

Upper Miocene endemic lacustrine gastropod fauna of the Turiec Basin: addressing taxonomic, paleobiogeographic and stratigraphic issues

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Abstract: The present work displays the first detailed taxonomic study on the freshwater gastropod fauna of the Upper Miocene Lake Turiec. Apart from several mentions of species and genus names in the literature, the mollusc fauna has been poorly studied up to now. Some of the cited genera implied peculiar paleobiogeographic relationships, urging a taxonomic investigation to either prove or revise such arising claims. Variable degrees of preservation, however, limited the possibility to identify all the fossils at species level. The fauna includes at least ten species, of which five turned out to be new to science. Four of those were sufficiently well preserved to be described as new species, namely *Viviparus pipiki* Neubauer & Harzhauser nov. sp., *Melanopsis glaubrechtii* Neubauer & Harzhauser nov. sp., *Tournouerina turiecensis* Neubauer & Harzhauser nov. sp., and *Radix kovaci* Neubauer & Harzhauser nov. sp. Additionally, the new genus *Popovicia* Neubauer & Harzhauser nov. gen. is introduced for the primary homonym *Metohia* Popović, 1964 non Absolon, 1927. Most importantly, this taxonomic study revises many of the names cited in the literature and proves most of the alleged paleobiogeographic relationships wrong. The only biogeographic and stratigraphic surprise is the record of *Popovicia* cf. *compressa*, a species described from lower Pliocene deposits of the Metohia Basin in Kosovo. The majority of the fauna, however, has only been documented for the Turiec Basin, once more confirming the high degree of its endemism. The faunal relationships indicate a latest Middle to early Late Pannonian (Middle to Late Tortonian) age, which is in agreement with available age models.

Key words: freshwater molluscs, taxonomy, endemism, paleobiogeography, stratigraphy, Western Carpathians, Neogene.

Introduction and taxonomic history

The Turiec Basin, located in the Western Carpathians in northern Slovakia (Fig. 1), harboured a closed, long-lived freshwater lake during the Late Miocene (Pipík et al. 2012). Data quality about its fauna and flora is, however, quite varied. The best known fossil group is the ostracods, documented in several successive papers by Pipík (2002, 2004, 2005), Pipík & Bodergat (2003a,b, 2004a,b, 2006, 2007, 2008), and Pipík et al. (2012). The fauna revealed a high degree of endemism, which makes the Lake Turiec a particularly interesting research field and a potential equivalent to comparable extant and fossil long-lived systems.

In contrast, the published data on the mollusc fauna of Lake Turiec is mostly imprecise and contains many misidentifications. The first work dates back to the 19th century and only mentions the bivalve *Congeria triangularis* (Andrian 1865). Based on determinations by Štúr (1860) — Andrian (1866) gave more detailed information and additionally recorded *Planorbis pseudoammonius*, *Paludina sadleri*, and unidentifiable remains of the genera *Paludina*, *Planorbis*, *Melanopsis*, and *Valvata* from the Bystrička locality (see also Vetter 1910). Half a century later, Vigh (1915) mentioned viviparids, melanopsids, neritids, hydrobiids, planorbids, and dreissenids from Martin brickyard. After determinations by Wenz, who compared the fauna with the much older Moravian

“*Oncophora* beds” (today known as the *Rzehakia* beds, Čtyroký et al. 1973), Remeš (1923) recorded the species *Viviparus oncophorae*, *Melanoptychia pseudoscalaria*, *Theodoxis (Neritodonta) aff. crenulata*, *Hydrobia* sp., *Theodoxis* sp., *Congeria subclaviformis*, and *Oncophora* sp. from the Hrby locality near Bystrička. Additionally he mentioned *Stalioia gracilis* from the Dolina locality near Martin.

The first “real” taxonomic work with synonymy lists, short descriptions and illustrations was performed by Andrusov (1954). He clearly discussed previous misidentifications and partly synonymized them with the species observed by himself, namely *Succinea (Amphibina) primaeva*, *Viviparus neumayri*, *Melanoptychia* sp., *Theodoxus (Calvertia) crenulatus crenulatus*, and *Congeria* sp. ex gr. *C. ornithopsis*. In the same year Pokorný (1954) reported a few terrestrial gastropods and a sphaeriid bivalve with determinations on genus or family level only. Further studies were carried out by A. Ondrejčková and M. Rakús, who produced manuscripts that were unfortunately never published (see Kováč et al. 2011).

Some genus names deriving from published as well as unpublished data were mentioned by Kováč et al. (2011) and Pipík et al. (2012), namely *Viviparus*, *Theodoxus*, *Melanopsis*, *Hydrobia*, *Pyrgula*, *Lymnaea*, *Ancylus*, *Gyraulus*, *Planorbis*, *Kosovia*, *Congeria*, *Unio*, and *Anodonta*. Especially the record of the genus *Kosovia* was eye-catching, since it is a known endemite for basins in Kosovo and southern Serbia.

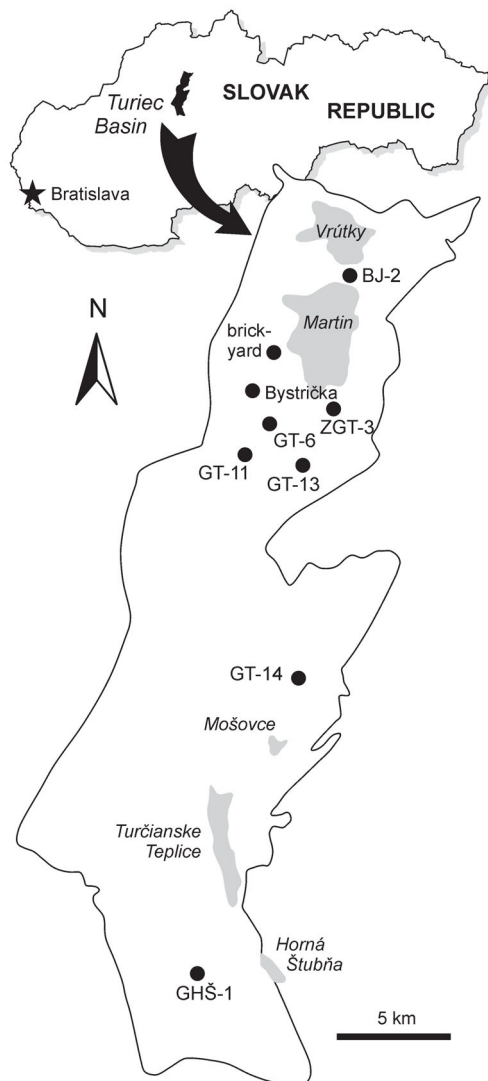


Fig. 1. Geographical sketch of the Turiec Basin in northern Slovakia with indication of sampled localities (modified after Kováč et al. 2011; Pipík et al. 2012). Grey areas display larger villages, filled circles the localities mentioned in the text.

Krstić et al. (2012) determined the species as *Kosovia strophostomopsis* Milošević, 1965, which was originally described from the Late Pontian (Early Pliocene) of the Metohia Basin. Additionally they mentioned *Lithoglyphus nanus* Roshka, 1973, a Maeotian species of the region SE of Odessa.

In summary, the few papers mentioning molluscs from the Turiec Basin produce quite a motley collection of names deriving from various stratigraphic levels and geographical regions. On the one hand, many of these names might raise doubts about the identifications, given the deviating paleobiogeographic distribution. On the other hand, if these molluscs were correctly determined, these findings would reshuffle parts of the Late Miocene paleobiogeographic framework. Consequently, one main task of this taxonomic work is to clarify these and other ambiguities to straighten up the paleobiogeographic framework of the Late Miocene in this region. The second point regards taxonomy itself — since

the fauna has never been studied in detail and rarely figured, this paper presents an important contribution to our knowledge of Miocene freshwater faunas and to our understanding of endemic faunas in the Miocene of Europe.

Geological setting

The geological history of the Turiec Basin is well understood, supported by data from structural geology, sedimentology, paleoecology, geochronology, geophysics, and geomorphology (Buday 1962; Gašparík et al. 1974, 1995; Konečný et al. 1983; Hók et al. 1998; Rakús et al. 2005; Kováč et al. 2011; Pipík et al. 2012; Králiková et al. 2014). The basin is a 40 km long and 10 km wide westward-dipping halfgraben system with a sedimentary infill of up to 1200 m thickness. It is enclosed by the Krivánska Malá Fatra Mts in the north, the Lúčanská Malá Fatra Mts in the west, the Veľká Fatra Mts in the east, and the Kremnické vrchy Mts in the southeast. Its southwestern part is delimited from the Horná Nitra Basin by the Žiar Mts. The basement consists mainly of the Mesozoic complexes of the Central Western Carpathian paleo-Alpine tectonic units and in its northern part also of Paleogene post-nappe sedimentary cover. The basin became restricted during the Middle Miocene as a result of rapid uplift of the surrounding mountain chains and volcanic activity.

Neogene sedimentation started during the late Middle Miocene. The transtensional to extensional tectonic regime during that time resulted in the subsidence of the southern part of the basin. The initial phase of sedimentation is characterized by a volcano-sedimentary complex in the southern region, lacustrine fine-grained sedimentation in the northern region, and subsequent alluvial fan deposits during the Late Badenian to Early Pannonian (Early Serravallian to Early Tortonian — Kováč et al. 2011). The main part of the Neogene sediments is represented by the lacustrine Martin Formation, reaching from the late Middle Miocene up to the earliest Pliocene (Kováč et al. 2011). Increased subsidence along the uplifted mountains led to accumulations of its clayey infill. Most of the known freshwater biota, including the herein presented molluscs, derives from this unit, reflecting the deposits of an isolated freshwater lake. On the basis of the rich ostracod assemblages Pipík et al. (2012) defined six paleoecological communities, allowing the ecological and bathymetrical zonation of Lake Turiec during the Late Miocene. Rapid uplift of the surrounding mountain chains during the latest Miocene and Early Pliocene resulted in the deposition of alluvial fans along the western, southwestern, and northwestern basin margins. This is followed by Pleistocene alluvial and river terrace deposits, which cover large parts of the basin at present. For a detailed reconstruction of the sedimentary history of the basin see Kováč et al. (2011).

