



Taxonomy, palaeoecology and stratigraphy of the middle Miocene mollusk fauna from the Gračanica coal pit near Bugojno in Bosnia and Herzegovina

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Received: 5 December 2019 / Revised: 17 February 2020 / Accepted: 11 March 2020 / Published online: 17 June 2020

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Abstract

During the early and middle Miocene, the Dinarides Lake System (DLS) was a major hotspot of freshwater mollusk diversity in southeastern Europe. The numerous intramontane lake basins, originating by combined effects of tectonic subsidence and humid climate, accumulated thick lacustrine successions. Diagenetic overprint and leaching of these carbonate-rich deposits have facilitated insights to faunal contents for only a few basins up to the present. We contribute to filling this gap by documenting for the first time a mollusk fauna from the Bugojno Basin in Bosnia and Herzegovina. The fauna originates from a coal-bearing succession representing a gradual flooding of the coastal wetlands followed upwards by the establishment of perennial lacustrine settings in the basin. Our taxonomic analyses documents 17 gastropod and two bivalve species. New to science are *Illyricocongeria forcakovici* nov. sp., *Prososthenia krijgsmanni* nov. sp. and *Bania goehlichae* nov. sp. The palaeoecological analysis based on quantified samples shows distinct shifts in mollusk composition and abundance. The terrestrial taxa are restricted to the coal-bearing interval of the section; melanopsids, neritids and hydrobiids are abundant in deltaic and littoral settings, whereas bivalves are frequent in littoral and sublittoral environments. In line with previous results, which have evidenced a high degree of intralacustrine radiation in the DLS, the Lake Bugojno fauna shows a low to moderate level of similarity to other DLS faunas. The dissimilarity may partly also result from its younger age as suggested by the presence or absence of regional biostratigraphic marker species.

Keywords Long-lived lakes · Gastropoda · Bivalvia · Environmental change · Dinarides Lake System · Southeastern Europe

Abbreviations

Bivalve dimensions

Ada Angle of the junction between dorsal and anterior shell margins
Adp Angle of the junction between dorsal and posterior shell margins

AV Articulated valves
C Convexity of the single valve
H Shell height
L Shell length
La Length of the anterior shell part
Lt Length of the diagonal thread/ridge
LV Left valve

This article is a contribution to the special issue “The drowning swamp of Gračanica (Bosnia-Herzegovina) - a diversity hotspot from the middle Miocene in the Bugojno Basin”

This article is registered in Zoobank under urn:lsid:zoobank.org:pub:B5A71F0C-FEDB-4EE0-BD84-EDFC7A692C20

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s12549-020-00423-6>) contains supplementary material, which is available to authorized users.

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RV Right valve
 Ts (Distal) shell thickness
 * Fragmented

Sample codes

BU Bugojno
 d Debris
 LS Lateral section
 M Mollusk
 yymm Year and month of sampling
 NHMW Naturhistorisches Museum Wien

Introduction

The mollusk fauna of the Dinarides Lake System (DLS, Fig. 1a, b) is striking for its high diversity and endemism (Harzhauser and Mandić 2008, 2010; Neubauer et al. 2015a, b). During the early and middle Miocene, the DLS represented a unique evolutionary hotspot within the continental biota of southeastern Europe. Its outstanding prominence was first recognised through the pioneering works of Neumayr (1869, 1880, 1883b) and Brusina (1874, 1884, 1897, 1902), introducing an immense number of previously unknown species to science.



Fig. 1 a–c Geographic, geologic and palaeogeographic setting of the Gračanica coal pit (Bugojno basin, BIH) (modified after Mandić et al. 2012b, 2016, 2019)

The DLS originated through the combined effects of a tectonic extension of the Dinarides during the early and middle Miocene and a long-lasting humid climate interval of the Miocene Climate Optimum between 17 and 15 Ma (van Unen et al. 2019a, b). The NW–SE elongated intramontane basins initiated by that extension accommodated a series of perennial lakes. Owing to their isolated, geologically long-lived character, the mollusk faunas underwent intralacustrine radiations in several of these basins, generating a high number of species endemic to DLS (Harzhauser and Mandić 2008).

Recently, the DLS mollusk fauna was subjected to a thorough taxonomic revision pointing out the individual basins as isolated palaeobiogeographic entities with their own evolutionary histories and only minor interbasinal migration (Neubauer et al. 2011, 2013a, b, 2016a, 2016b). Given the fact that merely a few basins have been studied in such a detail, i.e. Sinj and Drniš of southern Croatia, and Gacko, Konjic (Džepi) and Kupres of southern Bosnia and Herzegovina (Fig. 1b), further data are necessary to understand in more detail the DLS diversity and its development. Such a case providing new insights is presented by a mollusk fauna recently excavated at the Gračanica coal pit in the Bugojno Basin in Bosnia and Herzegovina.

Except for a few species mentioned by Katzer (1903, 1918), the only available record of the Miocene lacustrine and terrestrial mollusk fauna of the Bugojno Basin goes back to Muftić and Behlilović (1966). In an exploration study on the geology of the Gračanica coal pit, these authors listed ten gastropod and seven bivalve species from this site. The present study, dealing with the same succession, allows now a critical revision of that record.

Thus, the main goal of the present study is a careful taxonomic analysis and documentation of the Miocene mollusks from the Bugojno Basin. Besides this, the study establishes their vertical distribution in the Gračanica coal pit succession. Stratigraphical and palaeoecological interpretation of these data allows a reconstruction of regional environmental history during the initial lacustrine flooding of the basin. Finally, the comparison of the new mollusk fauna with records published from other DLS basins allows a discussion on their biostratigraphic and palaeobiogeographic relations.

Material and methods

The Gračanica coal pit is located SSE from Bugojno on the main road to Gornji Vakuf-Uskoplje in central Bosnia and Herzegovina (Fig. 1b, c). The about 40-m-thick succession exposed in the coal pit (Fig. 2) represents the lower part of the Bugojno Basin infill, characterised by the frequent occurrence of large vertebrate remains of middle Miocene age typical for the mammal units MN5 to MN6 (Aiglstorfer and Mayda *in press*, this issue; Bastl et al. *in press*, this issue;

Coombs and Göhlich *in press*, this issue; Becker and Tissier *in press*, this issue).

Mollusk sampling was done in five field campaigns from 2007 to 2009 and from 2016 to 2017 (Fig. 2). Altogether, 27 samples have been collected. Due to continuous progradation of the coal mining, the location of the NE–SW-oriented excavation front moved during this period about 500 m to the SSE. The detailed sedimentological logging was carried out in 2009, when stratified mollusk samples were taken from the mollusk-bearing layers (Fig. 2). The positions of samples from other campaigns were correlated to that section based on the stratigraphic position estimated in the field, additionally controlled by lithology and fossil content.

Only samples BU0708/368 and BU1610/LS were taken outside the coal pit's excavation front. The former one originated from an exploration well cored by the mining company, and its position is documented in the well-log. The latter one was taken from a small outcrop at the SSE prolongation of the mining front, directly at the NE basinal margin showing tectonically disturbed Miocene strata. Its correlation with the section is reconstructed by its fossil content and lithology.

Preservation of the mollusk shells is of moderate quality. Although the shell aragonite is mostly preserved, only a few complete specimens were obtained because of strong postsedimentary fragmentation and sediment compaction. Besides, the matrix sediment is mostly well lithified and not suitable for fossil extraction. Therefore, besides sediment bulk samples, mollusk shells were, where possible, also picked in the field and/or hand samples were taken for subsequent laboratory preparation. Suitable bulk samples, of several kilograms each, were washed and sieved, over 0.5 mm mesh size. Other samples were prepared by standard mechanical tools. The counting incorporated specimens won by sieving as well as those identified on hand sample surfaces.

Gastropod systematics follow Bouchet et al. (2017), and bivalve systematics follow Bouchet and Rocroi (2010), Bieler et al. (2014) and MolluscaBase (2019). Hinge description of Sphaeriidae follows Herrington (1962).

