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

Thomas A. Neubauer 1,2, Oleg Mandic 3, Mathias Harzhauser 3 and Gordana Jovanović 4

1 Department of Animal Ecology and Systematics, Justus-Liebig University, Heinrich-Buff-Ring 26-32 IFZ, 35392 Gießen, Germany; 2 Naturalis Biodiversity Center, PO Box 9517, 2300 RA Leiden, The Netherlands; 3 Geological-Palaeontological Department, Natural History Museum Vienna, Burggring 7, 1010 Vienna, Austria; and 4 Natural History Museum, Njegoševa 51, 11000 Belgrade, Serbia

Correspondence: T.A. Neubauer; e-mail: thomas.a.neubauer@allzool.bio.uni-giessen.de

(Received 22 August 2016; editorial decision 26 March 2017)

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 matejic 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; Miličević & Miličević, 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. 13.3.5). 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 armata 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 (Miličević, 1974). (Note that following ICZN, 1999: Art. 29, the correct spelling is Kosovinae.) Zilch (1959–1960) and Miličević & Miličević (1974), again without any explanation, placed the genus in the planorbid tribe Camptoceratinī, apparently suggesting a relationship with the sinistral, elongate Camptoceras 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 & Zanuleac, 1985; Mandic 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 & Eremita, 1977) or late Miocene (Milaković, 1983), based on biostatigraphic correlations of dreissenic 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°11'49"N 21°30'54"E), Material of *Bulinus* and Planorbus 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 snegulansis Müller, 1781; by Limnaeae tautonomy (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*—Miloshević, 1962: 32. Milaković & Miloshević, 1974: 69, text-fig. 3. Milaković cl. matejici—Miloshević, 1967: 5; text-fig. 2.

_Description:* Shell sinistral, buliniform, gradate, of up to five whors. Lectotype 15.0 × 12.0 mm. Protoconch planispiral, about 0.8 whors, 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 0.6 whors; 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 0.7 whors) 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, Madare and Pardik in central Serbia (Pavlović, 1931; Miloshević, 1967; Milaković & Miloshević, 1974). Additional records from Serbia not identified to species level (Miloshević, 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 undoubt- edly 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 sub- jective synonym of *Bulinus*. The subfamily Kosovinae is considered a junior synonym of Bulininae accordingly.

In both *Planorbarius* and *Bulinus*, the embryonic shell consists of a similar number of whors 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; Martinez-Orti, 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. 2I). 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 apertures 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 vari- ability (see Discussion). Nonetheless, some of the late Miocene species from the Kosovo Basin previously attributed to *Kosovia* (K. pavlovici Atanacković, 1959 and K. stevanovic Atanacković, 1959), which are characterized by non-graduate 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 Mađare, 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) |
|--------------------------------------|-------------------------------|----------------|------------------|------------------------|-----------------------|
| *Bulinus matejici* (Pavlović, 1931) | Madare, Serbia                | Late Langhian | 0.8              | 890                    | 270                   |
| *Bulinus corici* Harzhauser & Neubauer in Harzhauser et al., 2012 | Jauring, Austria            | Early Langhian | 0.9              | 910                    | 250                   |
| *Planorbarius mantelli* (Dunker, 1848) | Rein, Austria                | Early Langhian | 0.9              | 540                    | 140                   |
| *Planorbarius* 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 *Bulimus* and *Planorbarius*. A, B. *Bulimus corici* Harzhauser & Neubauer in Harzhauser et al., 2012, holotype, NHMW 2011/0021/0006; Jauring, Allenz Basin. C. *Bulimus corici* Harzhauser & Neubauer in Harzhauser et al., 2012, paratype, NHMW 2011/0021/0007; Jauring, Allenz 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 2012/0134/0028; Enzenbach, Rein Basin. H. *Planorbarius mantelli* (Dunker, 1848); NHMW 2012/0134/0029; Enzenbach, Rein Basin. I, L. *Bulimus corici* Harzhauser & Neubauer in Harzhauser et al., 2012, NHMW 2011/0021/0009; Jauring, Allenz Basin; pitted surface is visible opposite the nucleus under high magnification. J. *Planorbarius* sp., apical fragment, NHMW 2011/0130/0164; 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 μm.
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 subhypnorum* (Gottschick, 1920) which differs considerably from coexisting *Bulinus* (including *Kosovia*) species in its bulbous, smooth protocochle, 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 Aalen Basin in Austria (Harzhauser et al., 2012). *Bulinus trogus* (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., 2013a, 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 polyplody greatly contributed to the success of the genus and enabled dispersal into stressful and colder environments (see also Van Damme & Van Boxder, 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 ‘*Gammothorium 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 to keeled, 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 biostatigraphic 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; Miluković, 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 biostatigraphic 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 Kosovian 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.