Material and methods

The studied material is stored in the collection of the Múzeum Andreja Kmeťa in Martin, Slovak Republic. It de-

rives from drill cores and several outcrops sampled by Miloš Rakús in the 1950s and 1990s in the Turiec Basin (Fig. 1). Consequently any quantitative study is not possible. Some specimens were cleaned from sediment particles with an ultrasonic device. The SEM-photos were produced with a JEOL JSM-6610LV at the Natural History Museum Vienna using an output voltage of 15 kV.

Systematic paleontology

The systematical arrangement follows Bouchet & Rocroi (2005), Jörger et al. (2010), Criscione & Ponder (2013), and the FreshGEN database (Neubauer et al. 2014b).

Class: **Gastropoda** Cuvier, 1795

Subclass: **Neritimorpha** Golikov & Starobogatov, 1975

Order: **Cycloneritimorpha** Frýda, 1998

Superfamily: **Neritoidea** Rafinesque, 1815

Family: **Neritidae** Rafinesque, 1815

Subfamily: **Neritinae** Poey, 1852

Genus: *Theodoxus* Montfort, 1810

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

Theodoxus cf. *postcrenulatus* Papp, 1953
(Fig. 2A–C)

1923 *Theodoxis* (*Neritodonta*) aff. *crenulata* Klein — Remeš, p. 113
?cf. 1953 *Theodoxus* (*Theodoxus*) *postcrenulatus* n. sp. Papp, p. 96, pl. 2, figs. 1–3

1954 *Theodoxus* (*Calvertia*) *crenulatus crenulatus* (Klein) — Andrusov, p. 257 [non *Neritina crenulata* Klein, 1853]

?cf. 1997 *Theodoxus* (*Theodoxus*) *postcrenulatus* Papp, 1953 — Fordinál, p. 267, pl. 1, fig. 1

?cf. 2004 *Theodoxus postcrenulatus* Papp — Harzhauser & Tempfer, p. 60

Material: 10 specimens from Martin brickyard, coll. nos. SNM 9/2011 (PZ-696), SNM 12/2011 (PZ-699a–d); 1 specimen from Trebostovo (Drill core GT-11), coll. no. SNM 171/2006 (PZ-573); height: 5.5 mm, width: 6.5 mm (largest specimen).

Description: Shell small, sturdy, with ca. 2.5 whorls. Apex very low, in some specimens fully immersed. Apical region slightly flattened to convex; grades over a highly convex shoulder into the steep, straight base. Aperture inclined with about 60°; perfectly semicircular in shape. Callus moderately thickened, with weakly granulated surface; forms a shallow ramp towards a sharp, densely but weakly serrated edge, which lies below the plane formed by the aperture. This inclination produces weak incisions, where the callus touches the apertural margin (adapically as well as abapically). In a single specimen colouring is preserved as dark, broad, widely-spaced zigzag lines on white ground.

Remarks: It is extremely difficult to distinguish the many *Theodoxus* species-group taxa that have been introduced for the Miocene of the Pannonian region (e.g. Handmann 1887;

Brusina 1892, 1902; Jekelius 1944; Papp 1953). Since many of these were established based on different colour patterns only, which has been shown to be not taxonomically relevant (see e.g. Welter-Schultes 2012), many may actually represent junior synonyms of others. The present species fits morphologically (as well as concerning the colouring) well with the specimens described and illustrated by Papp (1953) as *Theodoxus postcrenulatus*. It corresponds in the presence of small teeth and a weakly granulated callus. The main difference is the distinctly larger size of the Austrian specimens (ca. 10 mm — Papp 1953). Therefore, the identification remains somewhat uncertain. It could be that the few available specimens are not fully grown individuals.

The present species differs from the similar *T. intracarpaticus* Jekelius, 1944, which has a more elongated shell, a more thickened callus and less distinct teeth (if at all), and *T. soceni* Jekelius, 1944, which has a higher apex and thus appears bulkier (see also Harzhauser et al. 2002).

Andrusov (1954) mixed up the species with *Theodoxus crenulatus* (Klein, 1853), a wide-spread species throughout the Middle Miocene of Central Europe (Wenz 1929; Schlickum 1976; Bartha 1979; Binder 2003; Harzhauser et al. 2012), which differs in its slightly more elevated spire.

Distribution: Up to now only recorded from Late Miocene localities of the Vienna Basin (Götzendorf, Austria, Pannonian F, Papp 1953; Pezinok, Slovakia, Pannonian E, Fordinál 1997).

Subclass: **Caenogastropoda** Cox, 1960

Superfamily: **Viviparoidae** Gray, 1847

Family: **Viviparidae** Gray, 1847

Subfamily: **Viviparinae** Gray, 1847

Genus: *Viviparus* Montfort, 1810

Type species: *Viviparus fluviatorum* Montfort, 1810 (currently considered as a synonym of *Viviparus viviparus* (Linnaeus, 1758)). Recent, Northern Eurasia, Europe, Anatolia and Northern America. Type by original designation (Welter-Schultes 2012).

Viviparus pipiki Neubauer & Harzhauser nov. sp.
(Fig. 2D–J)

1866 *Paludina Sadleri* — Andrian, p. 196 [non *Vivipara sadleri* Neumayr, 1869]

1923 *Viviparus oncophorae* Rzehak — Remeš, p. 113 [non *Vivipara oncophorae* Rzehak, 1893]

1954 *Viviparus neumayeri* [sic] (Brusina) — Andrusov, p. 257, pl. 16, figs. 12–13 [non *Vivipara neumayeri* Brusina, 1874]

Material: More than 100 specimens from Martin brickyard, coll. nos. SNM 1/2011 (PZ-688a–o), SNM 2/2011 (PZ-689a–ch), SNM 3/2011 (PZ-690a,b), SNM 4/2011 (PZ-691a–k), SNM 5/2011 (PZ-692a–c), SNM 11/2011 (PZ-698), SNM 16/2011 (PZ-703a–e).

Holotype: SNM 11/2011 (PZ-698); height: 28.8 mm, width: 22.3 mm (Figs. 2D–E).

Paratype: SNM 11/2011 (PZ-698); height: 32.5 mm, width: 23.7 mm (Figs. 2F–G).

Stratum typicum: Martin Formation, Upper Miocene.

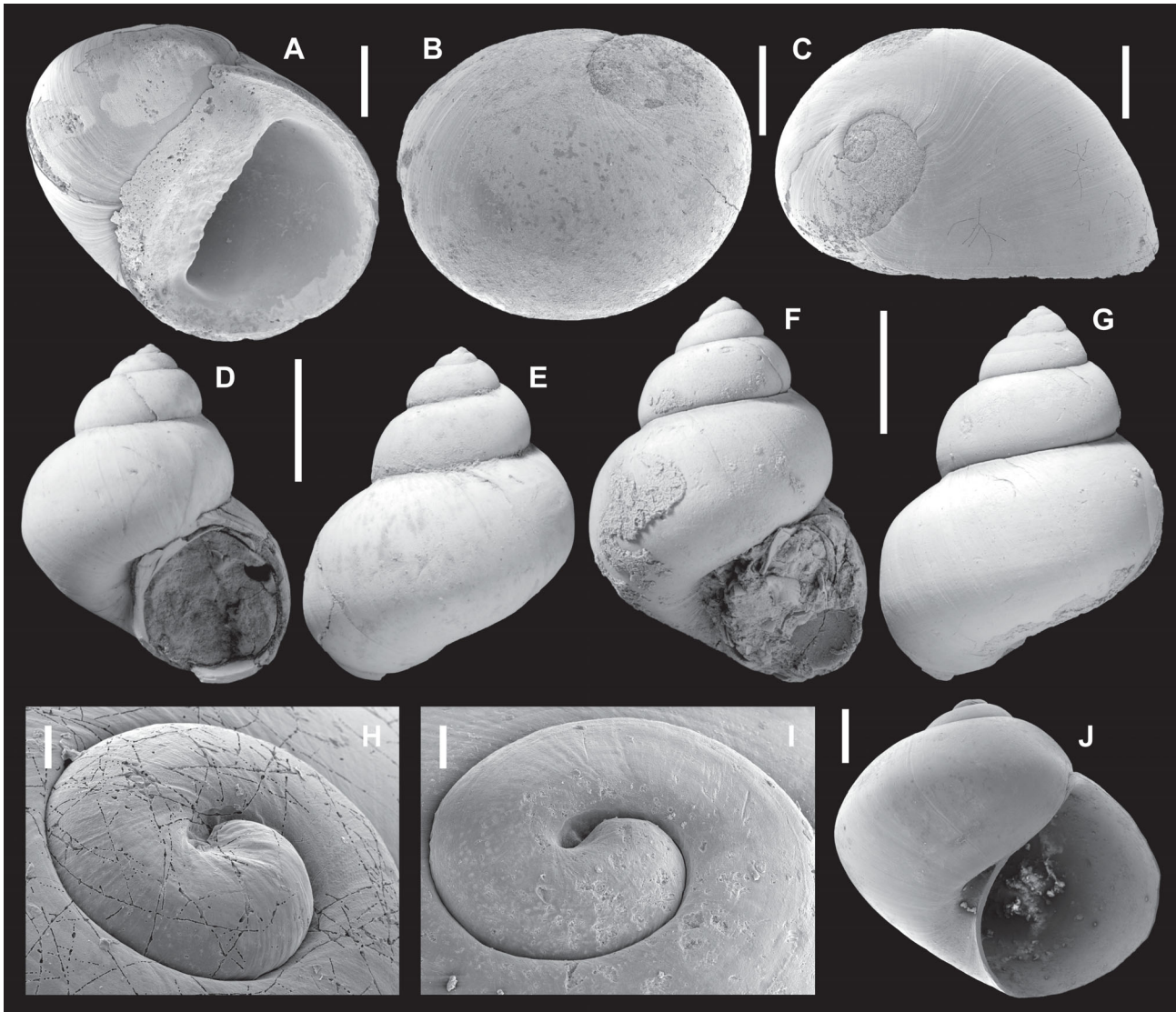


Fig. 2. **A** — *Theodoxus* cf. *postcrenulatus* Papp, 1953 (SNM 12/2011, PZ-699); **B** — *T.* cf. *postcrenulatus* (SNM 9/2011, PZ-696); **C** — *T.* cf. *postcrenulatus* (SNM 12/2011, PZ-699); **D–E** — *Viviparus pipiki* nov. sp., holotype (SNM 11/2011, PZ-698); **F–G** — *V. pipiki*, paratype (SNM 11/2011, PZ-698); **H** — *V. pipiki*, protoconch (SNM2/2011, PZ-689); **I** — *V. pipiki*, protoconch (SNM 2/2011, PZ-689); **J** — *V. pipiki*, juvenile specimen (SNM 3/2011, PZ-690). All specimens from Martin brickyard. Scale bars correspond to 100 μ m (H–I), 1 mm (A–C, J), and 10 mm (D–G).