Systematic palaeontology

Class Gastropoda Cuvier, 1795
 Subclass Neritimorpha Golikov and Starobogatov, 1975
 Order Cycloneritimorpha Frýda, 1998
 Superfamily Neritoidea Rafinesque, 1815
 Family Neritidae Rafinesque, 1815
 Genus *Theodoxus* Montfort, 1810

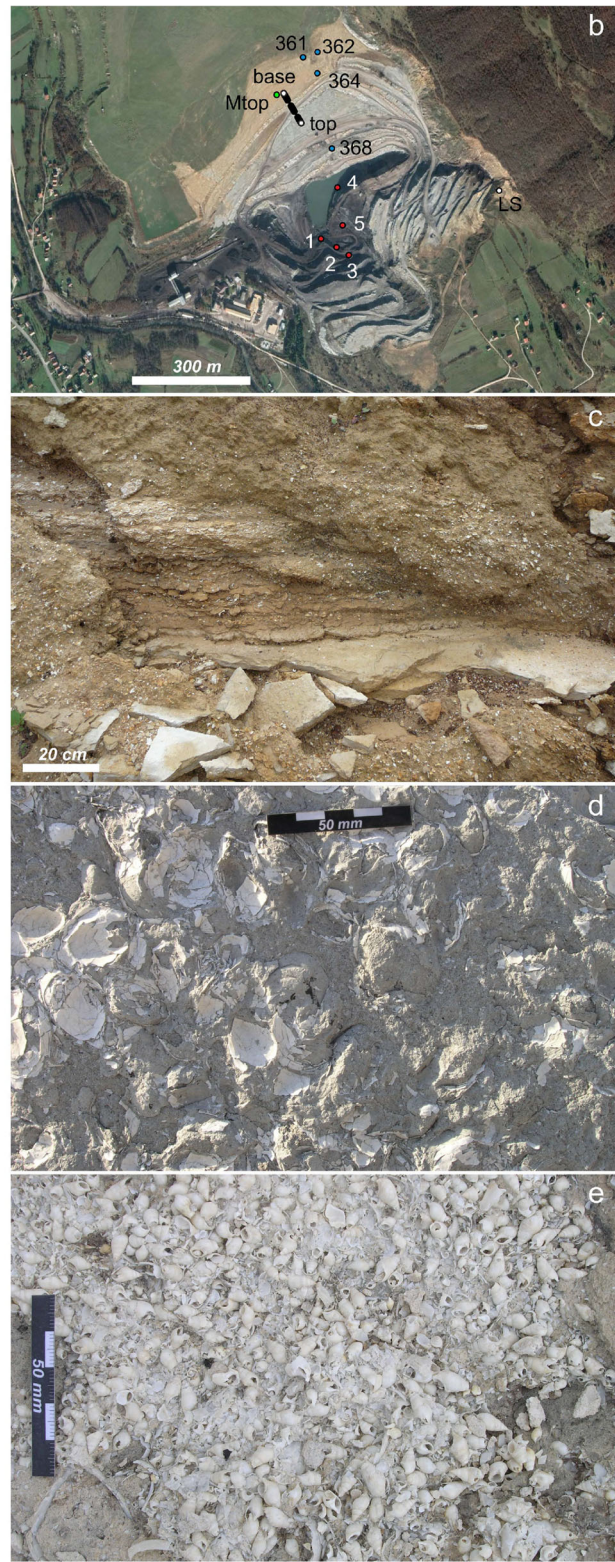
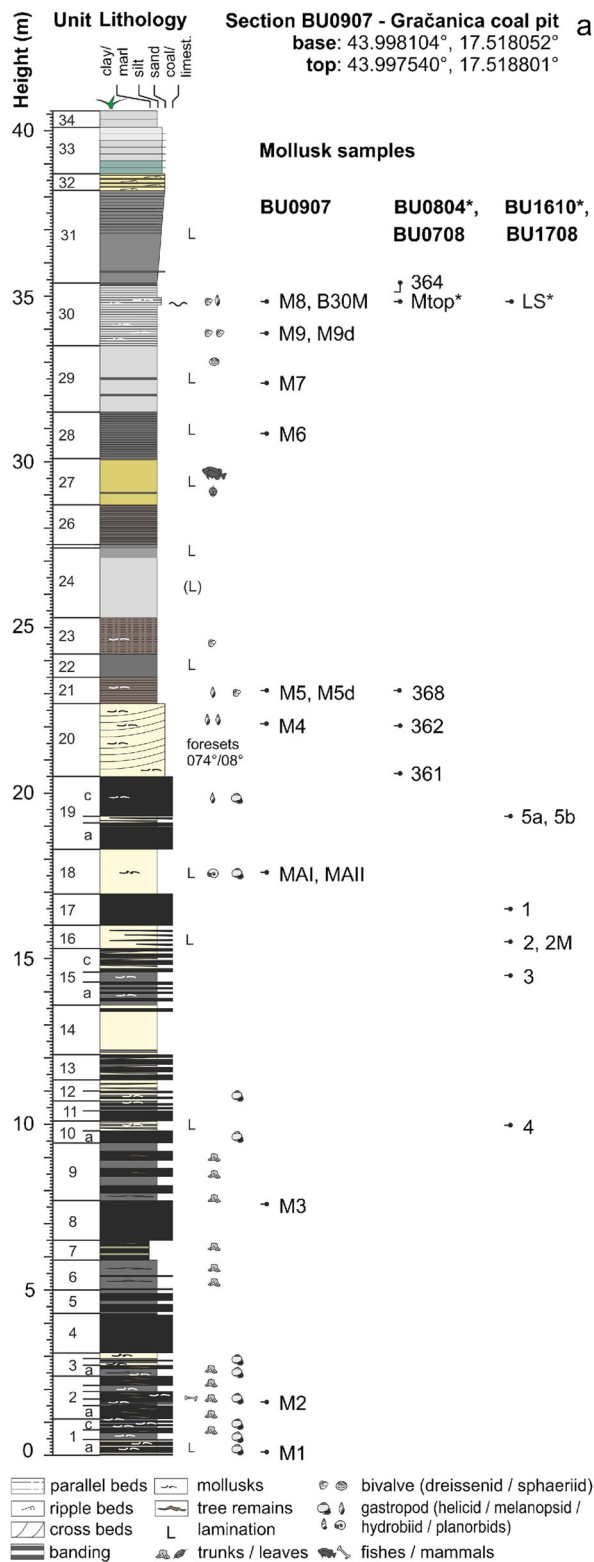


Fig. 2 **a** Section BU0907 with indicated position of mollusk samples. Position of samples from sections and sites BU0804, BU1610, BU0708 and BU1708 rely on lithostratigraphic correlation as indicated in the text. **b** Google Earth image (map data: Google, Maxar Technologies) showing Gračanica coal pit on 13 November 2018; position of BU0907 section is indicated by a dashed line, position of samples from other years by circles; position of the mine’s excavation front moved SSE from point

361 in 2007 to point 4 in 2017 (see text for more information). **c** Mollusk site LS showing rich shell accumulations in reddish and brownish marl on top of a marly limestone bed. **d** *Illyricocongeria forcakovici* accumulation on the bedding plane of unit 21. **e** *Melanopsis visianiana* accumulation on the bedding plane of unit 20, with single *Illyricocongeria forcakovici* valve on the lower left

Type species: *Theodoxus lutetianus* Montfort, 1810 [= *Theodoxus fluviatilis* (Linnaeus, 1758)]. Recent; Europe. Type by original designation.

Theodoxus sinjanus (Brusina, 1876)
(Fig. 3a–h)

*1876 *Neritina sinjana*, Brusina—Brusina, p. 113.
2016a *Theodoxus sinjanus* (Brusina, 1876)—Neubauer
et al., p. 20, fig. 2J–L (cum syn.).

Material: Four specimens from sample BU0708/364 (0101/0101/0108), 11 specimens from sample BU0907/M8 (0101/0101/0066, 0101/0101/0111), 15 specimens from sample BU0907/B30M (0101/0101/0065, 0101/0101/0109), 31 specimens from sample BU0804/Mtop (0101/0101/0051, 0101/0101/0064, 0101/0101/0115), 11 specimens from sample BU1610/LS (0101/0101/0050, 0101/0101/0052, 0101/0101/0053, 0101/0101/0063) and 1 specimen from sample BU0907/M9 (0101/0101/0116).

Dimensions: 0101/0101/0050: diameter 3.87 mm, height 3.78 mm (Fig. 3a, b); 0101/0101/0051: diameter 5.72 mm, height 6.08 mm (Fig. 3c–e); 0101/0101/0052: diameter 7.31 mm, height (fragmented) 5.70 mm (Fig. 3f–g); 0101/0101/0053: diameter 1.27 mm, height 1.32 mm (Fig. 3h).

Remarks: The studied specimens are attributed to the present species based on their oval shape, a shallow convex spire almost fully covered by the last whorl, and a laterally expanded semicircular aperture with demarcated callus pad displaying weak denticles. The species was originally described from the

early Langhian strata of Sinj–Župića potok (Brusina 1876, 1884; age after Kerner 1905 and de Leeuw et al. 2010). Recently, it was redescribed by Neubauer et al. (2011, 2016a). *Theodoxus sinjanus* (Brusina, 1884) of Kóckay (2006) from the Langhian of Nagygörbő in the Bakony Mts. (Hungary) differing in the upwards extruded apex is an erroneous identification.

