, **6**, xxii + 538.

TAKTAKISHVILI, I. G. 1973. *Pliotsenovyye dreyssenidy Zapadnoy Gruzii*. Metsniyereba, Tbilisi, 150 pp.

VERDUIN, A. 1977. On a remarkable dimorphism of the apices of sympatric closely-related marine gastropod species. *Basteria*, **41**, 91–95.

VESELINOVIĆ, M., ANTONIJEVIĆ, I., MILOŠAKOVIĆ, R., MIĆIĆ, I., KRSTIĆ, B., ČIČLIĆ, M., DIVLJAN, M. and MASLAREVIĆ, M. 1964. *Explanatory booklet of the basic geological map of the SFR Yugoslavia, Sheet Boljevac 1:100000. K 34-8*. Savezni geološki zavod, Beograd, 60 pp. [in Serbian with English summary]

—— —— KRSTIĆ, B., MIĆIĆ, I., MILOŠAKOVIĆ, R., RAKIĆ, M. and BANKOVIĆ, V. 1970. *Basic geological map of SFRY 1:100000, Boljevac sheet*. Savezni geološki zavod, Beograd. [in Serbian]

VESELINOVIĆ-ČIČULIĆ, M. 1952. Rezultati proučavanja tercijernih terena između Paraćina i Ražnja. *Zbornik Radova S.A.N.*, **23**, Geološki Institut S.A.N., 4, 207–226.

WELTER-SCHULTES, F. W. 2012. *European non-marine molluscs, a guide for species identification*. Planet Poster Editions, Göttingen, 679 pp.

WENZ, W. 1923–1930. *Fossilium Catalogus I: Animalia. Gastropoda extramarina tertiaria*. W. Junk, Berlin. Parts V: 1421–1734 (1923), VII: 1863–2230 (1926), X: 2887–3014 (1929).

ŽIVKOVIĆ, M. 1893. Über das Tertiär des mittleren Timok-Beckens. *Annales Géologiques de la Péninsule Balkanique*, **4**, 37–118, 147–168.

ŽUJOVIĆ, J. M. 1886. Geologische Uebersicht des Königreiches Serbien. *Jahrbuch der k. k. geologischen Reichsanstalt*, **36**, 71–126.

—— 1889. Osnovi za geologiju Kraljevine Srbije. *Geološki anali Balkanskoha poluostrva*, **1**, 1–130.