

The discovery of *Bulinus* (Pulmonata: Planorbidae) in a Miocene palaeolake in the Balkan Peninsula

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ABSTRACT

Large, sinistrally coiled gastropod species have been reported under the genus name *Kosovia* Atanacković, 1959 from middle and late Miocene palaeolakes of central Serbia and Kosovo. Despite several papers dealing with the taxonomy and evolution of this genus, its systematic position and possible ancestry have been unresolved. Previously, it has been suggested that it may be a member of the Viviparidae, Lymnaeidae or Planorbidae, but without morphological criteria to support these assertions. In order to elucidate the systematic position of the genus, we investigated type material of the type species *Kosovia matejici* Pavlović, 1931, which is the oldest representative and is restricted to middle Miocene deposits of central Serbia. Embryonic shell characters support membership of the Planorbidae. Based on the congruence of all evaluated morphological characteristics, we attribute the species to the genus *Bulinus*, which makes *Kosovia* a junior subjective synonym of *Bulinus*. We discuss potential ancestry of the oldest representative and relationships among the species previously attributed to *Kosovia*. Our study emphasizes the importance of SEM-based examination of the protoconch to clarify the systematic position of problematic freshwater gastropods, especially when molecular data are absent.

INTRODUCTION

The middle–late Miocene lacustrine deposits of central Serbia and Kosovo have yielded a number of large, sinistrally coiled, high-spired gastropod species that have been attributed to the genus *Kosovia* Atanacković, 1959. Several papers have dealt with taxonomy and hypotheses about evolutionary processes within the group (Pavlović, 1931; Atanacković, 1959; Milaković & Milošević, 1974; Krstić, Savić & Jovanović, 2012), but its systematic position has remained uncertain. Moreover, nomenclatural issues and stratigraphic uncertainties have precluded reliable conclusions.

The peculiar morphology of *Kosovia* was first mentioned by Boué (1840), who mistook the shells for sinistral aberrations of a co-occurring *Viviparus* species. Almost a century later, Pavlović (1931) described the genus *Kosovia* and four new species. Unfortunately, he did not designate a type species, thus the genus name was not available from that publication (ICZN, 1999: Art. 13.3). Moreover, Pavlović did not classify the genus, but compared it with Viviparidae, as well as with marine and terrestrial genera that share the sinistral coiling or the spiral keels. Atanacković (1959) made the name *Kosovia* available by indicating a type species, *Kosovia ornata* Pavlović, 1931 and by referring to Pavlović's earlier description (Art. 13.1.2). He placed *Kosovia* in a separate subfamily (Kosovinae) in the Viviparidae, largely based on comparison with

Recent *Lanistes* from Lake Malawi. Although neither Atanacković (1959) nor any later author formally described the subfamily, it is available from its original publication (ICZN, 1999: Art. 13.2.1), since it was used as valid after 1960 and before 2000 (Milošević, 1978). (Note that following ICZN, 1999: Art. 29, the correct spelling is Kosoviinae.) Zilch (1959–1960) and Milaković & Milošević (1974), again without any explanation, placed the genus in the planorbid tribe Campptoceratini, apparently suggesting a relationship with the sinistral, elongate *Campptoceras* from eastern Asia (see e.g. Walker, 1919). Most recently, Krstić *et al.* (2012) attributed *Kosovia* to the Lymnaeidae, once again without discussion.

In summary, the systematic position of *Kosovia* is highly uncertain. A relationship with Viviparidae seems doubtful, given that viviparids have little in common with *Kosovia* except for their size and, as we show here, differ in key taxonomic characters in early ontogeny. Moreover, morphological evolution in viviparids mostly involves variation of whorl cross-section and sculpture, while overall shell shape is less affected, as shown by the well-studied Plio–Pleistocene radiations in Croatia, Romania and Greece (Neumayr & Paul, 1875; Willmann, 1981; Lubenescu & Zazuleac, 1985; Mandić *et al.*, 2015). Furthermore, sinistral representatives are rare among Viviparidae (e.g. Tiemann & Cummings, 2008) and not known for European species.

In order to address the systematic position and evolutionary origin of *Kosovia*, we studied type material of the presumed oldest representative, *K. matejici* Pavlović, 1931. Earlier studies variously dated the Serbian ‘*Kosovia* beds’ as middle Miocene (Stevanović, Pavlović & Eremjia, 1977) or late Miocene (Milaković, 1983), based on biostratigraphic correlations of dreissenid bivalve faunas. Recent radioisotopic studies on nearby, presumably coeval, lacustrine deposits yielded a late Langhian (middle Miocene) age (Sant et al., 2016). Based on detailed study of the shell, particularly focusing on features of the protoconch, we show that *Kosovia* cannot be sufficiently distinguished from the planorbid genus *Bulinus* and should accordingly be considered its junior synonym.