Distribution: Endemic to DLS–middle Miocene (early Langhian): Drniš Basin (Miočić) and Sinj Basin (Župića potok, Novi bunar, Lučane, Brnaze, Crveni Klanac) (Jurišić-Polšak 1979; Neubauer et al. 2016a). This is the first published record of this species outside these two basins. Its occurrence at Ribarić in the Sinj Basin, indicated erroneously in Neubauer et al. (2016a), refers to *T. semidentatus* (see Brusina, 1884).

Subclass Caenogastropoda Cox, 1960

Order unassigned

Superfamily Cerithioidea Fleming, 1822

Family Melanopsidae Adams and Adams, 1854

Genus *Melanopsis* Férussac in Férussac and Férussac, 1807

Type species: *Melania costata* Olivier, 1804; Recent, Eastern Mediterranean and Middle East; type by subsequent designation by Gray (1847).

Melanopsis visianiana Brusina, 1874
(Fig. 4a–n)

*1874 *Melanopsis visianiana* Brusina—Brusina, p. 37, pl. 1, figs. 7–8.

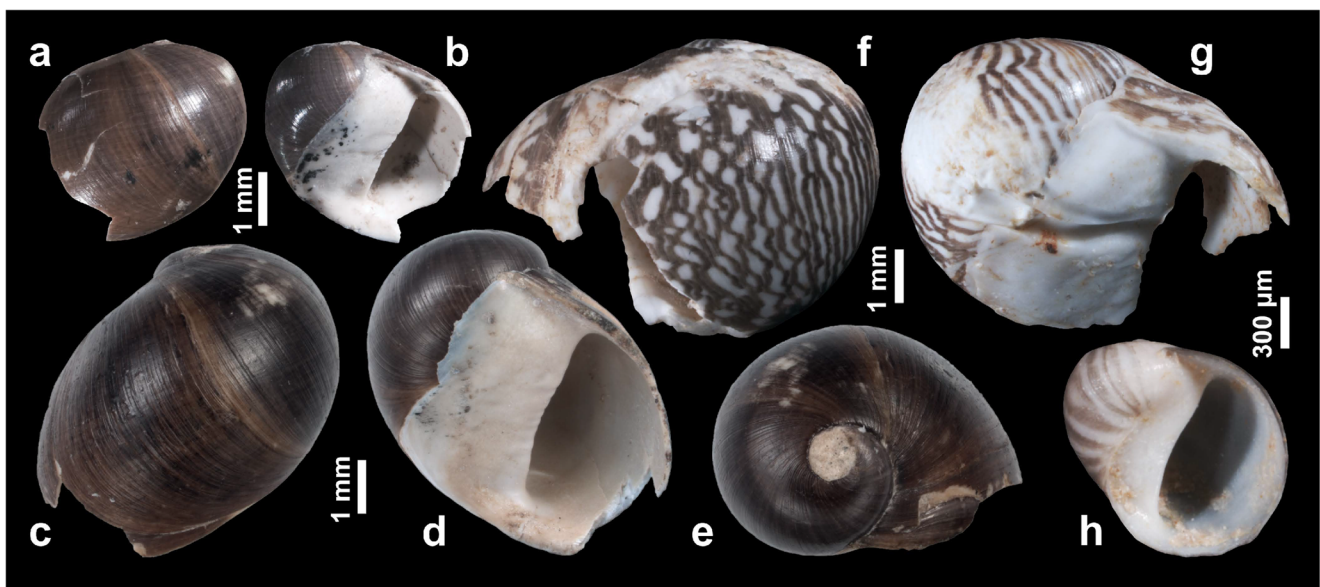


Fig. 3 *Theodoxus sinjanus* (Brusina, 1876): **a, b** specimen from sample BU1610/LS (NHMW 2018/0101/0050); **c–e** specimen from sample BU0804/Mtop (NHMW 2018/0101/0051); **f–g** largest but fragmented

specimen from sample BU1610/LS (NHMW 2018/0101/0052); **h** juvenile specimen from sample BU1610/LS (NHMW 2018/0101/0053)

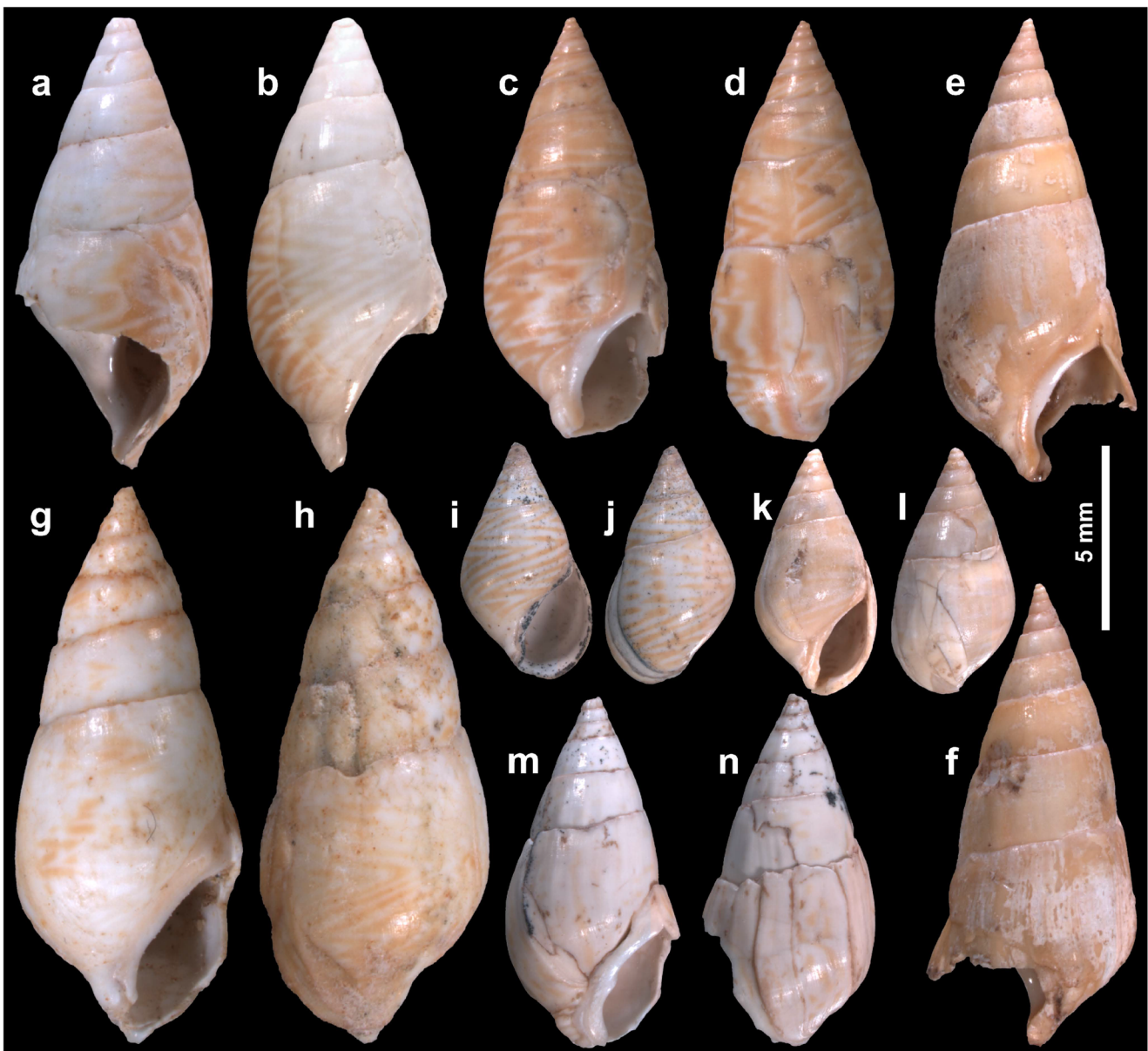


Fig. 4 *Melanopsis visianiana* Brusina, 1874: **a, b** BU1610/LS (NHMW 2018/0101/0054); **c, d** BU0907/M4 (NHMW 2018/0101/0055); **e, f** BU0907/M4 (NHMW 2018/0101/0056); **g, h** BU1610/LS (NHMW

2018/0101/0057); **i, j** BU0907/M8 (NHMW 2018/0101/0058); **k, l** BU0907/M8 (NHMW 2018/0101/0059); **m, n** BU0907/M8 (NHMW 2018/0101/0060)

2016a *Melanopsis visianiana* Brusina, 1874—Neubauer et al., p. 25, fig. 3S–X (cum syn.).