Type locality: Brickyard near the town of Martin, Turiec Basin, Slovak Republic; 49°04' N, 18°53' E.

Name: In honour of Radovan Pipík (Slovak Academy of Sciences, Banská Bystrica), who greatly contributed to our knowledge of Lake Turiec.

Diagnosis: Broad, conical viviparid with up to 6 whorls; spire angle distinctly decreases during ontogeny, while whorl convexity increases towards highly convex whorls in later ontogeny.

Description: Protoconch depressed, almost planispirally coiled, covered by weak axial wrinkles; termination indiscernible, whorl number unknown. Both degree of convexity and spire angle change distinctly during ontogeny: early whorls broadly conical (spire angle of ca. 120°), weakly convex, tightly coiled, with widely ovoid aperture (Fig. 2J). Adult

shells conical to weakly ovoid (ca. 50–60°) with strongly convex, entirely non-stepped whorls. Height-width ratio of adult shells slightly variable: shells usually rather broad, occasionally more slender specimens occur (Fig. 2F–G). Shell comprises up to 6 whorls. Last whorl attains 70–75 % of total height. Aperture broadly drop-shaped, with small posterior notch. Distinct sigmoidal growth lines (adapically opisthocyrt, abapically prosocyrt) cover shell.

Remarks: Owing to its thick shell this species is among the most common and best preserved ones in the Turiec Basin. It looks very similar to *Viviparus neumayri* Brusina, 1874 from the Pliocene “*Paludina* beds” of Croatia, matching in degree of convexity and shell shape (see also Neumayr & Paul 1875). However, this species is distinctly smaller and whorl height increases more slowly than in the present spe-

cies, resulting in a relatively shorter spire. Another comparable species is *Viviparus loczyi* Halaváts, 1903, from the Late Pannonian of the Balaton region, which has a similar shape, but it has less convex whorls and tends to be more slender.

Andrian (1866) confused the present species with *Viviparus sadleri* Neumayr, 1869, which differs in its distinctly stepped spire. Remeš (1923) in turn determined it as *V. oncophorae* Rzehak, 1893, which was described from the Early Miocene of Moravia and likewise has a stepped spire. Wenz (1928) erroneously introduced the replacement name *Viviparus oncophoriorum* for Rzehak's taxon to separate it from *Vivipara* (= *Viviparus*) *oncophora* Brusina, 1874. This error is probably based on a reading error by Wenz, who cited Rzehak's species also as "*Vivipara oncophora*" and thus referred to it as a primary homonym. This nomenclatural act, however, is invalid. The Code clearly states that a one-letter difference between species-group names combined with the same generic name is sufficient to prevent homonymy (ICZN 1999, Art. 57.6). The exceptions to this rule mentioned in Article 58 do not apply here. Hence, the name *Vivipara oncophorae* was validly introduced by Rzehak (1893). *Viviparus oncophoriorum* Wenz, 1928 is an objective synonym of *Viviparus oncophorae* Rzehak, 1893.

Distribution: Endemic to the Turiec Basin.

Genus: *Popovicia* Neubauer & Harzhauser nov. gen.

1964 *Metohia* nov. gen. — Popović, p. 47.

1968 *Metohia* nov. gen. — Popović, p. 206

Type species: *Metohia levantica* Popović, 1964. Pliocene (Early Dacian), Kosovo.

Other included species: *Kosovia compressa* Pavlović, 1931 (Late Pontian), *Metohia turriculoidea* Popović, 1964 (Late Dacian).

Name: In honour of Radmila Popović (formerly in the Institute of Geological and Geophysical Research, Belgrade), who intensively studied the Viviparidae of the Metohia Basin.

Diagnosis: Shell planispiral to trochiform, sinistrally coiled, attaining up to 4 whorls. Apex shallow to deeply immersed. Umbilicus immersed in planispiral shells, but raised and flattened in trochiform shells, producing pseudo-dextral appearance. Whorls regularly convex to angulated, but never resulting in offset keel; ramp above shoulder straight, whorl portion below convex. Sutures deep. Sculpture may be present as weak to distinct spiral keels.

Remarks: Several nomenclatorial issues concerning the alleged viviparid genera *Metohia* and *Kosovia* have strained the literature so far. First of all, *Metohia* Popović, 1964 is a primary homonym of *Metohia* Absolon, 1927 (Ostracoda), which is why we introduce *Popovicia* as a replacement name here. The second genus, *Kosovia*, with which the species discussed below was originally affiliated, is not available from the original publication (Pavlović 1931), since no type species was fixed (ICZN 1999, Art. 13.3). The first to indicate a type species, namely *Kosovia ornata* Pavlović, 1931, was Atanacković (1959). He clearly referred to Pavlović's work and description, which is sufficient as indication for the genus (Art. 13.1.2) and makes him the author of *Kosovia*. Zilch

(1959–1960), who claimed to fix the type species as well, was published later (17 July, 1959).

The subfamily Kosoviinae as found in the literature was never described and is therefore unavailable. Atanacković (1959) first uses the name (as "Kosovinae", but see Art. 29 of the Code), but did not describe it or added a bibliographic reference as indication. The only other mention in the literature is by Milošević (1978), who did not describe it either. Since we do not aim at a systematic revision, a solution to the systematic placements of *Kosovia* and *Popovicia* is still pending. Following Atanacković (1959), we place it preliminarily in the Viviparidae.

Distribution: Only known from the Metohia Basin, Kosovo, and the Turiec Basin.

Popovicia cf. *compressa* (Pavlović, 1931)
(Fig. 5B)

cf. 1931 *Kosovia compressa* nov. spec. Pavlović, p. 21, pl. 11, figs. 11–13
cf. 1964 *Metohia compressa* (Pavl.) — Popović, p. 50, 53, pl. 3, fig. 1, pl. 4, fig. 1

cf. 1965 *Kosovia strophostomopsis strophostomopsis* nov. spec. Milošević, p. 116, text-fig. 3, pl. 1, fig. 1

cf. 1965 *Kosovia strophostomopsis compressiforma* nov. s. spec. Milošević, p. 120, pl. 1, fig. 2

cf. 1965 *Kosovia compressa* Pavl. — Milošević, pl. 1, fig. 4

cf. 1967 *Kosovia strophostomopsis* V. Miloš. — Milošević, text-fig. 4a

cf. 1967 *Kosovia s. compressiforma* V. Miloš. — Milošević, text-fig. 4b
cf. 1968 *Metohia compressa* (Pavl.) — Popović, p. 208, 216, pl. 3, fig. 1, pl. 4, fig. 1

cf. 1970 *Kosovia strophostomopsis* V. Milošević — Milošević, text-fig. 2B

2011 *Kosovia* — Kováč et al., p. 371

2012 *Kosovia strophostomopsis* [sic] — Krstić et al., p. 44

Material: 1 specimen from Trebstovo (Drill core GT-11), coll. no. SNM 161/2006 (PZ-563); height: 4.5 mm, diameter: 11 mm (Fig. 5B).

Description: Small sinistral, planorbiform shell composed of 3.25 whorls. Protoconch unknown. Early whorls apically flattened, forming a weakly convex plane; traces of weak striation present. Last whorl overgrows previous ones, forms a distinct crest at its uppermost part, which separates an inner concave portion and an outer convex portion. Inner concave portion shows weak striation. In profile a weak angulation occurs slightly below whorl midline. In latest ontogeny the apertural margin starts to expand funnel-like: while the peristome becomes strongly inflated, the actual apertural opening inside retains its original width.

Remarks: The specimen from Turiec is highly reminiscent of *Popovicia compressa* (Pavlović, 1931), which was described from the Late Pontian (earliest Pliocene) of the Metohia Basin in Kosovo. It matches perfectly concerning general shape and apertural inflation. The main difference is the presence of seven distinct spiral keels in the Kosovan species, which could not be observed to such an extent on the Turiec specimen; this, however, could be a result of the moderate preservation. Moreover, like the mode of apertural inflation this feature seems to be quite variable (Popović 1964). The Turiec specimen is also generally smaller and probably reflects a subadult specimen (3.25 whorls at 11 mm diameter versus 4 whorls at ca. 15 mm for typical *P. compressa*).

The taxonomic history of the genus *Metohia* Popović, 1964 (= *Popovicia*) and the included species is very complicated and needs some discussion here in order to avoid future confusion. Popović (1964) described the new genus *Metohia* to separate planorbiform and low trochiform shells among the Kosoviinae from the high trochiform, sinistral *Kosovia* species (see also Pavlović 1931; Atanacković 1959). Additionally, she described the two new species *M. levantica* and *M. turriculoidea*. One year later Milošević (1965) introduced the new species *Kosovia strophostomopsis* and two new subspecies, *K. strophostomopsis compressiforma* and *K. strophostomopsis disjuncta*, all of which are strikingly similar to the two species of Popović. Despite citing the paper of Popović in the reference section, Milošević did not discuss it at all. Only two years later Milošević (1967) referred to the topic again, when discussing the systematic position of *Kosovia compressa*. Again he did not comment on the morphological similarities between Popović's and his species. To complete the confusion Popović (1968) re-published

exactly the same paper as in 1964 in a different journal. Unfortunately, all the names were again marked as new, misleadingly pretending first descriptions.