MATERIAL AND METHODS

We examined the syntype series of *Kosovia matejici* Pavlović, 1931 stored in the National History Museum Belgrade (NHMB). The collection comprises six specimens (NHMB 2521, 2870, 2871) from middle Miocene lacustrine deposits at Madare, NW Ražanj, central Serbia (c. 43°41′49″N 21°30′54″E). Material of *Bulinus* and *Planorbarius* species used for comparison derived from the collection of the National History Museum Vienna (NHMW). SEM images were made with a JEOL JSM-6610LV at the NHMW.

SYSTEMATIC DESCRIPTION

Family PLANORBIDAE Rafinesque, 1815
Subfamily BULININAE Fischer & Crosse, 1880

Genus *Bulinus* Müller, 1781

Type species: Bulinus senegalensis Müller, 1781; by Linnaean tautonymy (see ICZN, 1999: Art. 68.5).

***Bulinus matejici* (Pavlović, 1931)**
(Fig. 1)

Kosovia matejici Pavlović, 1931: 22, pl. 11, figs 14–16 (Madare, NW Ražanj, central Serbia; stratum typicum: lacustrine deposits of late Langhian (middle Miocene) age; lectotype (here designated) NHMB 2870, figured by Pavlović (1931: pl. 11, fig. 16); 5 paralectotypes: 4 juvenile and fragmentary shells NHMB 2871, 1 juvenile NHMB 2521).

Kosovia matejici—Milošević, 1962: 32. Milaković & Milošević, 1974: 69, text-fig. 3.

Kosovia cf. *matejici*—Milošević, 1967: 5; text-fig. 2.

Description: Shell sinistral, buliniform, gradate, of up to five whorls. Lectotype 15.0 × 12.0 mm. Protoconch planispiral, about 0.8 whorls, diameter 890 µm; nucleus immersed, bulbous, width 270 µm, with weakly, irregularly wrinkled surface; remaining part highly convex, densely covered by tiny, spirally arranged pits, which fade out after c. 0.6 whorls; at same time, an angulation appears between apical plane and whorl flank, forming a right angle after first protoconch whorl; shortly after onset of angulation (at c. 0.7 whorls) spiral ridges and furrows (5 in lectotype) appear on central part of apical plane, marking onset of teleoconch. Ridges and furrows increase in number and strength during ontogeny, covering entire apical plane and whorl flank after first half whorl of teleoconch. Topmost ridge on whorl flank (below angulation) is typically strongest. Growth lines cover teleoconch, producing irregularly reticulate pattern where they intersect with spiral sculpture. In adult specimens, very prominent, broad axial ribs appear (18 in lectotype, 24 in a paralectotype), extending across entire flank with almost

equal strength; in apical view, ribs form regularly undulating outline. Suture deeply incised in early stages, becoming very narrow in adult specimens as coiling tightens. Aperture widely elliptical with glossy, white, sheet-like inner lip; peristome not complete in any specimen. Umbilicus narrow, slit-like, almost fully covered by inner lip.

Distribution: Reported from middle Miocene lacustrine deposits of the Serbian Lake System (SLS) at Čerane near Kaona, Gornja Mutnica, Mađare and Pardik in central Serbia (Pavlović, 1931; Milošević, 1967; Milaković & Milošević, 1974). Additional records from Serbia not identified to species level (Milošević, 1967) are probably also referable to *B. matejici*.

Remarks: The protoconch of this species resembles those of Miocene species of the planorbid genera *Planorbarius* and *Bulinus* and undoubtedly classifies it in the family Planorbidae. Given the striking congruence of all the morphological characteristics assessed, we conclude that *Kosovia matejici* is a member of the genus *Bulinus*. Since it is the type species of *Kosovia*, the genus is herewith considered a junior subjective synonym of *Bulinus*. The subfamily Kosoviinae is considered a junior synonym of Buliniinae accordingly.