Material: Forty-five specimens from sample BU0907/M8 (NHMW 2018/0101/0058, NHMW 2018/0101/0059, NHMW 2018/0101/0060, NHMW 2018/0101/0068, NHMW 2018/0101/0111), 8 specimens from sample BU0907/B30M (NHMW 2018/0101/0072, NHMW 2018/0101/0109), 28 specimens from sample BU0804/Mtop (NHMW 2018/0101/0070, NHMW 2018/0101/0115), 105 specimens from sample BU1610/LS (NHMW 2018/0101/0054, NHMW 2018/0101/0057, NHMW 2018/0101/0069),

1 specimen from sample BU0907/M5, 1 specimen from sample BU0708/368 (NHMW 2018/0101/0008), 153 specimens from sample BU0907/M4 (NHMW 2018/0101/0055, NHMW 2018/0101/0056, NHMW 2018/0101/0067, NHMW 2018/0101/0123), 927 specimens from sample BU0708/362 (NHMW 2018/0101/0073), 200 specimens from sample BU0708/361 (NHMW 2018/0101/0121) and 23 specimens from sample BU0907/MA (NHMW 2018/0101/0071, NHMW 2018/0101/0126).

Dimensions: NHMW 2018/0101/0054: diameter 54.4 mm, height 123.3 mm (Fig. 4a, b); NHMW 2018/0101/0055: diameter 50.2 mm, height 114.3 mm (Fig. 4c, d); NHMW

2018/0101/0056: diameter 51.3 mm, height 125.8 mm (Fig. 4e, f); NHMW 2018/0101/0057: diameter 62.5 mm, height 150.8 mm (Fig. 4g, h); NHMW 2018/0101/005: diameter 35.5 mm, height 64.8 mm (Fig. 4i, j); NHMW 2018/0101/0059: diameter 33.7 mm, height 66.9 mm (Fig. 4k, l); NHMW 2018/0101/0060: diameter 47.0 mm, height 95.6 mm (Fig. 4m, n).

Remarks: The identification is based on comparison with topotypic material described by Neubauer et al. (2016a), which is characterised by a medium size, an elongated shape, the presence of up to nine flattened whorls delineated by shallow sutures, the last whorl attaining ~60% of the shell height, and a smooth exterior showing yellow zigzag lines. This is the most common species at Bugojno. It shows some variation in slenderness (Fig. 4) and sculpture. Except for samples from unit 18, its surface is smooth. In unit 18, the preservation is very bad and exclusively fragments are preserved showing however longitudinal ribs and zig-zag colour pattern typical for the morphotype *Melanopsis visianiana costulata* Brusina, 1897.

Distribution: Endemic to DLS–middle Miocene (early Langhian): Drniš Basin (Miočić, Biočić, Parčić) (Brusina 1874, 1884, 1897, 1907; Neubauer et al. 2016a). This is the first published record of this species outside the Drniš Basin.

Order Littorinimorpha Golikov and Starobogatov, 1975

Superfamily Truncatelloidea Gray, 1840

Family Hydrobiidae Stimpson, 1865

Genus *Bania* Brusina, 1896

Type species: *Bania prototypica* Brusina, 1872; by monotypy (ICZN, 2001); middle Miocene; Dalmatia (southern Croatia).

Bania goehlichae nov. sp.
(Fig. 5a–j, m, n)

Holotype: NHMW 2018/0101/0024: diameter 0.85 mm, height 1.07 mm (Fig. 5g, h, n; sample BU0907/M4).

Paratypes: NHMW 2018/0101/0021: diameter 1.1 mm, height 1.4 mm (Fig. 5a, b; sample BU0907/M8); NHMW 2018/0101/0022: diameter 1.0 mm, height 1.35 mm (Fig. 5c, d, m; sample BU0907/M8); NHMW 2018/0101/0023: diameter 1.05 mm, height 1.3 mm (Fig. 5e, f; sample BU0907/M8); NHMW 2018/0101/0025: diameter 0.88 mm, height 1.1 mm (Fig. 5i, j; sample BU0907/M4).

Additional material: Sixty-four specimens from sample BU0907/M8 (NHMW 2018/0101/0080, NHMW 2018/0101/0111), 1 specimen from sample BU0907/B30M (NHMW 2018/0101/0083), 2 specimens from sample BU0804/Mtop (NHMW 2018/0101/0114), 2 specimens from sample BU1610/LS (NHMW 2018/0101/0081), 2 specimens from sample BU0708/368 (NHMW 2018/0101/0120), 28 specimens from sample BU0907/

M4 (NHMW 2018/0101/0087), 14 specimens from sample BU0708/362 (NHMW 2018/0101/0086), 2 specimens from sample BU0708/361 (NHMW 2018/0101/0121), 1 specimen from sample BU1708/5 (NHMW 2018/0101/0135), 38 specimens from sample BU0907/MA (NHMW 2018/0101/0082, NHMW 2018/0101/0126), 11 specimens from sample BU1708/1 (NHMW 2018/0101/0085, NHMW 2018/0101/0130), 2 specimens from sample BU1708/3 (NHMW 2018/0101/0084, NHMW 2018/0101/0131) and 10 specimens from sample BU0907/M1 (NHMW 2018/0101/0127).

Type locality: Gračanica coal pit SE of Bugojno in central Bosnia and Herzegovina (coordinates: 43.99754° N, 17.51880° E, WGS84).

Type stratum: Unit 20 of the Gračanica section (Fig. 2).

Derivation of name: In honour of Ursula B. Göhlich, vertebrate palaeontologist at the Natural History Museum Vienna.

Diagnosis: Globular *Bania* species with deeply incised suture differing from related species by its broader last whorl and the lower and narrower penultimate whorl.

Description: Small globular shell with height/width ratio of c. 1.25. Protoconch comprising 0.75 convex whorls with deep suture and microsculpture of densely arranged wrinkles, fading out towards transition into teleoconch. Teleoconch consisting of 2.5 strongly convex whorls; deeply incised suture results in gradate spire outline. Maximum diameter of spire whorls in lower third; last whorl regularly convex attaining about 75% of total height. Sculpture consisting of prominent, densely spaced orthocone to slightly prosocline growth lines; few, very faint spiral cords appear on base, visible only in SEM pictures. Base slightly less convex than flank of last whorl. Position of posterior tip of aperture distinctly below periphery of preceding whorl. Aperture ovoid with weak posterior angulation; slightly detached from base in fully grown specimens. Peristome slightly reinforced, flaring with narrowly reflexed inner lip. Weak opercular ridge may be developed well behind peristome. Umbilicus open, deep, demarcated by blunt circumbilical ridge in fully grown specimens.

Remarks: This species displays little variability and is morphologically intermediate between *Bania valvatooides* (Brusina, 1874) and *B. torbariana* (Brusina, 1874), both from the middle Miocene of the DLS and revised by Neubauer et al. (2013b, 2016a). *Bania valvatooides* is known from the Drniš and Gacko basins and has an outstanding variability in shell shapes (Neubauer et al. 2013b). Nevertheless, it differs from *B. goehlichae* constantly in its broader last whorl and the lower and narrower penultimate whorl. Moreover, its protoconch microsculpture is more prominent and the protoconch consists of 1.1 whorls. *Bania torbariana*, from the Drniš Basin, differs in its higher spire with strongly convex whorls and even more incised suture and the regularly convex last whorl. *Bania stosciana* (Brusina, 1874), from