Subsequently, Popović (1969) synonymized *K. strophostomopsis* with *Metohia levantica* and regarded both *K. strophostomopsis compressiforma* and *K. strophostomopsis disjuncta* as intermediate stages between *Metohia levantica* and *M. turriculoidea*. This taxonomic act was rejected by Milošević (1970) for two reasons. First, he differentiated between his "pseudo-sinistral" *Kosovia* forms and the "dextral" *Metohia* species. Given the full correspondence of morphologies this differentiation is untenable. Second, Milošević (1970) stated stratigraphical discrepancies: while *K. strophostomopsis* and its two subspecies are described from Late Pontian (earliest Pliocene) strata, *M. levantica* and *M. turriculoidea* were recorded from Dacian deposits (middle Early Pliocene). He did not agree with the idea of Popović (1969) that all these species may actually derive from Dacian layers. More precisely, he stated that his species come from sediments above the main

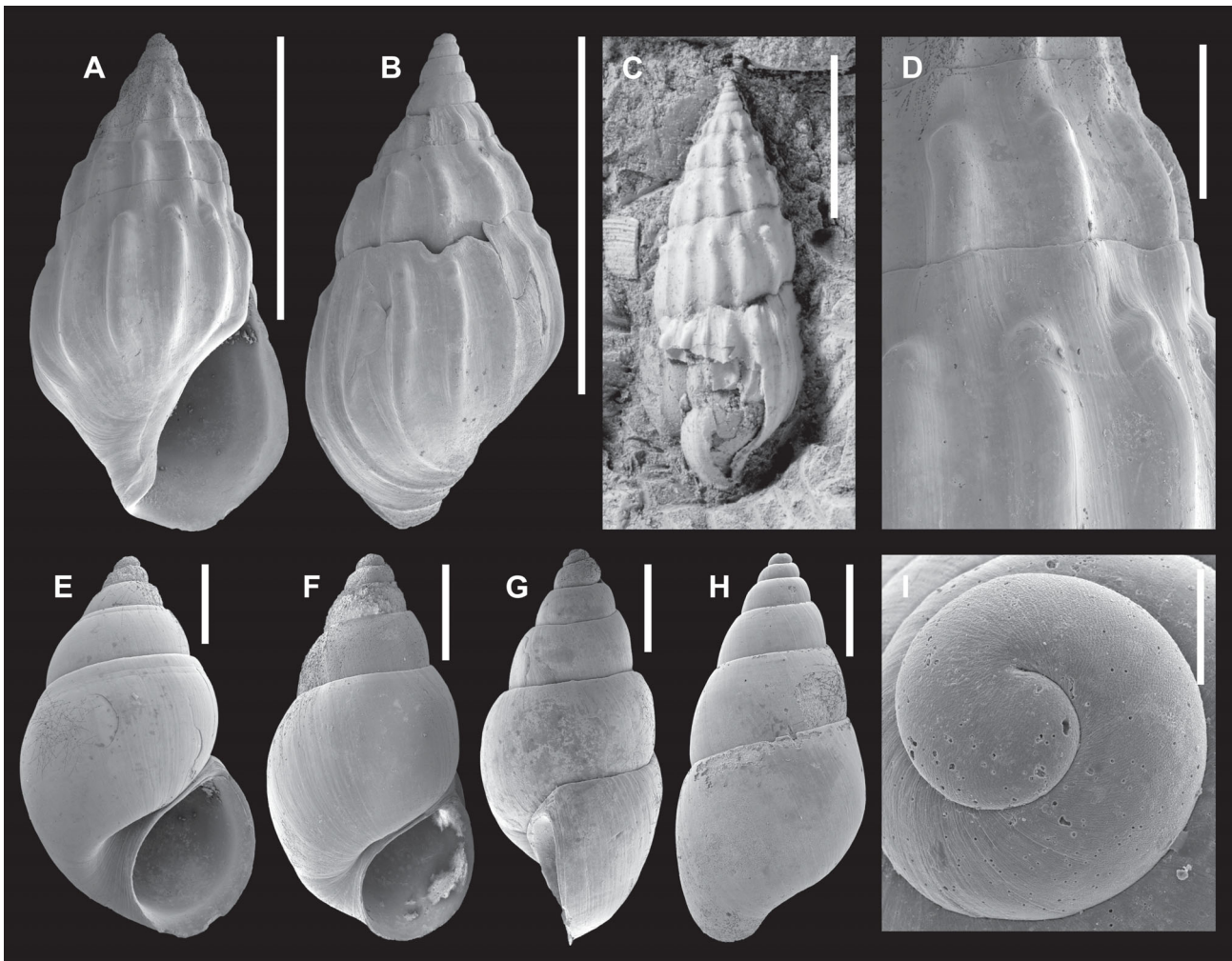


Fig. 3. A, D — *Melanospis glaubrechtii* nov. sp., paratype (SNM 10/2011, PZ-697), specimen digitally recombined from two separate images; B — *M. glaubrechtii*, juvenile shell (SNM 10/2011, PZ-697); C — *M. glaubrechtii*, holotype (SNM 16/2011, PZ-703g); E — *Tournouerina turiecensis* nov. sp., paratype 1 (SNM 10/2011, PZ-697); F — *T. turiecensis*, holotype (SNM 9/2011, PZ-696); G — *T. turiecensis*, paratype 2 (SNM 10/2011, PZ-697); H — *T. turiecensis*, paratype 3 (SNM 10/2011, PZ-697); I — *T. turiecensis*, protoconch (SNM 10/2011, PZ-697). All specimens from Martin brickyard. Scale bars correspond to 100 μ m (I), 1 mm (D-H), and 5 mm (A-C).

coal seam. However, the latest stratigraphical investigation by Elezaj et al. (2010) indeed confirmed the Dacian age of the deposits containing the *Metohia* (= *Popovicia*) species, with *P. levantica* marking Lower Dacian deposits and *P. turriculoidea* occurring in Upper Dacian layers.

Given the different extent of Pontian, Dacian, and Romanian deposits in the Metohia Basin it is most likely that Milošević misjudged the age of the deposits. The type localities of Popović's Dacian species are located in the south (Orahovac) and southwest (Trakanić brook at Čabrat hill near Gjakovë) of the Metohia Basin, where Pontian sediments are very restricted (S) to absent (SW) (Atanacković 1990). In contrast, the type locality of Milošević's species is right in the centre of the basin (Deiq), where Pontian to Romanian deposits have been documented (Popović 1970; Milošević 1983; Atanacković 1990). Geographically, all the type localities involved lie within a 30-km radius.

In summary, we fully agree with Popović (1969) concerning the stratigraphical attribution to the Dacian. However, we rather tend to synonymize *K. strophostomopsis strophostomopsis* and *K. strophostomopsis compressiforma* with *Popovicia compressa* and *K. strophostomopsis disjuncta* with *Popovicia levantica*. Since the evolutionary change throughout the Late Pontian and Dacian seems continuous, it is anyway difficult to draw a line between taxonomic entities (compare, e.g. Neubauer et al. 2013a,b). More detailed work on type material would be necessary to clarify this issue.

Distribution: Up to now only recorded for Upper Pontian deposits of the Metohia Basin (Pavlović 1931, 1932; Popović 1964) and the Turiec Basin.

Superfamily: **Cerithioidea** Fleming, 1822

Family: **Melanopsidae** H. Adams & A. Adams, 1854

Subfamily: **Melanopsinae** H. Adams & A. Adams, 1854

Genus: *Melanopsis* Férussac, 1807

Type species: *Melania costata* Olivier, 1804. Recent, Europe. Subsequent designation by Gray (1847, p. 153).

Melanopsis glaubrechtii Neubauer & Harzhauser nov. sp.
(Fig. 3A–D)

1923 *Melanoptychia pseudoscalaria* Sdbg. — Remeš, p. 113 [non *Melanoptychia pseudoscalaria* Sandberger, 1886]

1954 *Melanoptychia* sp. — Andrusov, p. 257, pl. 16, figs. 14–17

Material: More than 30 specimens and fragments from Martin brickyard, coll. nos. SNM 5/2011 (PZ-692), SNM 9/2011 (PZ-696), SNM 10/2011 (PZ-697), SNM 13/2011 (PZ-700), SNM 16/2011 (PZ-703a, f–g, ch).

Holotype: SNM 16/2011 (PZ-703g); height: 12.5 mm, width: 5 mm (Fig. 3C).

Paratype: SNM 10/2011 (PZ-697), juvenile shell; height: 8.8 mm, width: 4.6 mm (Fig. 3A,D).

Stratum typicum: Martin Formation, Upper Miocene.

Type locality: Brickyard near the town of Martin, Turiec Basin, Slovak Republic; 49°04' N, 18°53' E.

Name: In honour of Matthias Glaubrecht (Museum für Naturkunde Berlin), an expert for the living species of Melanopsidae.

Diagnosis: Small ovoid melanopsid with distinct ribs, which descend adapically over a small knob down to the suture. The ribs and the relief of the ribs of the penultimate whorl, which are clearly visible in early ontogeny, are not regularly aligned, producing irregular sculpture pattern below the sutures.