| Species* | Age | SLS | L. Kosovo | L. Metohia |
|---------|-----|-----|-----------|-----------|
| *Bulinus bouei* (Pavlović, 1931) | late Miocene | × | × |
| *Bulinus matejici* (Pavlović, 1931) | middle Miocene | x |
| *Bulinus ornatus* (Pavlović, 1931) | late Miocene | x |
| *Bulinus pavlovici* (Atanacković, 1959) | late Miocene | x |
| *Bulinus stevanovići* (Atanacković, 1959) | late Miocene | x |
| *Bulinus striatus* (Milošević, 1978) | late Miocene | x |
| *Popovicia compressa* (Pavlović, 1931) | late Miocene | x |
| *Popovicia levantica* (Pavlović, 1964) | early Pliocene | x |
| *Popovicia tuniculoides* (Pavlović, 1964) | early Pliocene | x |

*Note that the species name ‘*Kosovia praepontica*’ mentioned by Krstić et al. (2012) is a *nomum 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 *Planorbis* species.*
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 levanica 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-spired, 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. levanica (Popović, 1964) and later P. turriculaoides (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 ‘Kosova’, 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

Planorbid gastropods 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, Planorbifera, Planorbiida) and limpet-like shapes (e.g. Ancylus, Ferrissia), they have produced buliniform (e.g. Bulinus, Glyphophysa, Kessneria, Miratesta), corkscrew-like (e.g. Gyraulus), slightly to almost entirely uncoiled (e.g. Gyraulus) to dentaliform (Oxyoceras) shells, as well as all kinds of shell sculpture (e.g. Baker, 1945; Nutzel & Bandel, 1993; Finger, 1998; Walker & Ponder, 2001; Albrecht, Kuhn & Streit, 2007; Neubauer, Mandic & 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 generic diversity (e.g. Reif, 1985; Rasser, 2013; Clew,
PAPP, A. 1962. Die systematische Stellung von Gyraulus aus dem Steinheimer Becken. Archiv für Molluskenkunde, 91: 203–206.

PAVLOVIĆ, P.S. 1903. Grada za poznavanje tercijska u Starij Srbiji. Annales Géologiques de la Péninsule Balkanique, 6: 155–189.

PAVLOVIĆ, P.S. 1931. O fosilnoj fauni mekušaca iz Skopske Kotline. Glasnik Skopskog naučnog društva, Odjeljenje prirodnih Nauka, 9: 1–28.

PAVLOVIĆ, P.S. 1932. Novi prilozi za poznavanje fosilne faune iz Kosovske i Metohiskopodrimske Kotline. Bulletin du Service Géologique du Royaume de Yougoslavie, 1: 231–253.

PAVLOVIĆ, P.S. 1933. O fosilnoj fauni mekušaca iz okoline Peči. Glas Spske Krajevne Akademije, 138: 73–91.

PAVLOVIĆ, P.S. 1935. Sur la faune fossile de Mallusques des environs de Peć (Serbie du Sud). Bulletin de l’Académie Serbe des Sciences Mathématiques et Naturelles, B. Sciences Naturelles, 2: 43–50.