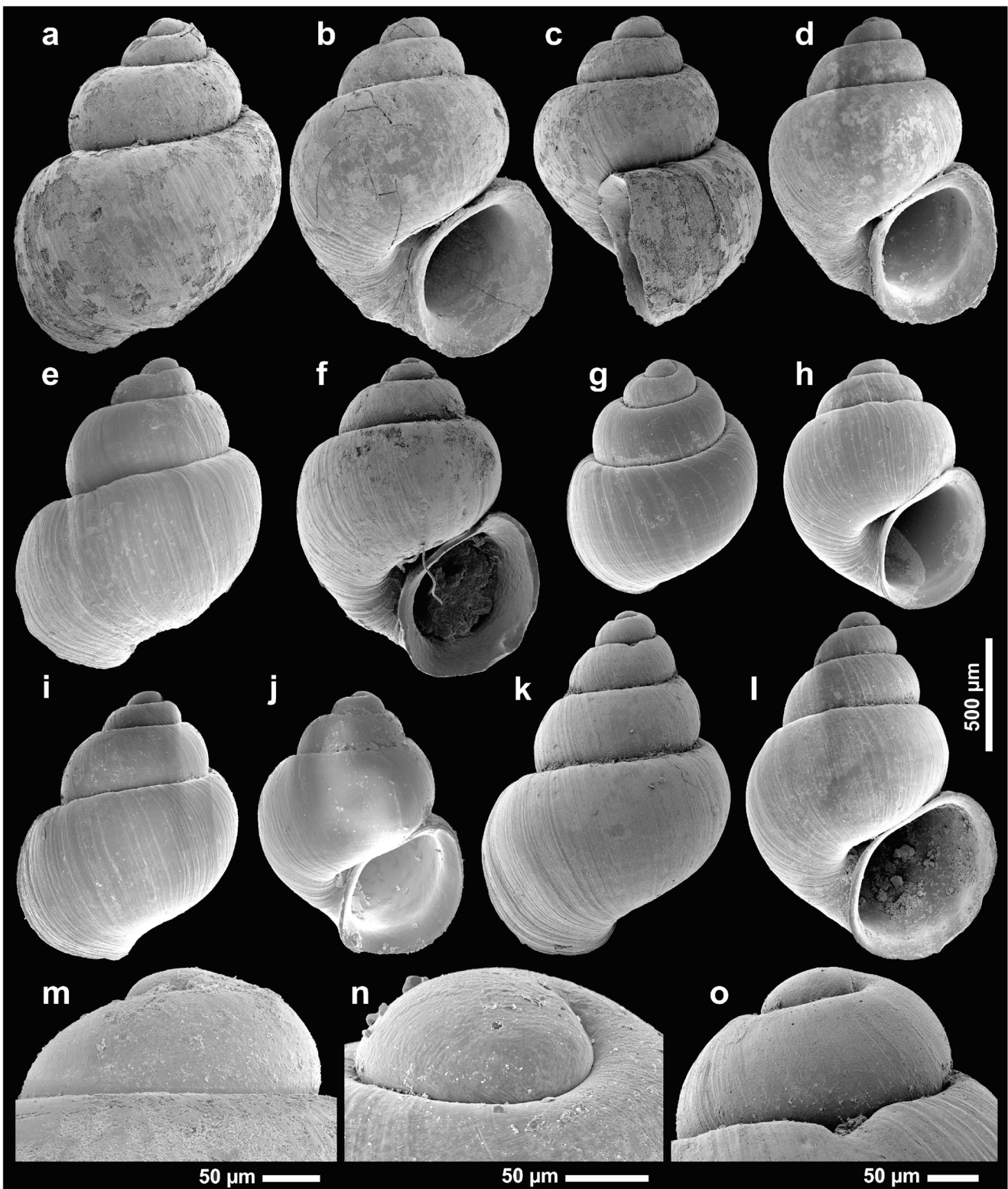


Fig. 5 *Bania* species: **a–j, m, n** *Bania goehlichae* nov. sp.; **a, b** paratype, BU0907/M8 (NHMW 2018/0101/0021); **c, d, m** paratype, BU0907/M8 (NHMW 2018/0101/0022); **m** protoconch in side view; **e, f** paratype, BU0907/M8 (NHMW 2018/0101/0023); **g, h, n** holotype, BU0907/M4

(NHMW 2018/0101/0024); **n** protoconch in side view; **i, j** paratype, BU0907/M4 (NHMW 2018/0101/0025); **k, l, o** *Bania* sp., BU0907/M4 (NHMW 2018/0101/0026); **o** protoconch in side view

the middle Miocene of the Drniš Basin has an even higher conical spire with gradate outline (Neubauer et al. 2016a). Outside of the DLS, *Bania pseudoglobula* (d'Orbigny, 1852), from the middle Miocene of Steinheim (Germany), is most similar to *Bania goehlichae* concerning general outline (see Finger 1998, pl. 5, figs. D–E), but it differs in its much larger size, the slightly higher and narrower last whorl, the higher base and the larger protoconch with a coarser microsculpture.

Distribution: Only known from the type locality.

Bania sp.

(Fig. 5k, l, o)

Material: One specimen from sample BU0907/M4 (NHMW 2018/0101/0026).

Dimensions: NHMW 2018/0101/0026: diameter 1.1 mm, height 1.5 mm (Fig. 5k, l, o).

Description: Small shell of 4.5 whorls with moderately high conical spire; apical angle c. 60°. Protoconch consisting of one convex whorl with delicate wrinkles. Teleoconch whorls regularly convex with incised suture, covered by densely spaced orthocone to weakly prosocline growth lines. Last whorl attaining 72% of total height. Ovoid aperture; peristome weakly reinforced, slightly reflexed; weak opercular ridge. Umbilicus narrow and deep.

Remarks: The outline with the rather high conical spire is highly reminiscent of the middle Miocene *Bania torbariana* (Brusina, 1874) and *B. stosiciana* (Brusina, 1874), as revised by Neubauer et al. (2016a). Nevertheless, *B. torbariana* differs in its higher, broader and more convex spire whorls and the lower base. *Bania stosiciana* differs in its markedly gradate and higher spire. This species differs from the syntopic *Bania goehlichae* nov. sp. in its larger size, higher and regularly conical spire, the less reinforced peristome and the less angulated aperture. Therefore, the shell from Bugojno most probably represents a new species. Nevertheless, we cannot exclude that it is only an aberrant specimen of *B. goehlichae*. More material would be necessary to describe its intraspecific variability.

Genus *Cyclothyrella* Neubauer, Mandić, Harzhauser and Hrvatović, 2013a

Type species: *Litorinella candidula* Neumayr, 1869, type by original designation. Middle Miocene; Dalmatia (southern Croatia).

Cyclothyrella tryoniopsis (Brusina, 1874)

(Fig. 6a–e)

*1874 *Prososthenia tryoniopsis* Brusina—Brusina, p. 50, pl. 3, figs. 5–6.

1902 [*Prososthenia*]? *humilis* [Brus.]—Brusina, pl. 8, figs. 24–26.

2016b *Cyclothyrella tryoniopsis* (Brusina, 1874)—Neubauer et al., p. 281, fig. 5A–B (cum syn.).

Material: One specimen from sample BU0708/364 (NHMW 2018/0101/0108), 1033 specimens from sample BU0907/M8 (NHMW 2018/0101/0027, NHMW 2018/0101/0028, NHMW 2018/0101/0029, NHMW 2018/0101/0078, NHMW 2018/0101/0111), 5 specimens from sample BU0907/B30M (NHMW 2018/0101/0079, NHMW 2018/0101/0109), 3 specimens from sample BU0804/Mtop (NHMW 2018/0101/0114) and 2 specimens from sample BU1610/LS (NHMW 2018/0101/0077).

Dimensions: NHMW 2018/0101/0027: diameter 1.2 mm, height 2.9 mm (Fig. 6a, b); NHMW 2018/0101/0028: diameter 1.4 mm, height 2.9 mm (Fig. 6c); NHMW 2018/0101/0029 (spire fragment): diameter 0.75 mm (Fig. 6d, e).

Description: See Neubauer et al. (2013a, 2016a, b) for detailed descriptions.

Remarks: This species was widespread in the DLS during the early middle Miocene and is characterised by the slender shell with strong, blunt axial ribs, its wrinkled protoconch sculpture and the slightly detached aperture. A delicate sculpture of spiral threads may cover the entire teleoconch or may be partially or completely reduced. Therefore, “*Prososthenia? humilis*”, which was introduced by Brusina (1902) as name for the smooth morphotype from the Džepi Basin, is considered to be a junior synonym of *Cyclothyrella tryoniopsis* (Neubauer et al. 2013a, 2016a, b).

Distribution: Endemic to DLS–middle Miocene (early Langhian): Kupres Basin (Fatelj), Konjic Basin (Džepi), Drniš Basin (Miočić, Parčić) and Sinj Basin (Trnovača) (Neubauer et al. 2016a). Its occurrence in the lowermost upper Miocene of Tomislavgrad Basin reported in Jurišić-Polšak and Slišković (1989) needs objective verification.

Genus *Prososthenia* Neumayr, 1869

Type species: *Prososthenia schwartzi* Neumayr, 1869; subsequent designation by Clessin (1880). Middle Miocene; Dalmatia (southern Croatia).

Prososthenia krijgsmani nov. sp.

(Fig. 6f–m)

Holotype: NHMW 2018/0101/0030: diameter 1.5 mm, height 3.65 mm (Fig. 6i–l; sample BU0907/M8).

Paratypes: NHMW 2018/0101/0031: diameter 1.6 mm, height 3.5 mm (Fig. 6k–m; sample BU0907/M8); NHMW 2018/0101/0034: diameter 1.8 mm, height 4.2 mm (sample BU0907/M8).