Description: Slender, drop-like shell, attaining its maximum diameter on the penultimate whorl and maintains this on the last whorl, which attains almost 50 % of total height. Protoconch poorly preserved but small and smooth. Including the protoconch, the shell comprises up to 9 whorls. The typical features are the strong axial ribs, which start faintly on the 3rd to 4th whorl. They form a strong crest of uniform elevation in the lower (abapical) three quarters of the whorls. Above, the ribs terminate in a small knob; in the uppermost quarter, the ribs rapidly slope down from the knob towards suture. In early ontogeny this produces a thin, weakly sculptured band in the uppermost part of the whorl. This weak sculpture is not produced by down-sloping ribs, but by ribs of the penultimate whorl, whose abapical portions can be traced beyond a thin shell layer. Since the number of ribs is not equal on each whorl, ribs and relief of ribs of penultimate whorl are not regularly aligned (Fig. 3D). In such cases, where “pseudo-ribs” run between two ribs, they may reach down to the level of knobs but never beyond. Aperture ovoid, sometimes with columellar fold; no thickened callus present.

Remarks: This species is reminiscent of specimens from the Pannonian F of Götzendorf in the Vienna Basin illustrated by Papp (1953, pl. 12, figs. 16–17), determined as *Melanopsis bouei sturii* Fuchs, 1873. A very similar specimen as shown by Papp was documented by Fordinál (1993, pl. 12, fig. 4) from the Pannonian of the Bratislava area. Both correspond to *M. glaubrechtii* concerning the general outline and the arrangement of the ribs with terminating adapical knobs. However, direct comparison with material from Götzendorf shows subtle but consistent differences: *M. sturii* has a highly regular morphology, with even suture, smooth subsutural band, and often intentions of a second row of weak knobs near the whorl base. In contrast, *M. glaubrechtii* has a fairly irregular suture line, the typical irregular sculpture pattern below the sutures, and just one row of knobs. The overall similarity still hints at a close phylogenetic relationship between the two species.

The present species also differs from “*M. boettgeri* Halaváts, 1903”, which has a conical shell and distinctly stronger knobs forming a spruce-like outline. This species name is a primary homonym of *M. boettgeri* Klika, 1891 and was replaced by Cossmann (1909) with the new name *M. balatonensis*. Both Wenz (1929) and Papp (1953), who obviously overlooked this, synonymized this species with *M. sturii*. The similar species *M. pseudoaustriaca* Sauerzopf, 1952 differs in its distinctly conical outline and the entirely smooth subsutural band.

Remeš (1923) refers to this species as *Melanoptychia pseudoscalaria*, which was described from the Lower Miocene “*Oncophora* beds” (*Rzehakia* beds) of Moravia. This species can be distinguished based on its much higher last whorl and the considerably thickened callus. Moreover, the ribs terminate directly at the upper suture (Rzehak 1893, pl. 2, fig. 7).

Distribution: Endemic to the Turiec Basin.

Order: **Littorinimorpha** Golikov & Starobogatov, 1975
 Superfamily: **Truncatelloidea** Gray, 1840
 Family: **Hydrobiidae** Stimpson, 1865
 Subfamily: **Hydrobiinae** Stimpson, 1865
 Genus: *Tournouerina* Schlickum, 1971

Type species: *Nematurella lugdunensis* Tournouër, 1879. Pliocene, France. Type by original designation.

Tournouerina turiecensis Neubauer & Harzhauser nov. sp.
 (Fig. 3E-I)

?2012 *Lithoglyphus nannus* [sic] — Krstić et al., p. 44 [non *Lithoglyphus nanus* Roshka, 1973]

Material: 35 specimens from Martin brickyard, coll. nos. SNM 9/2011 (PZ-696), SNM 10/2011 (PZ-697), SNM 13/2011 (PZ-700).

Holotype: SNM 9/2011 (PZ-696); height: 4.0 mm, width: 2.2 mm (Fig. 3F).

Paratype 1: SNM 10/2011 (PZ-697); height: 4.8 mm, width: 3.0 mm (Fig. 3E).

Paratype 2: SNM 10/2011 (PZ-697); height: 4.5 mm, width: 2.1 mm (Fig. 3G).

Paratype 3: SNM 10/2011 (PZ-697); height: 4.2 mm, width: 2.1 mm (Fig. 3H).

Stratum typicum: Martin Formation, Upper Miocene.

Type locality: Brickyard near the town of Martin, Turiec Basin, Slovak Republic; 49°04' N, 18°53' E.

Name: After the Turiec Basin.

Diagnosis: Small, ovoid hydrobiid with up to 6 convex whorls, separated by moderately deep sutures, a large last whorl, and an inclined, broadly drop-shaped aperture with a thickened posterior tip.

Description: Shell small, composed of 6 whorls. Shell shape is variable, reaching from rather broadly ovoid to slender, almost conical. Protoconch low trochiform, consisting of exactly 1 highly convex whorl with a diameter of 300 µm; termination indicated by indistinct growth rim; surface throughout covered with small, densely arranged, weak but consistent wrinkles, which partly merge into irregular, indistinct axial riblets. Teleoconch whorls distinctly and regularly convex, separated by moderately deep sutures. Last whorl attains ca. 70 % of total height. Aperture broadly, regularly drop-shaped, weakly inclined (20–30° to axis), with uninterrupted, slightly reflected peristome. Inner lip weakly protruding below posterior tip. Aperture growing increasingly in anterior direction in latest stage, producing a thickened posterior tip, with former shell layers distinctly visible. Umbilicus narrow; in slender specimens almost fully covered by aperture. Faint, weakly prosocyrte growth lines cover shell.

Remarks: After detailed literature review and study of fossil material, we are not aware of a single hydrobiid species in the Mio-Pliocene of Europe that might be conspecific with the present one. The characteristic ovoid aperture with the thickened posterior tip and the narrow umbilicus argues for an affiliation with the genus *Tournouerina* (e.g. Schlickum 1971, 1978; Schlickum & Puisségur 1977, 1978; Meijer

1989). Even the curvature of the aperture in side-view matches perfectly with the illustrations of Schlickum (1978). Especially the type species *T. lugdunensis* (Tournouër, 1879) from the Pliocene of Miribel (Ain, France) is very similar in terms of outline shape, but it has less convex whorls and a less bulbous last whorl.

Some species of the genus *Prososthenia* Neumayr, 1869 also exhibit certain similarities, like *P. sepulcralis* Partsch in Čížek, 1848 from Lake Pannon. This species differs in its clearly less convex whorls, the less inclined aperture, and the weak angle at the base, producing a conical outline (Papp 1953; Harzhauser & Binder 2004). The Pannonian *Hydrobia testulata* Papp, 1953, which was synonymized with *Hydrobia pseudocornea* Brusina, 1902 by Harzhauser & Binder (2004), has similar shape and size, but clearly differs in the aperture, which lacks the thickened posterior tip, and the more convex whorls. Another very similar Pannonian species is *Caspia boeckhi* (Lörenthey, 1902) from Tinnye, Hungary, which can be distinguished by the more conical outline, formed by a distinct angle on the last whorl, and the whorl convexity, which lies below the median. The quite variable Middle Miocene *Prososthenia neutra* Brusina, 1897 from Miočić, Croatia, has a less bulbous last whorl and a stronger inclined aperture resulting in an almost covered umbilicus. The likewise variable Dacian species *Hydrobia arminiensis* Jekelius, 1932 from the Braşov Basin has a wider aperture that almost or fully covers the umbilicus, in most cases a bigger last whorl, and more convex whorls.

Most likely the identification of Krstić et al. (2012) as *Lithoglyphus nanus* Roshka, 1973 [misspelt as “nannus”] actually reflects the present species. *Lithoglyphus nanus* is a Late Miocene taxon from the Eastern Paratethys and has a much bulkier shell with bigger last whorl and strongly inclined aperture. Whether or not the records of *Hydrobia* sp. from Hrby and “*Stalioia* [sic] *gracilis*” from Dolina by Remeš (1923) correspond to the present species could not be verified. The material from Dolina available to us comprises lithified freshwater limestones with unidentifiable fragments of shelly impressions and molds. As correctly pointed out by Andrusov (1954), the name *Stalioia gracilis* has to be replaced with *Stalioia rzehaki*. Wenz (1925) considered *Staliopsis gracilis* Rzehak, 1893 and *Euchilus gracile* Sandberger, 1875 congeneric, making the former a secondary homonym of the latter. For *Staliopsis gracilis* he introduced the replacement name *Stalioia rzehaki* Wenz, 1925. Currently it is again affiliated with *Staliopsis* (Čtyroký 1972).

Distribution: Endemic to the Turiec Basin.