In both *Planorbarius* and *Bulinus*, the embryonic shell consists of a similar number of whorls and bears spirally arranged tiny pits of similar size (6–7 µm, measured on c. 0.5 whorl) (Table 1; Fig. 2G, H, J–L; see also Riedel, 1993; Bandel, 2010; Harzhauser et al., 2012, 2014a, b; Martínez-Ortí, BARGUES & MAS-COMA, 2015). A major difference is that the pits are much more widely spaced and more regularly aligned in *Planorbarius*, while they are densely spaced in *Bulinus*, including *B. matejici*. Moreover, the embryonic shell of *B. matejici* is much larger than those of Miocene *Planorbarius* species, while it is similar to the size of early middle Miocene *Bulinus corici* Harzhauser & Neubauer in Harzhauser et al., 2012 (Table 1). Protoconch size, however, seems to vary considerably among species in both genera as there are also species with distinctly smaller embryonic shells in *Bulinus* (e.g. Brown, 1994) and larger ones in *Planorbarius* (e.g. Riedel, 1993). *Bulinus matejici* also shares with *B. corici* the typical pattern of grooves and ridges on the early teleoconch, which is restricted to the central region of the apical plane, as well as the angulation between whorl flank and apical plane emerging on the first whorl (Fig. 2L). In *Planorbarius*, in contrast, grooves and ridges cover the entire (visible) shell surface and the angulation is much less pronounced (Fig. 2G, H, J, K; Riedel, 1993). The detachment of the aperture reported for several species of *Kosovia* (e.g. Pavlović, 1931; Atanacković, 1959) has also been documented for species of *Bulinus* (Brown, 1994), but not for *Planorbarius*. Finally, the axial sculpture on the teleoconch that is typical of *B. matejici* has never been found in *Planorbarius*, but is present, albeit weaker, in some recent African *Bulinus* species (e.g. Brown, 1994).

Overall shell shape might be considered a crucial (and obvious) reason to differentiate between discoidal *Planorbarius* and *Bulinus* with a high last whorl and raised spire (Fig. 2A–F), but the family Planorbidae is widely known for its extreme morphological variability (see Discussion). Nonetheless, some of the late Miocene species from the Kosovo Basin previously attributed to *Kosovia* (*K. pavlovici* Atanacković, 1959 and *K. stevanovici* Atanacković, 1959), which are characterized by non-gradate spires and less pronounced axial sculpture, closely resemble some Recent African species of *Bulinus*. As far as we are aware, no *Planorbarius* species has been reported to form a raised spire.

Classification in the families Viviparidae and Lymnaeidae, as proposed earlier, is ruled out by the strongly differing protoconchs. *Viviparus*, for instance, has a low domed to pointed protoconch that bears axial folds or narrow spiral threads (e.g. Riedel, 1993; Neubauer et al., 2015b). Lymnaeidae, on the other hand, bear only growth lines on the protoconch (Riedel, 1993). Similarly, members of the family Physidae, which also consist of sinistrally coiled species, have entirely smooth or weakly striate protoconchs (Riedel, 1993;