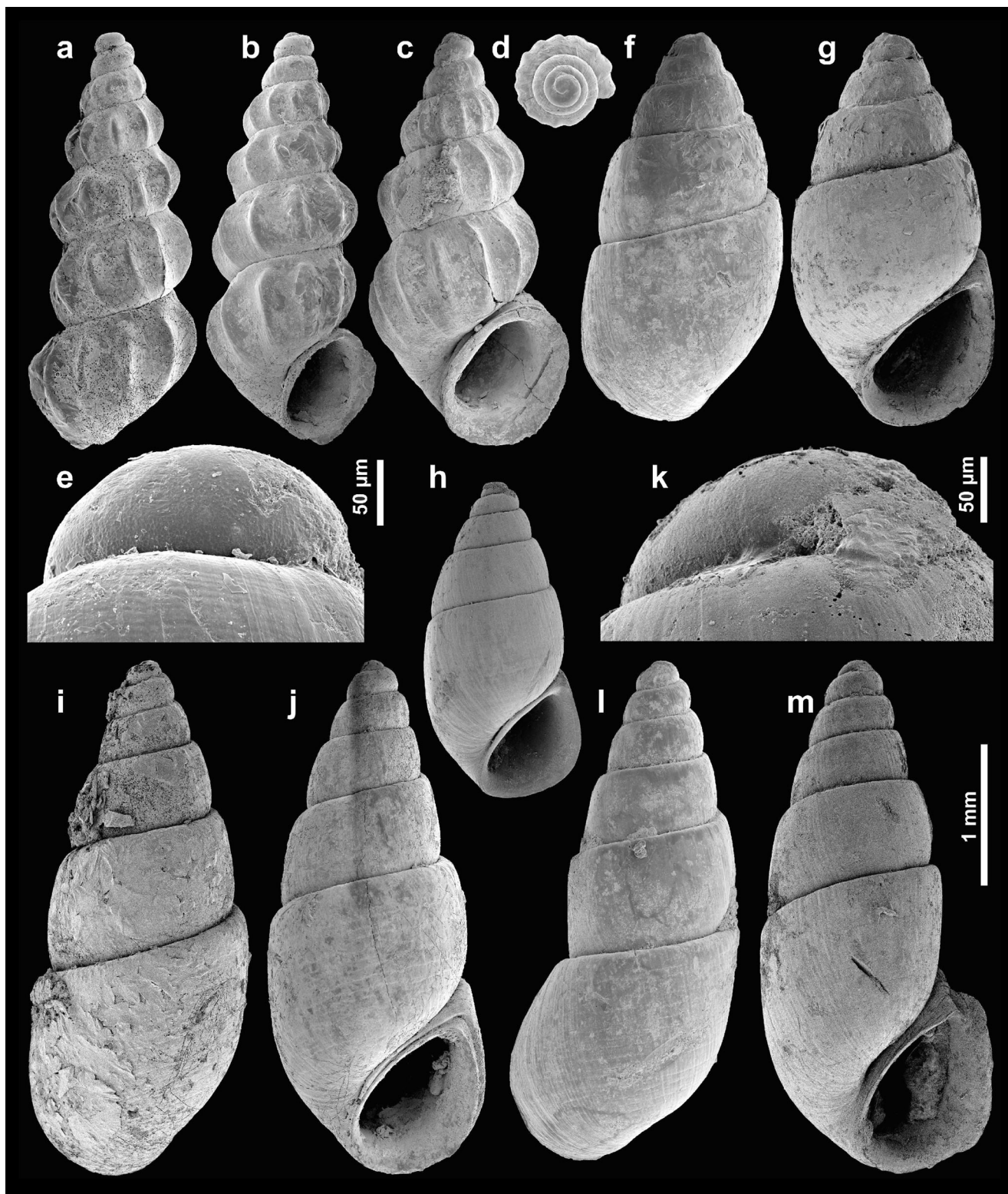


Fig. 6 *Cyclothyrella* and *Prososthenia* species: **a–e** *Cyclothyrella tryoniopsis* (Brusina, 1874); **a, b** specimen from sample BU0907/M8 (NHMW 2018/0101/0027); **c** BU0907/M8 (NHMW 2018/0101/0028); **d, e** spire fragment from sample BU0907/M8 (NHMW 2018/0101/0029); **e** protoconch in side view; **f–m** *Prososthenia krijgsmani* nov. sp.; **f, g**

BU0907/M8 (NHMW 2018/0101/0032); **h** BU0907/M8 (NHMW 2018/0101/0033); **i, j** holotype, BU0907/M8 (NHMW 2018/0101/0030); **k–m** paratype, BU0907/M8 (NHMW 2018/0101/0031); **k** protoconch in side view

Additional material: Three specimens from sample BU0708/364 (NHMW 2018/0101/0108), 30 specimens from sample BU0907/M8, 1 specimen from sample BU0907/B30M (NHMW 2018/0101/0074), 2 specimens from sample BU0804/Mtop (NHMW 2018/0101/0114), 5 specimens from sample BU1610/LS (NHMW 2018/0101/0075) and 1 specimen from sample BU0907/M7 (NHMW 2018/0101/0117).

Type locality: Gračanica coal pit SE of Bugojno in central Bosnia and Herzegovina (coordinates: 43.99389° N, 17.52028° E, WGS84).

Type stratum: Unit 30 of the Gračanica section (Fig. 2).

Derivation of name: In honour of Wout Krijgsman from Utrecht University, for his enormous contributions to unravelling Europe's Neogene stratigraphy.

Diagnosis: Elongate drop-shaped *Prososthenia*, differing from other species by its gradate spire and/or the spiral grooves on the teleoconch.

Description: Elongate drop-shaped, solid shell comprising 5.5 whorls. Protoconch consisting of c. one low, convex whorl with granular microsculpture; poorly preserved in available material. First and second teleoconch whorl moderately convex, regularly increasing in height. Convexity decreasing on later whorls resulting in nearly straight-sided flanks and cylindrical spire whorls; slightly gradate spire with impressed suture. Last whorl height variable, subcylindrical in profile; slightly expanding in last quarter close to aperture. Base high, moderately convex. Sculpture consisting of delicate, weakly prosocline growth lines on entire teleoconch. Faint spiral grooves may appear on entire teleoconch but are most prominent on last whorl and base, cutting growth lines. Aperture ovoid with marked posterior angulation, not detached from base. Peristome strongly thickened, shifting downwards at adapical suture, terminating in thin outer and basal lips. Parietal lip thick, separated from base by narrow groove. No umbilicus.

Remarks: This species is characterised by the gradate spire and the spiral sculpture. *Prososthenia neutra* Brusina, 1897 and *P. eburnea* Brusina, 1897 are both stout drop-shaped and smaller (see Neubauer et al. 2016a). *Prososthenia dalmatina* (Neumayr, 1869) tends to form a slightly gradate spire but is much larger and has a narrower aperture. The slender *Prososthenia* from Lake Gacko, erroneously identified as *P. neutra* by Neubauer et al. (2013b, fig. 7E), is also reminiscent of the species from Bugojno in general shape and microsculpture but lacks a gradate spire.

Distribution: Only known from the middle Miocene of the Gračanica coal pit near Bugojno.

Family Bithyniidae Gray, 1857

Genus *Bithynia* Leach in Abel, 1818

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

Bithynia sp.
(Fig. 7a, b)

Material: Five opercula from sample BU0907/M8 (NHMW 2018/0101/0034, NHMW 2018/0101/0088, NHMW 2018/0101/0111) and 1 operculum from sample BU1708/1 (NHMW 2018/0101/0130).

Dimensions: NHMW 2018/0101/0034: height of the operculum 1.6 mm.

Remarks: Only a single fragmentary *Bithynia* operculum was found, which lacks diagnostic features. As pointed out by Neubauer et al. (2016a), *Bithynia jurinaci* Brusina, 1884 is the only known *Bithynia* species from the Miocene of the DLS, and the specimen from Bugojno might be conspecific with this abundant and widespread species.

Distribution: *Bithynia jurinaci* is recorded from the Miocene of the Sinj Basin, Drniš Basin and Gacko Basin (Brusina 1884; Neubauer et al. 2013b).

Subclass Heterobranchia Burmeister, 1837

Order Hygrophila Férussac, 1822

Suborder Branchiopulmonata Morton, 1955

Superfamily Lymnaeoidea Rafinesque, 1815

Family Lymnaeidae Rafinesque, 1815

Lymnaeidae gen. et sp. indet.

(Fig. 8a, b)

Material: Eight specimens from sample BU1708/5 (NHMW 2018/0101/0036, NHMW 2018/0101/0089, NHMW 2018/0101/0134), 1 specimens from sample BU0907/MA (NHMW 2018/0101/0126), 4 specimens from sample BU1708/1 (NHMW 2018/0101/0035, NHMW 2018/0101/0062, NHMW 2018/0101/0130), 5 specimens from sample BU1708/3 (NHMW 2018/0101/0131, NHMW 2018/0101/0132), 3 specimens from sample BU0907/M3 (NHMW 2018/0101/0128) and 2 specimens from sample BU0907/M1 (NHMW 2018/0101/0127).