PICKFORD, M. 2008. Freshwater and terrestrial Mollusca from the Early Miocene deposits of the northern Spergebiet, Namibia. Memoirs of the Geological Survey of Namibia, 20: 65–74.

POPOV, S.V., RÖGL, F., ROZANOV, A.Y., STEININGER, F.F., POPOVIĆ, P.S., REIF, W.-E. 1985. Endemic evolution of species from the Neogene Metohia Basin, the Balkan Peninsula. Nioš Hidrogeol., Beliščko, 143: 53–62.

PAPP, A. 1962. Die systematische Stellung von Gyraulus aus dem Steinheimer Becken. Archiv für Molluskenkunde, 91: 203–206.

PAVLOVIĆ, P.S. 1903. Grada za poznavanje tercijska u Starij Srbiji. Annales Géologiques de la Péninsule Balkanique, 6: 155–189.

PAVLOVIĆ, P.S. 1931. O fosilnoj fauni mekušaca iz Skopske Kotline. Glasnik Skopskog naučnog društva, Odjeljenje prirodnih Nauka, 9: 1–28.

PAVLOVIĆ, P.S. 1932. Novi prilozi za poznavanje fosilne faune iz Kosovske i Metohiskopodrimske Kotline. Bulletin du Service Géologique du Royaume de Yougoslavie, 1: 231–253.

PAVLOVIĆ, P.S. 1933. O fosilnoj fauni mekušaca iz okoline Peči. Glas Spske Krajevne Akademije, 138: 73–91.

PAVLOVIĆ, P.S. 1935. Sur la faune fossile de Mallusques des environs de Peć (Serbie du Sud). Bulletin de l’Académie Serbe des Sciences Mathématiques et Naturelles, B. Sciences Naturelles, 2: 43–50.

PICKFORD, M. 2008. Freshwater and terrestrial Mollusca from the Early Miocene deposits of the northern Spergebiet, Namibia. Memoirs of the Geological Survey of Namibia, 20: 65–74.

POPOV, S.V., RÖGL, F., ROZANOV, A.Y., STEININGER, F.F., POPOVIĆ, P.S., REIF, W.-E. 1985. Endemic evolution of species from the Neogene Metohia Basin, the Balkan Peninsula. Nioš Hidrogeol., Beliščko, 143: 53–62.

PAPP, A. 1962. Die systematische Stellung von Gyraulus aus dem Steinheimer Becken. Archiv für Molluskenkunde, 91: 203–206.

PAVLOVIĆ, P.S. 1903. Grada za poznavanje tercijska u Starij Srbiji. Annales Géologiques de la Péninsule Balkanique, 6: 155–189.

PAVLOVIĆ, P.S. 1931. O fosilnoj fauni mekušaca iz Skopske Kotline. Glasnik Skopskog naučnog društva, Odjeljenje prirodnih Nauka, 9: 1–28.

PAVLOVIĆ, P.S. 1932. Novi prilozi za poznavanje fosilne faune iz Kosovske i Metohiskopodrimske Kotline. Bulletin du Service Géologique du Royaume de Yougoslavie, 1: 231–253.

PAVLOVIĆ, P.S. 1933. O fosilnoj fauni mekušaca iz okoline Peči. Glas Spske Krajevne Akademije, 138: 73–91.

PAVLOVIĆ, P.S. 1935. Sur la faune fossile de Mallusques des environs de Peć (Serbie du Sud). Bulletin de l’Académie Serbe des Sciences Mathématiques et Naturelles, B. Sciences Naturelles, 2: 43–50.

PICKFORD, M. 2008. Freshwater and terrestrial Mollusca from the Early Miocene deposits of the northern Spergebiet, Namibia. Memoirs of the Geological Survey of Namibia, 20: 65–74.