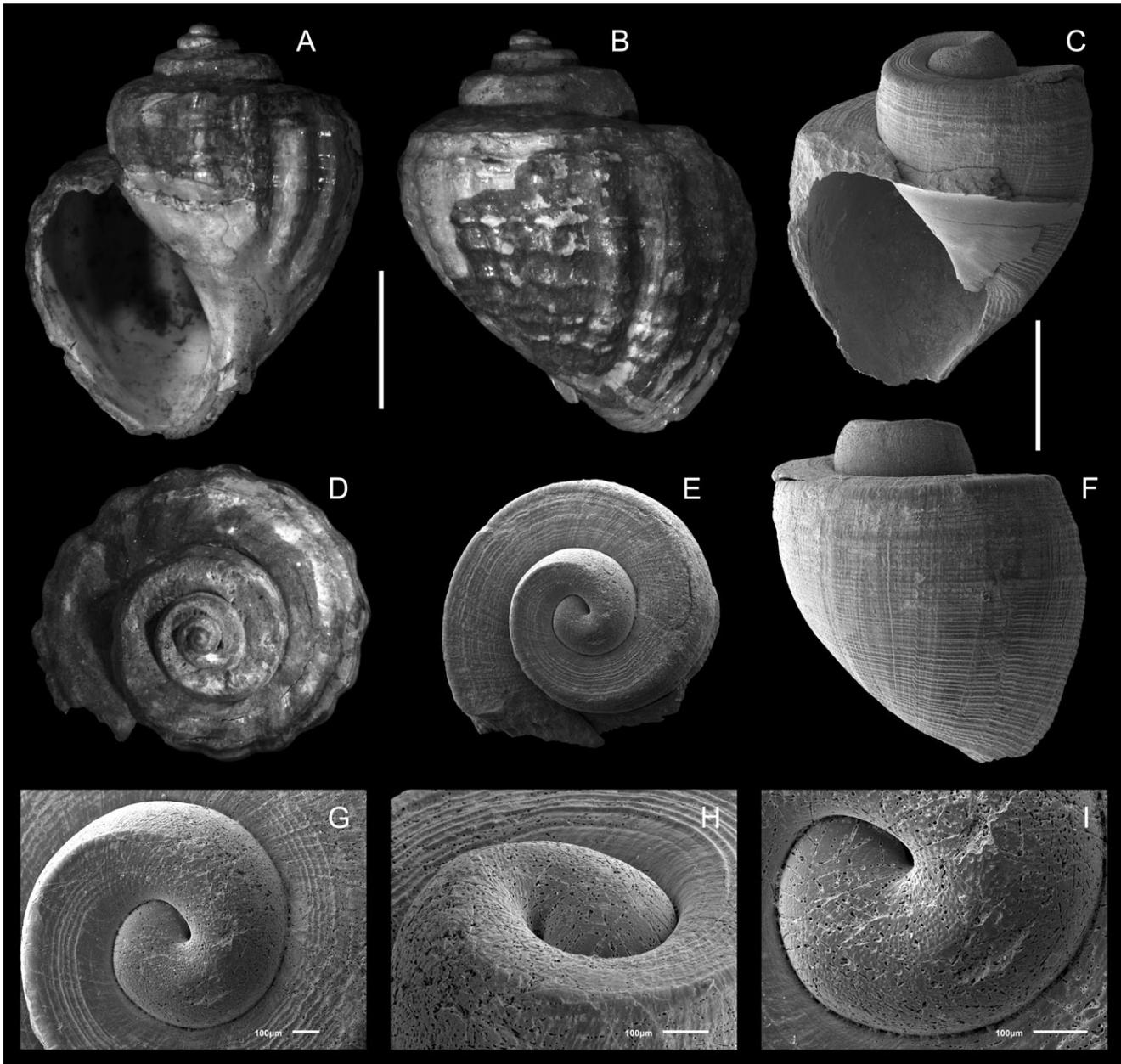


Figure 1. *Bulinus matejici* (Pavlović, 1931) from Madare, NW Ražanj, central Serbia. **A, B, D.** Lectotype, NHMB 2870. **C, E–I.** Paralectotype, NHMB 2521; juvenile specimen, showing details of the protoconch. Note that the poor preservation of the early shell slightly obscures the pitted surface. Scale bars: **A, B, D** = 5 mm; **C, E, F** = 1 mm; **G–I** = 100 µm.

Table 1. Protoconch measurements on *Bulinus matejici* and early middle Miocene *Bulinus* and *Planorbarius* species for comparison

Species	Locality	Age	Number of whorls	Maximum diameter (µm)	Width of nucleus (µm)
<i>Bulinus matejici</i> (Pavlović, 1931)	Madare, Serbia	Late Langhian	0.8	890	270
<i>Bulinus corici</i> Harzhauser & Neubauer in Harzhauser et al., 2012	Jauring, Austria	Early Langhian	0.9	910	250
<i>Planorbarius mantelli</i> (Dunker, 1848)	Rein, Austria	Early Langhian	0.9	540	140
<i>Planorbarius</i> sp.	Gacko, Bosnia and Herzegovina	Early Langhian	0.9	550	170

Note that due to preservation issues and the smooth P/T transition, some of the numbers are approximate. Measurements are based on specimens studied by Neubauer et al. (2013) and Harzhauser et al. (2014a, b), some of which are illustrated in Figure 2. Counting of protoconch whorls follows the method proposed by Verduin (1977).



Figure 2. Early middle Miocene (early Langhian) representatives of *Bulinus* and *Planorbarius*. **A, B.** *Bulinus corici* Harzhauser & Neubauer in Harzhauser *et al.*, 2012, holotype, NHMW 2011/0021/0006; Jauring, Aflenz Basin. **C.** *Bulinus corici* Harzhauser & Neubauer in Harzhauser *et al.*, 2012, paratype, NHMW 2011/0021/0007; Jauring, Aflenz Basin. **D, E.** *Planorbarius mantelli* (Dunker, 1848), adult specimen, UMJ 60.461; Hörgas (= Enzenbach), Rein Basin. **F, G.** *Planorbarius mantelli* (Dunker, 1848), juvenile specimen, NHMW 2012/0154/0028; Enzenbach, Rein Basin. **H.** *Planorbarius mantelli* (Dunker, 1848); NHMW 2012/0154/0029; Enzenbach, Rein Basin. **I, L.** *Bulinus corici* Harzhauser & Neubauer in Harzhauser *et al.*, 2012, NHMW 2011/0021/0009; Jauring, Aflenz Basin; pitted surface is visible opposite the nucleus under high magnification. **J.** *Planorbarius* sp., apical fragment, NHMW 2011/0138/0164; Gračanica section in Gacko Basin, sample 0804/039b. **K.** *Planorbarius* sp., early protoconch and nucleus, NHMW 2011/0138/0163; Gračanica section in Gacko Basin, sample 0804/039 coal. For details, see Neubauer *et al.* (2013) and Harzhauser *et al.* (2012, 2014a). Scale bars (unless indicated otherwise): **A–E** = 5 mm; **F, I** = 500 μ m.