Dimensions: Largest incomplete specimen (NHMW 2018/0101/0036): height 47 mm, diameter (compacted) 22.5 mm (Fig. 8b).

Description: Large lymnaeid attaining estimated total height of c. 50 mm. Shell morphology strongly obscured by compaction, but fragments suggest slender outline with high spire whorls and moderately convex last whorl. Last whorl sculpture composed of delicate axial growth lines interrupted by few narrow spiral furrows. Inner lip narrow, thickened, well demarcated from base; columella strongly twisted.

Remarks: According to Jackiewicz and Koralewska-Batura (1995), the microsculpture is characteristic for *Stagnicola* Jeffreys, 1830, which is also supported by the height of the aperture (Glöer 2002). The preservation, however, does not

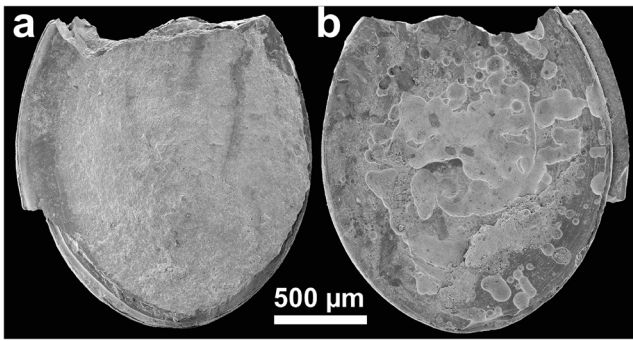


Fig. 7 *Bithynia* sp., operculum, BU0907/M8 (NHMW 2018/0101/0034): **a** inner surface; **b** outer surface

allow a clear generic identification. The specimens might be conspecific with *Stagnicola klaici* (Brusina, 1884), which is widespread during the middle Miocene in the DLS (e.g. Drniš Basin, Sinj Basin) (Neubauer et al. 2016a), but several early and middle Miocene *Stagnicola* species develop comparable shapes and attain about the same size: e.g. *Stagnicola subpalustris* (Thomä, 1845), as described by Harzhauser et al. (2014b) from the early Miocene of the North Bohemian Lake, and *Stagnicola armaniensis* (Noulet, 1857), from the early middle Miocene of Lake Rein (Austria) (Harzhauser et al. 2014a). *Radix korlevici* (Brusina, 1884), from Miočić in Croatia and Gacko in Bosnia and Herzegovina, differs in its lower spire (see Neubauer et al. 2013b, 2016a).

Superfamily Planorboidea Rafinesque, 1815

Family Planorbidae Rafinesque, 1815

Genus *Ferrissia* Walker, 1903

Type species: *Ancylus rivularis* Say, 1817; original designation. Recent, North America.

Ferrissia illyrica (Neumayr, 1880)

(Fig. 8c–f)

*1880 *Ancylus illyricus* n. f.—Neumayr, p. 486, pl. 7, fig. 16.

2016a *Ferrissia illyrica* (Neumayr, 1880)—Neubauer et al., p. 44, fig. 8F, P (cum syn.).

Material: One specimen from sample BU1708/3 (NHMW 2018/0101/0061) and 2 specimens from sample BU0907/M3 (NHMW 2018/0101/0090).

Dimensions: The only specimen free of sediment (NHMW 2018/0101/0061; Fig. 8c–f): length 2.8 mm, width 1.8 mm, height 0.7 mm.

Remarks: The identification is based on comparison with conspecific specimens described by Neubauer et al. (2016a). The species is characterised by a small and narrow ancylid shell with rounded and blunt apex inclined to the right, bearing a shallow pit in its centre surrounded by a collar-like array of

thin radial threads, not interfering with the growth lines and restricted to the proximal shell part. This species was discussed in detail by Neubauer et al. (2013b, 2016a). It is generally a rare, although geographically widespread DLS species. Its presence in the middle Miocene of southeastern Europe challenges the North American cryptic invader hypothesis for the extant European *Ferrissia* (Walther et al. 2006; Welter-Schultes 2012), suggesting that at least some of the species might have an autochthonous European origin.

Distribution: Endemic to DLS—middle Miocene (early Langhian): Gacko Basin (Avtovac-Gacko, Gračanica, Vrbica), Drniš Basin (Miočić, Parčić) and Sinj Basin (Lučane, Ruduša, Strmendolac-Crveni klanac) (Neubauer et al. 2016a). Genus *Planorbarius* Duméril, 1806

Type species: *Helix cornea* Linnaeus, 1758. Recent, Europe; by subsequent designation (Froerip, 1806).

Planorbarius mantelli (Dunker, 1848)

(Fig. 8g, h)

*1848 *Planorbis mantelli*, Dkr.—Dunker, p. 159, pl. 21, figs. 27–29.

2016a *Planorbarius mantelli* (Dunker, 1848)—Neubauer et al., p. 739, fig. 8K–M.

2017 *Planorbarius mantelli* (Dunker, 1848)—Neubauer et al., p. 739, fig. 3G, H, P (cum syn.).

Material: Four specimens from sample BU1708/5 (NHMW 2018/0101/0036, NHMW 2018/0101/0037, NHMW 2018/0101/0091), 17 specimens from sample BU1708/1 (NHMW 2018/0101/0038, NHMW 2018/0101/0130), 22 specimens from sample BU1708/3 (NHMW 2018/0101/0131, NHMW 2018/0101/0132), 2 specimens from sample BU1708/4 (NHMW 2018/0101/0133), 6 specimens from sample BU0907/M3 (NHMW 2018/0101/0128), 6 specimens from sample BU0907/M2 (NHMW 2018/0101/0129), 2 specimens from sample BU0907/M1 (NHMW 2018/0101/0127).

Dimensions: Largest specimen diameter 33.2 mm.

Remarks: The typical protoconch sculpture of spiral rows of pits places this large planorbid in *Planorbarius*. The last teleoconch whorls are slightly shouldered, the flanks are only weakly convex and the entire teleoconch bears prominent spiral cords. The morphology and sculpture agree with *Planorbarius mantelli* (Dunker, 1848) as described by Neubauer et al. (2016a) from the middle Miocene of the DLS.

Distribution: *Planorbarius mantelli* appeared during the late early Miocene in the North Alpine Foreland Basin and the Korneuburg Basin (Austria), became ubiquitous in central and south-eastern Europe during the middle Miocene and disappeared during the late Miocene (see Neubauer et al. 2017 for references). Within the DLS, the species was reported from