Clade: **Panpulmonata** Jörger et al., 2010

Order: **Hygrophila** Férussac, 1822

Superfamily: **Lymnaeoidae** Rafinesque, 1815

Family: **Lymnaeidae** Rafinesque, 1815

Subfamily: **Lymnaeinae** Rafinesque, 1815

Genus: *Radix* Montfort, 1810

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

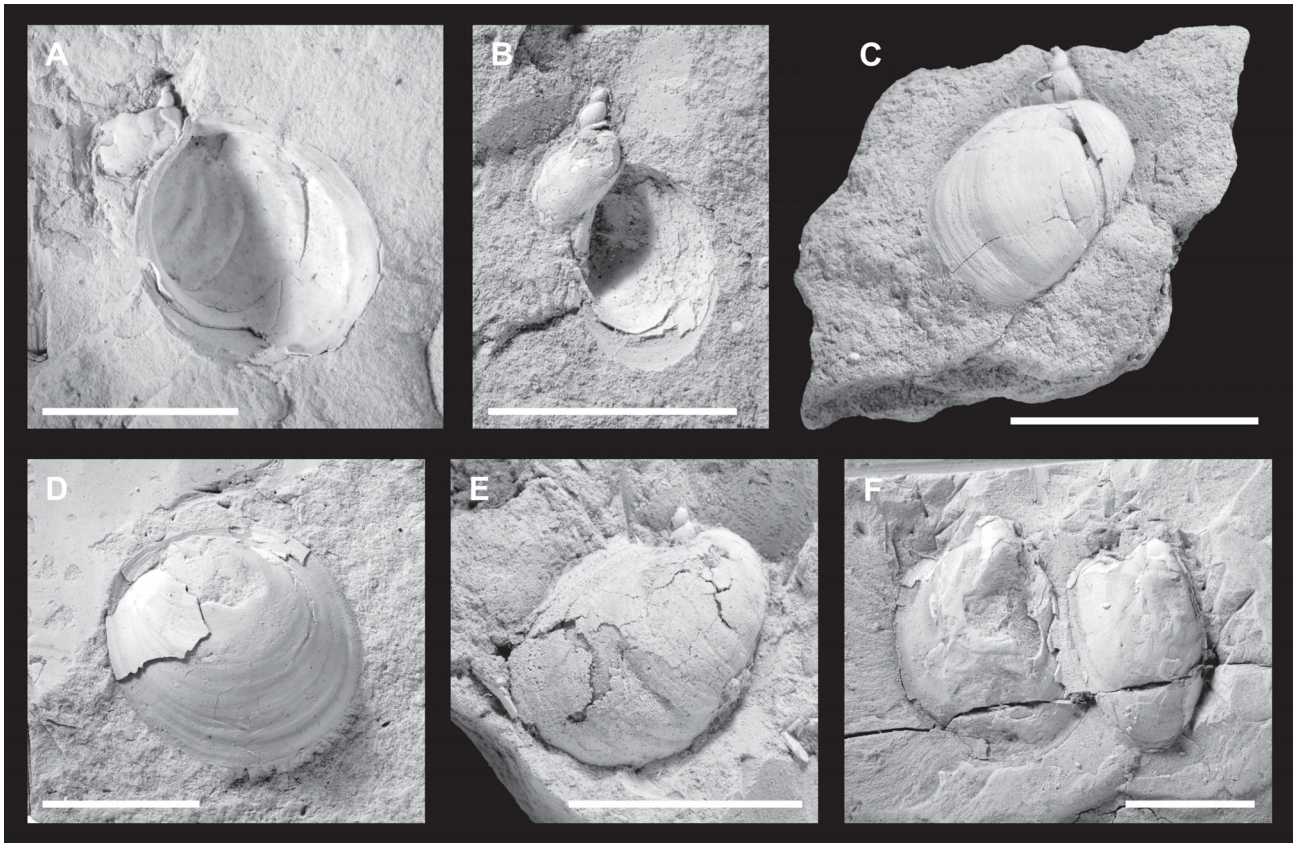


Fig. 4. *Radix kovaci* nov. sp. **A** — Holotype (SNM 114/2006, PZ-517), Mošovce (GT-14); **B** — Juvenile specimen (SNM 148/2006, PZ-550), Horná Štubňa (GHŠ-1); **C** — Paratype 1 (SNM 155/2006, PZ-557), Horná Štubňa (GHŠ-1); **D** — Paratype 3 (SNM 121/2006, PZ-524a), Mošovce (GT-14); **E** — Paratype 2, (SNM 153/2006, PZ-555), Horná Štubňa (GHŠ-1); **F** — Sediment infills of apertures of two specimens (SNM 118/2006, PZ-521), Mošovce (GT-14). Scale bars correspond to 10 mm.

Radix kovaci Neubauer & Harzhauser nov. sp.
(Fig. 4A–F)

Material: Several tens of specimens in different ontogenetic stages, from following localities: Mošovce (Drill core GT-14), coll. nos. SNM 114/2006 (PZ-517), SNM 117-119/2006 (PZ-520-522), SNM 121/2006 (PZ-524b), SNM 120/2006 (PZ-523); Horná Štubňa (Drill core GHŠ-1), coll. nos. SNM 144-145/2006 (PZ-546-547), SNM 146-154/2006 (PZ-548-561), SNM 136-143/2006 (PZ-538-545); Košťany nad Turcom (Drill core GT-13), coll. nos. SNM 107-113/2006 (PZ-510-516).

Holotype: SNM 114/2006 (PZ-517); height: 14 mm, diameter: 16 mm (Fig. 4A).

Paratype 1: SNM 155/2006 (PZ-557), from drill core GHŠ-1, Horná Štubňa; height: 10.8 mm, diameter: 8.5 mm (Fig. 4C).

Paratype 2: SNM 153/2006 (PZ-555), from drill core GHŠ-1, Horná Štubňa; height: 11.4 mm, diameter: 11.2 mm (Fig. 4E).

Paratype 3: SNM 121/2006 (PZ-524a), from type locality; sediment infill of aperture; height: 15.5 mm, diameter: 16.6 mm (Fig. 4D).

Stratum typicum: Martin Formation, Upper Miocene (drilling depth 229.5–229.6 m).

Type locality: Mošovce (Drill core GT-14), Turiec Basin, Slovak Republic; 48°54' N, 18°53' E.

Name: In honour of Michal Kováč (Univerzita Komenského, Bratislava), who intensively worked on the sedimentary evolution and stratigraphy of the Pannonian Basin System and adjacent areas.

Diagnosis: Moderately sized *Radix* with rapidly expanding whorls towards an extremely large aperture, finally overgrowing the spire.

Description: Most of the material does not allow a proper description. The few complete or nearly so specimens show a shell with ca. 4 whorls, a very small and short spire, and an extremely rapidly expanding last whorl. The direction of expansion forms an angle of usually around 55° to the columella. Aperture prominent, elliptical to almost round, terminates in sharp peristome. Where it touches base of penultimate whorl it forms small notch. Degree and direction of apertural expansion as well as apertural shape highly variable. Apparently expansion continues throughout ontogeny, so that aperture even overgrows entire spire in latest ontogeny; in abapertural view this produces bulky, cap-like appearance. Some specimens show elongate shape due to stronger lateral expansion of the aperture.

Remarks: After careful review of the rich literature we are still not aware of any lymnaeid species of the Mio-



Fig. 5. **A** — *Radix* sp. (SNM 183/2006, PZ-520), Martin (ZGT-3); **B** — *Popovicia* cf. *compressa* (Pavlović, 1931) (SNM 161/2006, PZ-563), Trebstovo (GT-11); **C** — *Planorbarius* nov. sp. (SNM 160/2006, PZ-562a), Horná Štubňa (GHŠ-1). Scale bars correspond to 10 mm.

Pliocene of Europe that might be conspecific with this shell. The uniquely formed aperture distinguishes it from all other known species. Most of the available specimens are preserved as mere impressions or sediment fillings of the last aperture, which form cap-like molds. The alleged records of *Ancylus* mentioned in the literature probably refer to these fillings as indicated by the museum labels. The final growth stage with the inflated aperture is also reminiscent of species of the genus *Hiscerus* Gorjanović-Kramberger, 1923, a lymnaeid with cap-shaped, oval shells (see Gorjanović-Kramberger 1923; Moos 1944). These, however, are much more bulbous and usually have a wrinkled surface.

The only rather similar taxon is *Radix kobelti* (Brusina, 1884) from the Pannonian of the Zagreb area, which also exhibits a very wide aperture, but differs in the lower spire and the almost horizontally oriented and stronger expressed expansion. Moreover, shells of *R. kobelti* are distinctly larger (see also Brusina 1897; Gorjanović-Kramberger 1923).

Distribution: Endemic to the Turiec Basin.

Radix sp.
(Fig. 5A)

Material: 1 specimen from Martin (Drill core ZGT-3), coll. no. SNM 183/2006 (P-520a); height: 27 mm, width 15.5 mm.

Remarks: A second *Radix* species is documented by a single, moderately preserved specimen. It can be easily distinguished from the co-occurring *R. kovaci* by its huge but

slender shell. A determination at species level is not possible as the aperture is covered with sediment.

Superfamily: **Planorboidea** Rafinesque, 1815

Family: **Planorbidae** Rafinesque, 1815

Genus: *Planorbarius* Duméril, 1806

Type species: *Helix cornea* Linnaeus, 1758. Recent, Europe. Subsequent monotypy by Froriep (1806, p. 165).

Planorbarius nov. sp.
(Fig. 5C)

?1866 *Planorbis pseudoammonius* — Andrian, p. 196 [non *Helicites pseudoammonius* Schlotheim, 1820]

Material: Several fragments and impressions from the following localities: Horná Štubňa (Drill core GHŠ-1), coll. no. SNM 160/2006 (PZ-562a,b); Martin (Drill core ZGT-3), coll. no. SNM 190/2006 (PZ-579); Martin brickyard (compressed), coll. no. SNM 13/2011 (PZ-700); Turčiansky Peter (Drill core GT-6, 37.2–37.3 m), coll. no. SNM 180/2006 (PZ-517); height: 6.5 mm, diameter: 18 mm (most complete specimen, Fig. 5C).