Appleton & Dana, 2005; De Paula & Silveira, 2005). Moreover, physid shells usually have shallower sutures and smoother surfaces (Brown, 1994). Physids are represented by a single species in the European middle Miocene, *Aplexa subhyponorum* (Gottschick, 1920) which differs considerably from coexisting *Bulinus* (including *Kosovia*) species in its bulbous, smooth protoconch, and in the elongate shape with well-rounded and entirely smooth whorls (Gottschick, 1920; cf. Harzhauser & Binder, 2004).

DISCUSSION

Potential ancestry of Bulinus matejici

The genus *Bulinus* is the only member of the Bulininae in Europe and is represented by only two rare coeval species, whereas other planorbid genera are common. *Bulinus corici* is endemic to the early middle Miocene Lake Groisenbach in the Aflenz Basin in Austria (Harzhauser *et al.*, 2012). *Bulinus trojanus* (Neumayr, 1883) was described from freshwater deposits near Assos (presently Behramkale) in northwestern Turkey, which probably are of early middle Miocene age (for the geology of the area see Yilmaz & Karacik, 2001; Gürdal & Bozcu, 2011; Bozcu, 2015). Given their globular shapes and lack of sculpture on the teleoconch, they are not likely to have been ancestors of *B. matejici*. The middle Miocene of Europe and especially the regions featuring *Bulinus*, i.e. central Europe, the Balkan Peninsula and the Aegean-Anatolian region, are represented by numerous well-sampled faunas (see reviews by Neubauer *et al.*, 2015a, b and references therein). We therefore do not expect a major sampling bias masking undetected *Bulinus* records and potential predecessors.

Given the unique morphology of *B. matejici* and the paucity of potential relatives in the European fossil record, the ancestor might have its roots outside the European continent. *Bulinus* very likely originated in Africa, where its fossil record dates back at least to the early Miocene (c. 19–20 Ma; Pickford, 2008). Recent molecular analyses suggest an even older origin (Jørgensen *et al.*, 2011). Brown (1994) postulated that the development of polyploidy greatly contributed to the success of the genus and enabled dispersal into stressful and colder environments (see also Van Damme & Van Bocxlaer, 2009). Today, *Bulinus* is represented by numerous species in Africa, southwestern Asia and Arabia, with one species also extending into the Mediterranean region (Brown, 1994). For it to reach remote, isolated European basins during the middle Miocene could have been possible by means of passive long-distance dispersal, probably by birds. There was a land bridge that connected Europe and Africa during the early Miocene and allowed repeated faunal exchange among mammals (c. 21–22 Ma, 19–18.5 Ma and 18–17.5 Ma; Harzhauser *et al.*, 2007). However, this ‘Gomphotherium land bridge’ did not offer hydrological connections allowing active

migration of freshwater gastropods. Moreover, no terrestrial pathway was available during the known geological duration of *B. matejici* (Popov *et al.*, 2004; Harzhauser *et al.*, 2007).

Avian dispersal is readily underestimated as an important vector and has been demonstrated for several species of gastropods living today (e.g. Green & Figuerola, 2005; Kappes & Haase, 2012; van Leeuwen & van der Velde, 2012; van Leeuwen *et al.*, 2012a, b, 2013). Recently, it was suggested as dispersal mode for a species of *Bulinus* in Nigeria (Salawu & Odaibo, 2013). Dispersal by waterfowl has also been invoked as factor explaining distributions of fossil freshwater snails (Wesselingh, Cadée & Renema, 1999; Harzhauser *et al.*, 2016). One case even involves the isolated occurrence of a presumed descendant of *B. matejici* in the late Miocene of the Turiec Basin in Slovakia, found at a distance of c. 700 km from its apparent origin in the Metohia Basin (Neubauer *et al.*, 2015b; see below).

Late Miocene to Pliocene evolution in palaeolakes Kosovo and Metohia

In addition to the type species, several species from late Miocene strata of the Kosovo and Metohia basins in Kosovo have been ascribed to the genus *Kosovia* by earlier authors (Pavlović, 1931; Atanacković, 1959; Milošević, 1978; Atanacković & Stevanović, 1990; Table 2; Fig. 3). Compared with *B. matejici*, these taxa cover a distinctly wider morphological spectrum, ranging from slender to stout forms and from coarsely ribbed or keeled to striate, almost smooth surfaces (Pavlović, 1931; Atanacković, 1959; Milošević, 1978). Many of the described species co-occur in the same localities and differ only in intensity of sculpture or height of the spire and might merely represent local phenotypes of a single species.

The poorly resolved stratigraphy of the deposits in the Kosovo and Metohia basins remains a major impediment to unravelling the evolutionary pattern among late Miocene forms and the connection to their presumed ancestor *B. matejici*. Based on biostratigraphic data from molluscs, ostracods and diatoms, the lacustrine deposits have been traditionally correlated with the regional stratigraphic stages of the Pannonian and Dacian basins, which correlate to the late Miocene to Pliocene (e.g. Pavlović, 1903; Atanacković, 1959; Milošević, 1966; Popović, 1970b, 1974; Milaković, 1983; Atanacković & Stevanović, 1990; Ognjanova-Rumenova, 2006, 2014; Elezaj, 2009; Elezaj *et al.*, 2010; Krstić *et al.*, 2012). Contrary to the middle Miocene SLS, no absolute age data are available for the lacustrine deposits in the two basins as yet. However, if the biostratigraphic correlations are correct, *Bulinus* populations from central Serbia and from the Kosovo and Metohia basins would have been separated by several million years. Although time-displaced phenotypic convergence cannot be ruled out, the high similarity between *B. matejici* and the Kosovan species (Pavlović, 1931; Atanacković, 1959) suggests that they belong to the same lineage. Until revised stratigraphic data and a detailed character analysis of all species are available, no firm conclusion can be drawn.

Table 2. List of presently accepted *Bulinus* and *Popovicia* species from Serbia and Kosovo, with indication of their temporal and geographic distributions.

Species*	Age	SLS	L. Kosovo	L. Metohia
<i>Bulinus bouei</i> (Pavlović, 1931)	late Miocene		x	x
<i>Bulinus matejici</i> (Pavlović, 1931)	middle Miocene	x		
<i>Bulinus ornatus</i> (Pavlović, 1931)	late Miocene		x	x
<i>Bulinus pavlovici</i> (Atanacković, 1959)	late Miocene		x	
<i>Bulinus stevanovici</i> (Atanacković, 1959)	late Miocene		x	
<i>Bulinus striatus</i> (Milošević, 1978)	late Miocene			x
<i>Popovicia compressa</i> (Pavlović, 1931)	late Miocene			x
<i>Popovicia levantica</i> (Popović, 1964)	early Pliocene			x
<i>Popovicia turriculoidea</i> (Popović, 1964)	early Pliocene			x

*Note that the species name ‘*Kosovia praepontica*’ mentioned by Krstić *et al.* (2012) is a *nomen nudum*, referring to a description in an unpublished manuscript by Milošević. Re-examination of the respective specimens from the middle Miocene of the Metohia Basin showed that they do not represent a *Bulinus* but are juveniles of an unidentified *Planorbarius* species.