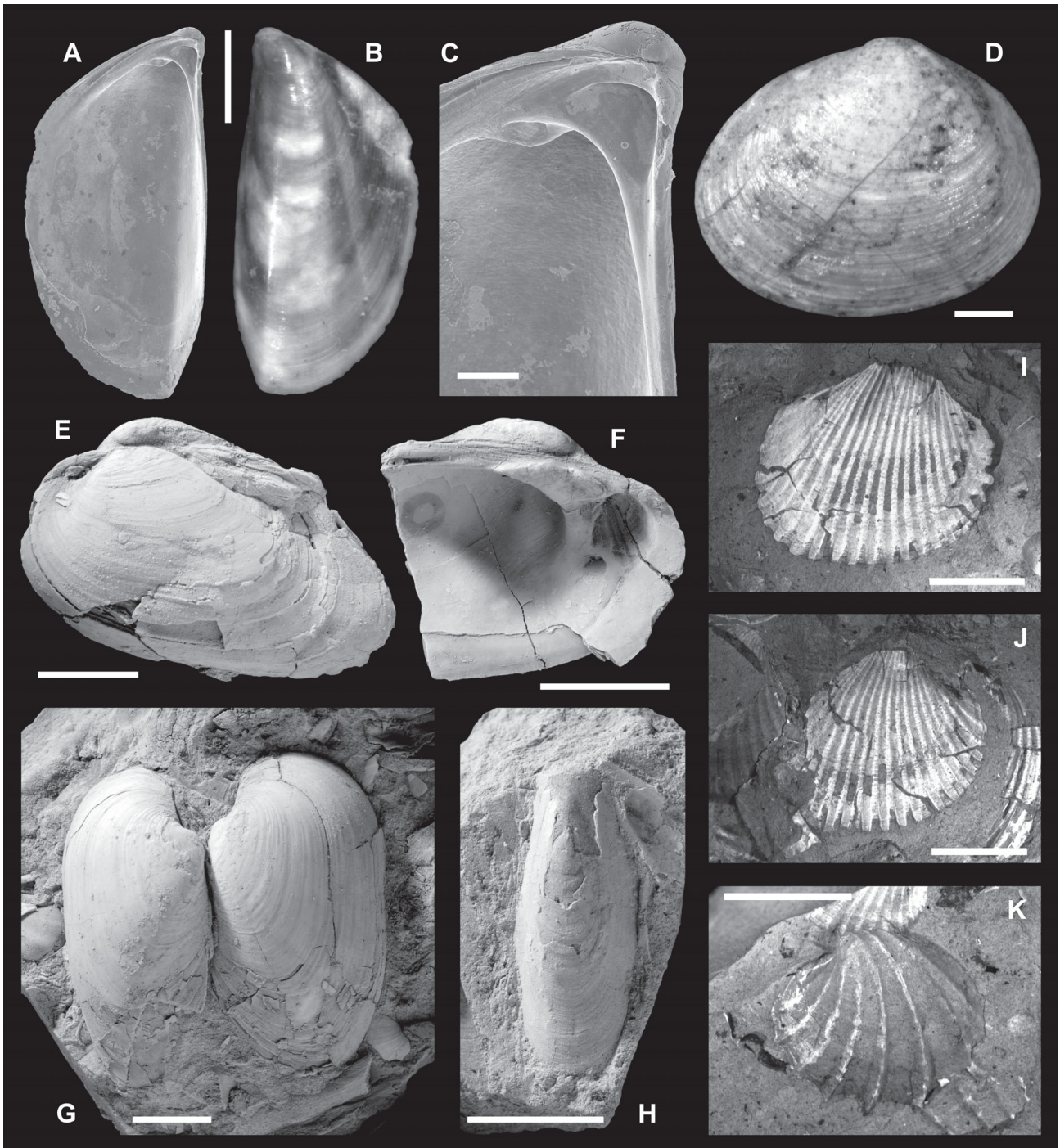
Description: Most complete specimen attains 4.5 whorls at a maximum diameter of 18 mm. Whorls appear regularly convex and increase regularly in diameter. Up to penultimate whorl apical region flat, not depressed; only last whorl distinctly elevated. Umbilical region unknown. Growth lines but no horizontal striation visible.

Fig. 6. Bivalves. **A–C** — *Mytilopsis?* sp. (SNM 9/2011, PZ-696), juvenile specimen, Martin brickyard; **D** — *Pisidium* sp. (SNM 13/2011, PZ-700b), Martin brickyard; **E** — *Unio* cf. *atavus* Hörmes, 1865 (SNM 14/2011, PZ-701), Martin brickyard; **F** — *U.* cf. *atavus* (SNM 7/2011, PZ-694c), Martin brickyard; **G** — *U.* cf. *atavus* (SNM 7/2011, PZ-694a), Martin brickyard; **H** — *Mytilopsis?* sp. (SNM 166/2006, PZ-568), Martin brickyard; **I** — Lymnocypridae gen. et sp. indet. 1 (SNM 380/1968, G-129), Martin-Záturčie (BJ-2); **J** — Lymnocypridae gen. et sp. indet. 1 (SNM 380/1968, G-129), Martin-Záturčie (BJ-2); **K** — Lymnocypridae gen. et sp. indet. 2 (SNM 380/1968, G-129), Martin-Záturčie (BJ-2). Scale bars correspond to 200 µm (C), 1 mm (A–B, D), 5 mm (I–K), and 10 mm (E–H).

Remarks: The most typical characteristic of this species is the non-depressed spire, which distinguishes it from all other Neogene *Planorbarius* species, e.g. *Planorbarius cornu* (Brongniart, 1810) from the Lower Miocene of France and Germany (e.g. Harzhauser et al. 2014b); *P. garsdorfensis* Schlickum & Strauch, 1979 from the Upper Pliocene of the open-cast mine “Fortuna-Garsdorf” near Bergheim, Germany; *P. grandis* (Halávats, 1903) [= *P. halavatsi* Neubauer, Harzhauser, Kroh, Georgopoulou & Mandic in Neubauer et al., 2014a] from the Upper Pannonian of Balatonfőkajár, Hungary; *P. heriacensis* (Fontannes, 1876) from the Upper

Miocene of Heyrieux, France; *P. mantelli* (Dunker, 1848) from the upper Lower Miocene (Kirchberg Fm) of Günzburg, Southern Germany (see, e.g. Harzhauser et al. 2014a); *P. thiollieri* (Michaud, 1855) from the Lower Pliocene of Hauterives, Southern France. This feature is certainly not an artefact from preservation, as this specimen is not deformed in any way. Still we refrain from introducing a new name based on a few incomplete specimens.

“*Planorbis pseudoammonius*” documented by Andrian (1866) is an Eocene species of France. The specimens studied by him are probably conspecific with *Planorbarius* sp.



Distribution: So far only known from the Turiec Basin.

Discussion

Faunal composition

The freshwater gastropod fauna consists of at least 10 species (Table 1). In many cases, the rather poor preservation of the fossils prevents precise determination. Therefore, some taxa could not be identified at the species level. Many fossils from drill cores are strongly compressed, deformed or preserved as shelly impressions only. The best preserved specimens derive from the Martin brickyard, including most of the thick-shelled *Viviparus* and the small *Theodoxus*, *Melanopsis*, and *Tournouerina*. Most of the species that have been determined at the species level are unknown from other European freshwater systems. This again confirms the high degree of endemism in Lake Turiec, as was already shown for the ostracod fauna (Pipík et al. 2012).

The composition above genus level is quite diverse with 7 families present (Viviparidae, Neritidae, Melanopsidae, Bithyniidae, Hydrobiidae, Lymnaeidae, and Planorbidae). This rather high number, however, must not be overestimated, since this diversity is never found in a single locality but is the sum of all species recorded from Upper Miocene deposits of the entire lake. The varied composition is certainly reflected in the paleoecological and/or stratigraphical differences throughout the basin. The ecological model established by Pipík et al. (2012) based on the ostracod fauna indicates the presence of quite diverse habitats in Lake Turiec. Most of the molluscs derive from marsh/wetland habitats or littoral to sublittoral areas in the north and are preserved as accumulations in sublittoral sediments (e.g. in Martin brickyard). More precise data, however, is not available, excluding reconstruction of the original habitats of the single species.

In addition to the freshwater gastropods, several fragments of terrestrial gastropods were found in the studied material, including a few opercula of *Pomatias* and remnants of helicids. None of these, however, allowed proper identification, in most cases not even at the family level. Bivalves are present as well and display a great systematic diversity similar to that of the gastropods. They are represented by at least one slender, elongate, triangular species of *Mytilopsis?* sp. (Dreissenidae), two single valves of *Pisidium* sp. (Sphaeriidae), several imprints of two species of Lymnocyprinae, and several shells and fragments of *Unio* cf. *atavus* Hörnes, 1865 (Unionidae) (Fig. 6). The overall rather poor preservation of the material makes more precise identifications difficult.

Stratigraphy

The earliest studies correlated the deposits with the Pannonian (“Congerienschichten”) based on elements of the mollusc fauna Štúr 1860; Andrian 1866; Vetter 1910; Fig. 7). Vigh (1915) in turn suggested a “Pliocene to Levantian” age. Remeš (1923), in contrast, indicated an Early Miocene age, based on the findings of the genus *Oncophora* (= *Rzehakia*) which is restricted to the late Oligocene (middle Burdigalian) (e.g. Čtyroký 1972). This implied a temporal shift of more than 7 Ma and naturally led to continuing discussions among later authors (Andrusov 1938; Čechovič 1948, 1954). Since not a single follow-up study could confirm the record of *Rzehakia*, it was and is considered a misidentification. Based on his determinations, Andrusov (1954) supported the former opinion and suggested an Early Pannonian age. More precise age constraints are provided from K-Ar radiometric dating by Konečný et al. (1983). They give an age of ca. 12.4–10.7 Ma (Late Sarmatian/Early Pannonian or Late Serravallian/Early Tortonian) for the rhyolitic formation of the Central Slovakia Volcanic Field underlying the Martin Formation, bounding the beginning of the Martin Formation and the main evolutionary episode of the endemic fauna

Table 1: Mollusc species present in the Turiec Basin. Counts are avoided here as the specimens derive from several non-quantitative collections.