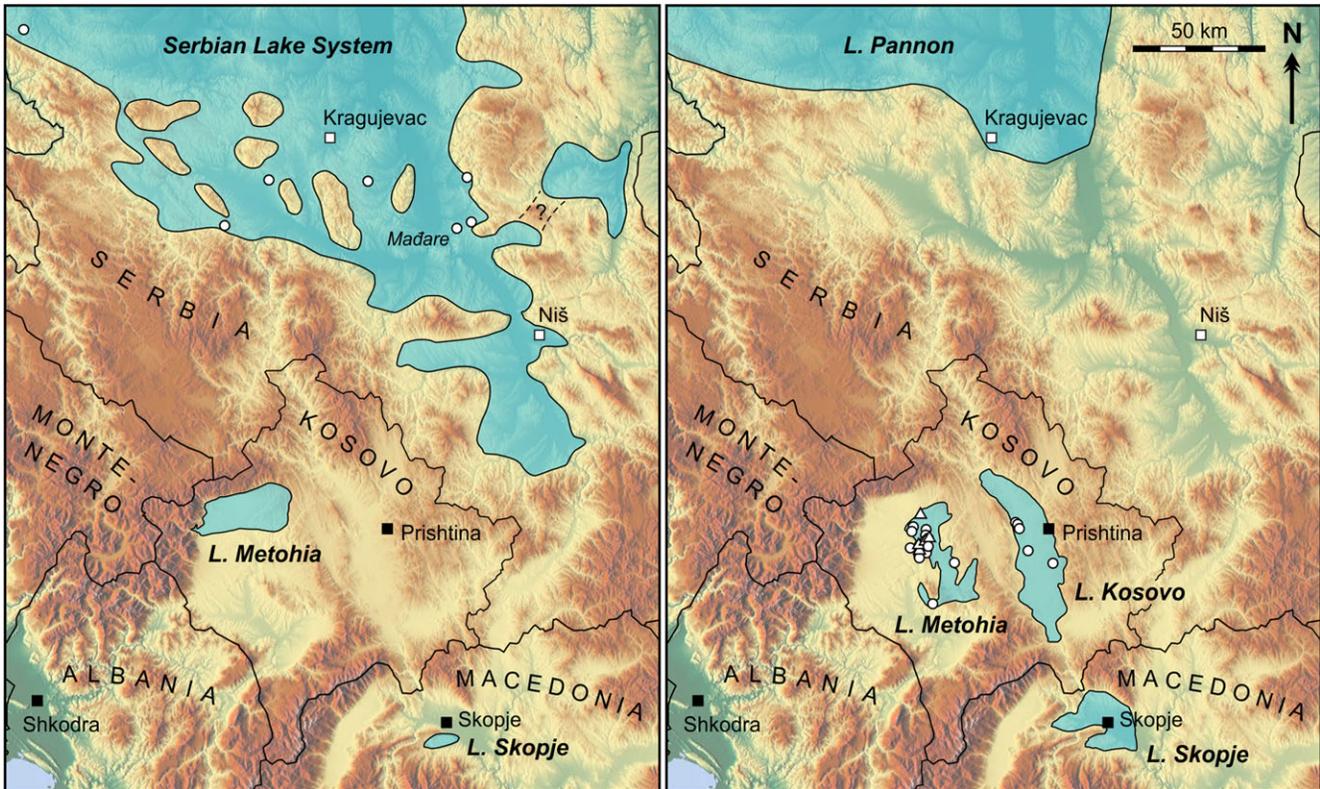


Figure 3. Topographic map of middle (left) and late (right) Miocene records of *Bulinus* (formerly *Kosovia*) (circles) and *Popovicia* (triangles) from Serbia and Kosovo as derived from the literature (Pavlović, 1931, 1932, 1935; Atanacković, 1959; Popović, 1964; Milošević, 1965, 1967, 1978; Milaković & Milošević, 1974; Atanacković & Stevanović, 1990). The list of occurrences forming the basis of this figure is provided in the Supplementary Material. Palaeolake outlines are tentative estimations based on available reconstructions, distributions of lacustrine sediments and localities with mollusc faunas, as well as present topography (see Popović, 1970a; Atanacković, 1990; Dumurdzanov, Serafimovski & Burchfiel, 2005; Neubauer *et al.*, 2015a). Contrary to this rather conservative reconstruction, 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. Mollusc faunas indicate little similarities between Serbian, Kosovan and Macedonian systems (Burgerstein, 1877; Pavlović, 1903, 1931, 1932, 1933, 1935), while the presumed connection to Bulgaria and Greece is based on outdated stratigraphy (Neubauer *et al.*, 2015a). Note that the northern boundary of the Serbian Lake System is unknown, but probably did not extend north of the Belgrade region.

Coexisting with *Bulinus* during the late Miocene, another group of sinistrally coiled gastropods appeared in the Metohia Basin (Fig. 3). Representatives of that group have been previously attributed to the genus *Metohia* Popović, 1964, which was recently shown to be a junior homonym and, thus, invalid. Neubauer & Harzhauser in Neubauer *et al.* (2015b) introduced *Popovicia* as a replacement name, with *Metohia levantica* Popović, 1964 as type species.

Compared with the still uncertain phylogenetic relationship of late Miocene Kosovan *Bulinus* species, the evolution of the genus *Popovicia* is better understood. The oldest known species, *P. compressa* (Pavlović, 1931), has an almost entirely planispiral coiled shell. Only in latest ontogeny does the shell start to grow slightly in an adapical direction (Popović, 1964, 1968; Neubauer *et al.*, 2015b). The shape of this species forms the basis for the morphological evolution of broad, occasionally quite high-spined, pseudodextral shells with bulbous, weakly flattened apex (Popović, 1964). Each of the three species ascribed to the *Popovicia* lineage is confined to a distinct horizon in the stratigraphic succession of the Metohia Basin. Following the stratigraphic classification of Elezaj *et al.* (2010), *P. compressa* appeared in the latest Miocene, while the succeeding *P. levantica* (Popović, 1964) and later *P. turriculoidea* (Popović, 1964) are confined to the Pliocene. Despite considerable discussion on evolutionary patterns within *Popovicia* (Popović, 1964, 1968, 1969; Milošević, 1967, 1970), little has been published about its potential ancestry. The only comprehensive work

dealing with this is an unpublished manuscript by Milošević from 1982 (who died before he could publish the rich information it contained). He provided numerous illustrations that convincingly demonstrate the continuous morphological transition between sinistral ‘*Kosovia*’, through planispiral forms to pseudodextral *Popovicia*. The extreme morphological variability and continuum between Kosovan *Bulinus* and *Popovicia* raises considerable doubt about the taxonomic separation of the two genera. However, more material, close examination of the protoconchs and detailed knowledge about the stratigraphic succession are required to properly address the evolutionary patterns in palaeolakes Kosovo and Metohia, and their relation to *B. matejici*.

Morphological disparity of the Planorbidae

Planorbids are known for their enormous morphological disparity in both Recent and fossil clades, exceeding those of most other freshwater gastropod families. Apart from the ubiquitous spirally coiled (e.g. *Anisus*, *Gyraulus*, *Planorbarius*, *Planorbis*) and limpet-like shapes (e.g. *Ancylus*, *Ferrissia*), they have produced buliniform (e.g. *Bulinus*, *Glyptophysa*, *Kesneria*, *Miratesta*), corkscrew-like (e.g. *Gyraulus*), slightly to almost entirely uncoiled (e.g. *Gyraulus*) to dentaliiform (*Orygoceras*) shells, as well as all kinds of shell sculpture (e.g. Baker, 1945; Nützel & Bandel, 1993; Finger, 1998; Walker & Ponder, 2001; Albrecht, Kuhn & Streit, 2007; Neubauer, Mandić & Harzhauser, 2013, 2016; Rasser, 2013;

Clewing *et al.*, 2015). However, little is understood about the causes of this extreme disparity and of the individual contributions of ecophenotypic versus genetic diversity (e.g. Reif, 1985; Rasser, 2013; Clewing *et al.*, 2015). Such uncertainty complicates taxonomic classifications, especially in the absence of molecular data. One of the most famous examples of phenotypic evolution in Planorbidae is the *Gyraulus* species flock in middle Miocene Lake Steinheim. Within a geologically short time, a single founder species gave rise to a diverse set of morphologies, many of which coexisted in the small lake (Hilgendorf, 1867; Mensink, 1984; Reif, 1985; Gorthner, 1992; Nützel & Bandel, 1993; Rasser, 2013). Tens of species- and subspecies-level taxa have been introduced over the past 150 years to categorize this vast morphological diversity and many of them have already been considered junior synonyms (e.g. Rasser, 2013). A comparable example of high morphological disparity is provided by the *Gyraulus* populations of Recent Lake Bangong on the Tibetan Plateau (Clewing *et al.*, 2015). There, typical planispiral forms co-occur with corkscrew-like and partly open-coiled morphologies and a series of transitional shapes (Clewing *et al.*, 2015). Molecular analyses indicate that phenotypic evolution in that clade is not genetically determined, but likely caused by the rapid ecophenotypic response of a single species to ecological stress.

Examples of scalariform specimens of the genera *Anisus* or *Biomphalaria* have been reported from breeding experiments in the laboratory (Boettger, 1949; Basch, 1968), emphasizing once more that morphological disparity does not necessarily have a genetic basis. A case similar to that documented here is the evolution of high-spired forms in North American *Planorbella*, which seem to have appeared at least twice independently in that genus during Pliocene to Recent times (Burch, 1982). In fact, the high-spired morphologies closely resemble *B. matejici*, particularly in the marked angulation between whorl flank and apical plane. *Planorbella* is, however, unknown from fossil European deposits; it has been introduced artificially into European waterbodies with aquarium plants (Glöer, 2002).

A case of extraordinary convergence with present *B. matejici* is shown by *Miratesta* P. & F. Sarasin, 1898, a genus endemic to ancient Lake Poso (Walker & Ponder, 2001). The shell of its only representative, *M. celebensis* P. & F. Sarasin, 1898, has a very similar shape and shows the same type of ornamentation, featuring broad axial ribs and numerous thin spiral keels (P. Sarasin & F. Sarasin, 1898). A marked difference is the wide anterior emargination of the peristome.

Co-occurring with *B. matejici* in the SLS, the genus *Orygoceras* is a representative of uncoiled Planorbidae (Papp, 1962; Harzhauser, Kowalke & Mandic, 2002; Neubauer, Mandic & Harzhauser, 2011; Neubauer *et al.*, 2016). The dentaliform-to-curved morphology probably originated in one of the slightly older lakes of the nearby Dinaride Lake System in Croatia and Bosnia and Herzegovina. Earlier authors have attributed the genus variously to valvatids, planorbids and even the marine Caecidae (Harzhauser *et al.*, 2002). In this case, again, the protoconch has shed light on its systematic classification. The presence of widely spaced faint spiral striae on its planispiral protoconch suggests placement in the Planorbidae (Harzhauser *et al.*, 2002; Neubauer *et al.*, 2011).

The present study demonstrates and further expands our knowledge of the extraordinary range of morphological disparity of the Planorbidae. Moreover, the present taxonomic revision reveals the only phenotypic radiation of the genus *Bulinus* on the European continent. This conclusion was only possible because of the detailed assessment of the embryonic shell. Especially in the absence of molecular data, SEM-based examination of the early shell should be preferred over morphological assessment of the highly variable characteristics of the adult shell when trying to unravel the systematic position of problematic freshwater gastropods.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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