Species	Martin brickyard	Horná Štubňa (GHŠ-1)	Turčiansky Peter (GT-6)	Trebstovo (GT-11)	Mošovce (GT-14)	Košťany nad Turcom (GT-13)	Martin (ZGT-3)	Martin-Záturčie (BJ-2)
<i>Theodoxus</i> cf. <i>postcrenulatus</i> Papp, 1953	x			x				
<i>Viviparus pipiki</i> Neubauer & Harzhauser nov. sp.	x							
<i>Popovicia</i> cf. <i>compressa</i> (Pavlovič, 1931)				x				
<i>Melanopsis glaubrechti</i> Neubauer & Harzhauser nov. sp.	x							
<i>Tournouerina turiecensis</i> Neubauer & Harzhauser nov. sp.	x							
<i>Bithynia</i> sp.							x	
<i>Radix kovaci</i> Neubauer & Harzhauser nov. sp.		x			x	x		
<i>Radix</i> sp.							x	
<i>Gyraulus</i> sp.						x		
<i>Planorbarius</i> nov. sp.	x	x	x				x	
Lymnocyprinae gen. et. sp. indet. 1								x
Lymnocyprinae gen. et. sp. indet. 2								x
<i>Mytilopsis?</i> sp.			x	x				
<i>Pisidium</i> sp.	x							
<i>Unio</i> cf. <i>atavus</i> Hörnes, 1865	x							

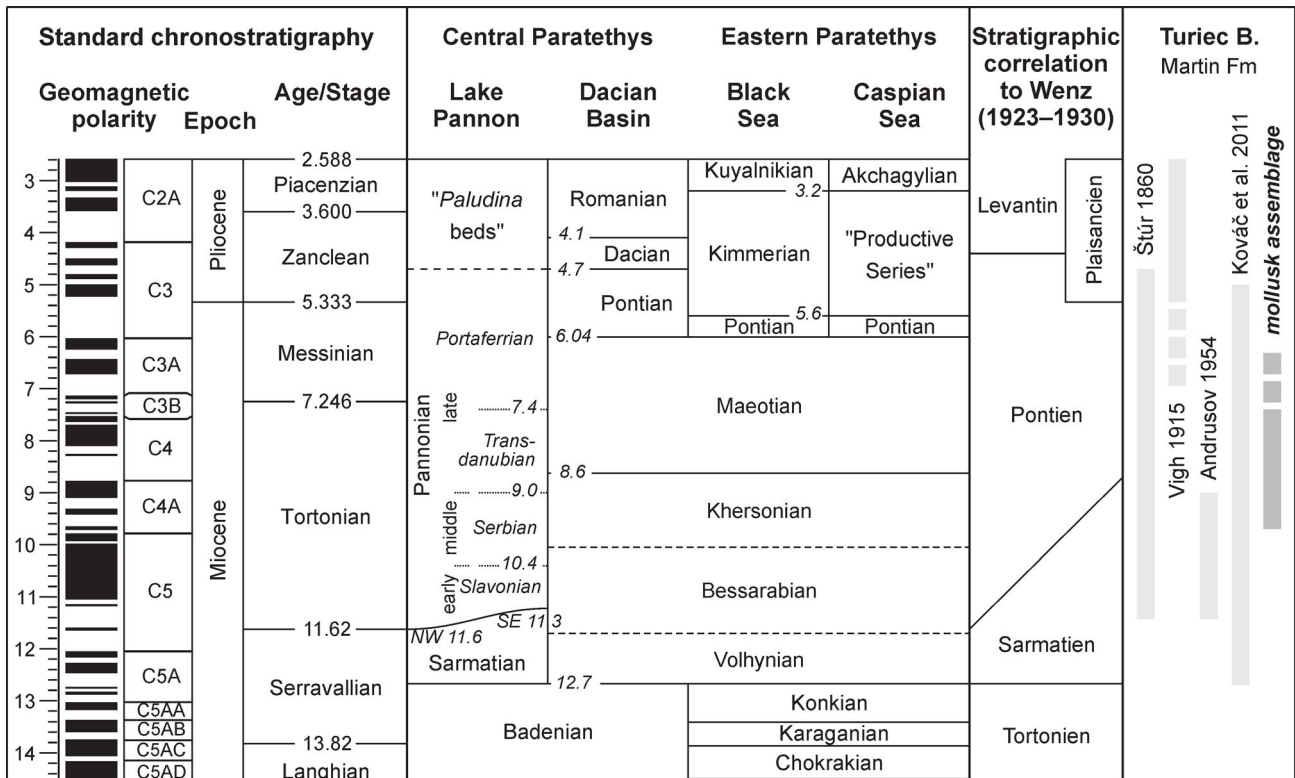


Fig. 7. Compiled stratigraphic chart based on the Geological Time Scale 2012 (Gradstein et al. 2012) with correlation of regional units and biozones. Regional correlations follow Sacchi & Horváth (2002), Krstić (2003), Popov et al. (2006), Harzhauser & Mandić (2008), Krijgsman et al. (2010), Vasiliev et al. (2011), Magyar & Geary (2012), Andreescu et al. (2013), Stoica et al. (2013), and ter Borgh et al. (2013). The boundaries of the intervals used by Wenz (1923-1930) are adapted to those of the current stages. Ranges of former and present stratigraphic classifications of the Martin Formation are given to the right.

of Lake Turiec. An age of 6.0 Ma (Late Pannonian, earliest Pontian or Late Messinian) is indicated by Konečný et al. (1983) and Kováč et al. (2011) for the Abramová Member, which is correlated to the top of the formation. A similar age, documenting the upper boundary of the formation and an approximate end of Lake Turiec, derives from radiometric data from zircon and apatite fission track thermochronology of the rhyolite tuffs and breccias from the south margin of the basin (Králíková et al. 2014). Detailed lithostratigraphic divisions were provided by Rakús et al. (2005) and Kováč et al. (2011).

The given age constraints are in good agreement with the majority of the fauna of the Martin Formation, including the species *Theodoxus cf. postrenulatus*, *Viviparus pipiki* nov. sp., *Melanopsis glaubrechtii* nov. sp., *Tournouerina turiecensis* nov. sp., *Planorbarius* nov. sp., *Mytilopsis?* sp., and *Unio cf. atavus*. In neighbouring



Fig. 8. Map of sediment distributions of Late Miocene lakes referred to in the discussion. Lake Pannon: extent for the early late Pannonian (ca. 8 Ma), after Magyar et al. (1999). Lake Metohia: extent for the Pontian, after Atanacković (1990), Elezaj et al. (2010), and Neubauer et al. (2015). Lake Turiec: after Pipík et al. (2012). Note that the lake outlines do not necessarily correspond to the basin boundaries.

Lake Pannon *Theodoxus postcrenulatus* is recorded for Pannonian biozones E–F, corresponding to the upper *Lymnocardium conjungens* Zone to *Mytilopsis neumayri|zahalkai* Zone or to the Middle Pannonian (Papp 1953; Fordinál 1997; for a biostratigraphic correlation chart see Magyar et al. 1999 and Harzhauser et al. 2004). Likewise, the first viviparids occur in Lake Pannon during zone F (e.g. Strausz 1942; Papp 1953). *Melanopsis sturii*, probably a close relative or even ancestor of the here described *M. glaubrechtii*, is documented for the Pannonian F as well (Papp 1953). *Unio atavus* is an Early-Middle Pannonian species (Harzhauser et al. 2007). This pattern suggests a similar temporal range of the deposits from Martin brickyard. The genus *Tournouerina* is unknown so far from Miocene localities but is widespread during the Pliocene (Schlickum 1978). In contrast, *Popovicia* cf. *compressa* rather indicates a younger age. This species was described from Upper Pontian deposits of the Metohia Basin (Pavlović 1931; Popović 1969), which can be roughly correlated with the latest Pannonian, and so earliest Pliocene (Elezaj et al. 2010). Since the fauna of the Metohia Basin shows a highly endemic development (e.g. Pavlović 1931, 1932; Milošević 1962; Popović 1964, 1970; Atanacković & Stevanović 1990), a reliable biostratigraphical correlation is not feasible. Absolute datings are also not available for the Metohia Basin, lowering the biostratigraphic value of its fauna. At present, this discrepancy remains unsolved.

Based on these considerations, the mollusc-bearing layers of the Martin Formation can be roughly correlated with the latest Middle or early Late Pannonian, corresponding to the Middle and Late Tortonian of the International Timescale.

Paleobiogeography

One of the most important results of this taxonomic work is the revision of species and genus names erroneously stated for the Turiec Basin. Names like *Ancylus*, *Hydrobia*, *Kosovia*, *Melanoptychia*, *Lithoglyphus*, *Lymnaea*, and *Pyrgula* greatly biased the picture of factual biodiversity, paleobiogeography, and paleoecology. Most of the available determinations and names in the literature represent misidentifications, partly even on the genus level. “*Hydrobia*” and “*Pyrgula*” as well as “*Lithoglyphus nannus*” mentioned by Krstić et al. (2012) most likely reflect the here described *Tournouerina turiecensis* nov. sp.; “*Lymnaea*” corresponds to one of the described *Radix* species; “*Ancylus*” turned out to be sedimentary infills of the inflated apertures of *Radix kovaci* nov. sp.; “*Planorbis pseudo-ammonius*” most probably reflects *Planorbarius* sp.; the alleged occurrence of the Early Pannonian endemic *Papyrotheca* was based on a misidentified fragment of a dreissenid bivalve.

Certainly, the most interesting fact is the record of *Popovicia* cf. *compressa*. This species belongs to an evolutionary lineage seemingly endemic to the Metohia Basin in Kosovo (Fig. 8). Probably originating from the Middle-Late Miocene *Kosovia* lineage, the planorbiform *P. compressa* evolved during the Late Pontian (earliest Pliocene), followed by the planorbiform to low trochiform *P. levantica* in the Early Dacian, and terminating with the high trochiform *P. turriculoidea* in the Late Dacian (middle Early Pliocene) (Popović 1969; Elezaj et al. 2010). It remains unclear how a member

of this lineage could enter the Turiec Basin. Direct dispersal is impossible, since neither the Lake Turiec nor the Lake Metohia had any hydrological connections to the interjacent Lake Pannon, where this genus is absent. One possible explanation is transport via birds, which seems to account for several present and past distribution patterns of freshwater gastropods (Wesselingh et al. 1999; Figuerola & Green 2002; van Leeuwen et al. 2012).

Especially in this light it is notable that apart from the somewhat doubtful record of *Theodoxus postcrenulatus* none of the species was found in the nearby, coeval Lake Pannon. In contrast to the situation for Lake Turiec, the fauna of Lake Pannon, whose shore line was some 160 km to the southeast during the Late Pannonian (Magyar et al. 1999; Fig. 8), is particularly well known. Presently a statement on such discrepancies and paleobiogeographical relationships in general would be premature, since our knowledge about the Turiec mollusc fauna is still incomplete. The collection and evaluation of more and better preserved fossils would certainly allow a more detailed analysis of the paleobiogeographical picture as well as a reconstruction of the lake’s paleoecological settings. Nevertheless, the present work contributes to the still fragmentary puzzle of the actual biodiversity of the Late Miocene Lake Turiec — and once more the high degree of its endemism has been proven.

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