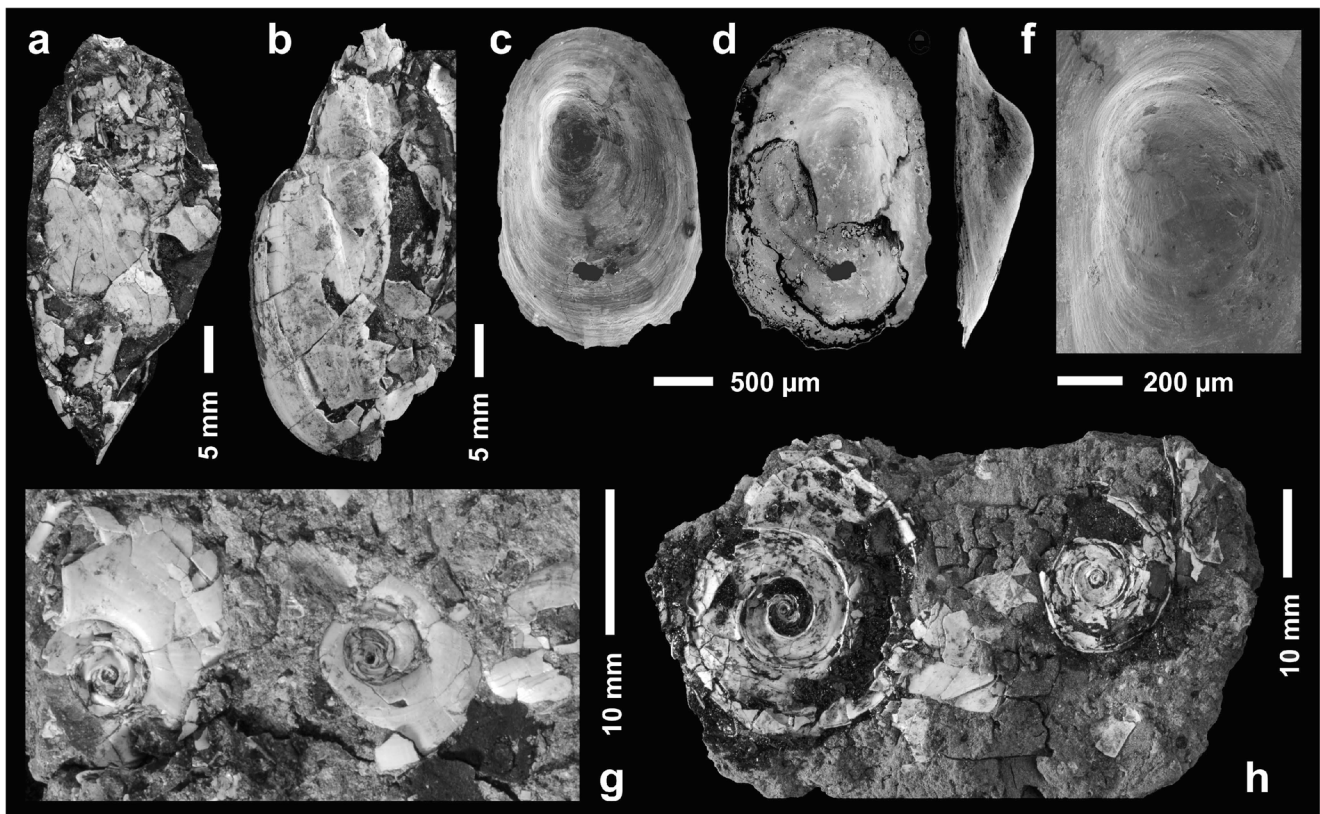


Fig. 8 Lymnaeidae and *Planorbarius* species: **a, b** Lymnaeidae gen. et sp. indet.; **a** fragmented specimen, BU1708/1-5 (NHMW 2018/0101/0035); **b** fragmented specimen, BU1708/1-5 (NHMW 2018/0101/0036); **c–f** *Ferrissia illyrica* (Neumayr, 1880), BU1708/3 (NHMW

2018/0101/0061); **f** detail of exterior surface showing radial microsculpture; **g, h** *Planorbarius mantelli* (Dunker, 1848); **g** two fragmented specimens, BU1708/1-5 (NHMW 2018/0101/0037); **h** two fragmented specimens, BU1708/1-5 (NHMW 2018/0101/0038)

the Drniš Basin (Biočić, Miočić) and the Sinj Basin (Ruduša) (see Neubauer et al. 2016a for references).

Genus *Gyraulus* Charpentier, 1837

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

Gyraulus dalmaticus (Brusina, 1884)
(Fig. 9a–e)

- *1884 *Planorbis dalmaticus* Brusina—Brusina, p. 56.
- 2013 *Gyraulus dalmaticus* (Brusina, 1884)—Krstić et al., p. 15, pl. 3, fig. 7.
- 2016a *Gyraulus dalmaticus* (Brusina, 1884)—Neubauer et al., p. 44, fig. 8G, J (cum syn.).

Material: Four specimens from sample BU0708/364 (NHMW 2018/0101/0108), 65 specimens from sample BU0907/M8 (NHMW 2018/0101/0039, NHMW 2018/0101/0040, NHMW 2018/0101/0041, NHMW 2018/0101/0092, NHMW 2018/0101/0111), 1 specimen from sample BU0907/B30M (NHMW 2018/0101/0109), 1 specimen from sample BU0804/Mtop (NHMW 2018/0101/

0114), 3 specimens from sample BU1610/LS (NHMW 2018/0101/0095), 6 specimens from sample BU0907/M9 (NHMW 2018/0101/0016, NHMW 2018/0101/0116), 7 specimens from sample BU0907/M6 (NHMW 2018/0101/0125), 1 specimen from sample BU0907/M5 (NHMW 2018/0101/0125), 2 specimens from sample BU0708/368 (NHMW 2018/0101/0120), 5 specimens from sample BU0907/M4 (NHMW 2018/0101/0093), 36 specimens from sample BU0708/362 (NHMW 2018/0101/0094) and 1 specimen from sample BU0708/361 (NHMW 2018/0101/0121).

Dimensions: NHMW 2018/0101/0039: diameter 1.6 mm, height 0.55 mm (Fig. 9a, b); NHMW 2018/0101/0040: diameter 1.4 mm, height 0.5 mm (Fig. 9c + e); NHMW 2018/0101/0041: diameter 1.45 mm, height 0.5 mm (Fig. 9d).

Description: Small, discoid shell of up to three whorls with involute spire whorls and wide last whorl. Protoconch consisting of about 0.75 whorls; no spiral sculpture visible (maybe due to inadequate preservation). Whorls moderately convex in adapical and adumbilical quarter but nearly flat towards periphery, with faint concavity close to marked central angulation. Upper side slightly flattened. Aperture elongate heart-shaped. Sculpture consisting of prominent, prosocyrct growth lines.

Remarks: This species is easily distinguished from congeners by its flattened shell, prominent central angulation and prominent growth lines (see also Neubauer et al. 2016a).

Distribution: Endemic to DLS–middle Miocene (early Langhian): Kupres Basin (S Kupres), Drniš Basin (Miočić) and Sinj Basin (Trnovača, Crveni klanac?) (Brusina 1884, 1897; Jurišić-Polšak et al. 2000; Krstić et al. 2013; Neubauer et al. 2016a).

Gyraulus pulici (Brusina, 1897)
(Fig. 9f–i)

*1897 *Planorbis Pulici* Brus. n. sp.—Brusina, p. 6, pl. 2, figs. 8–10.

2013a *Gyraulus pulici* (Brusina, 1897)—Neubauer et al., p. 9 in supplementary material, fig. 10A–C, E–F (cum syn.).

2013 *Gyraulus pulici* (Brusina, 1897)—Krstić et al., 2013, p. 14–15, pl. 3, fig. 6.

Material: One specimen from sample BU1708/1-5 (NHMW 2018/0101/0042), 8 specimens from sample BU1708/5 (NHMW 2018/0101/0097, NHMW 2018/0101/0135), 9 specimens from sample BU0907/MA (NHMW 2018/0101/0096, NHMW 2018/0101/0126), 16 specimens from sample BU1708/1 (NHMW 2018/0101/0038, NHMW 2018/0101/0130), 3 specimens from sample BU1708/2 (NHMW 2018/0101/0098), 19 specimens from sample BU1708/3 (NHMW 2018/0101/0099, NHMW 2018/0101/0131, NHMW 2018/0101/0132), 4 specimens from sample BU1708/4 (NHMW 2018/0101/0133), 5 specimens from sample BU0907/M3 (NHMW 2018/0101/0128), 1 specimen from sample BU0907/M2 (NHMW 2018/0101/0129) and 26 specimens from sample BU0907/M1 (NHMW 2018/0101/0127).

Dimensions: NHMW 2018/0101/0042: diameter 2.0 mm, height 0.7 mm (Fig. 9f–i).

Description: Bulky *Gyraulus* comprising three convex whorls. Protoconch consisting of c. 0.7 whorls with few wide-spaced spiral striae. Teleoconch whorls strongly convex, involute with marked prosocyrte growth lines, being accentuated at suture. Last whorl attaining about 40% of shell diameter. Upper side only weakly less convex than lower side.

Remarks: The species was described in detail by Neubauer et al. (2013a). Within the DLS, *Gyraulus pulici* is recognised easily by its prominent growth lines at the suture and the strongly convex and overgrowing whorls.

Distribution: Endemic to DLS–middle Miocene (early Langhian): Kupres Basin (S Kupres) and Gacko Basin (Vrbica, Gračanica) (Brusina 1897; Krstić et al. 2009, 2013; Neubauer et al. 2013a).

Order Eupulmonata Haszprunar and Huber, 1990
Superfamily Ellobioidea Pfeiffer, 1854

Family Carychiidae Jeffreys, 1830

Genus *Carychium* Müller, 1773

Type species: *Carychium minimum* Müller, 1774; by subsequent monotypy. Recent, Europe.

Carychium nouleti Bourguignat, 1857
(Fig. 9j)

*1857 *Carychium Nouleti*—Bourguignat, p. 226.

1860 *Carychium Nouleti*—Bourguignat, p. 56, pl. 11, figs. 9–10.

1977 *Carychium (Saraphia) nouleti* Bourguignat, 1857 s.l.—Strauch, p. 162, pl. 15, figs. 24, 26–27, pl. 18, fig. 61, pl. 20, fig. 83 (partim; non pl. 15, fig. 25 = *C. gibbum*).

2017 *Carychium nouleti* Bourguignat, 1857 s.l.—Neubauer et al., p. 740, fig. 4A–E, J, O (cum syn.).

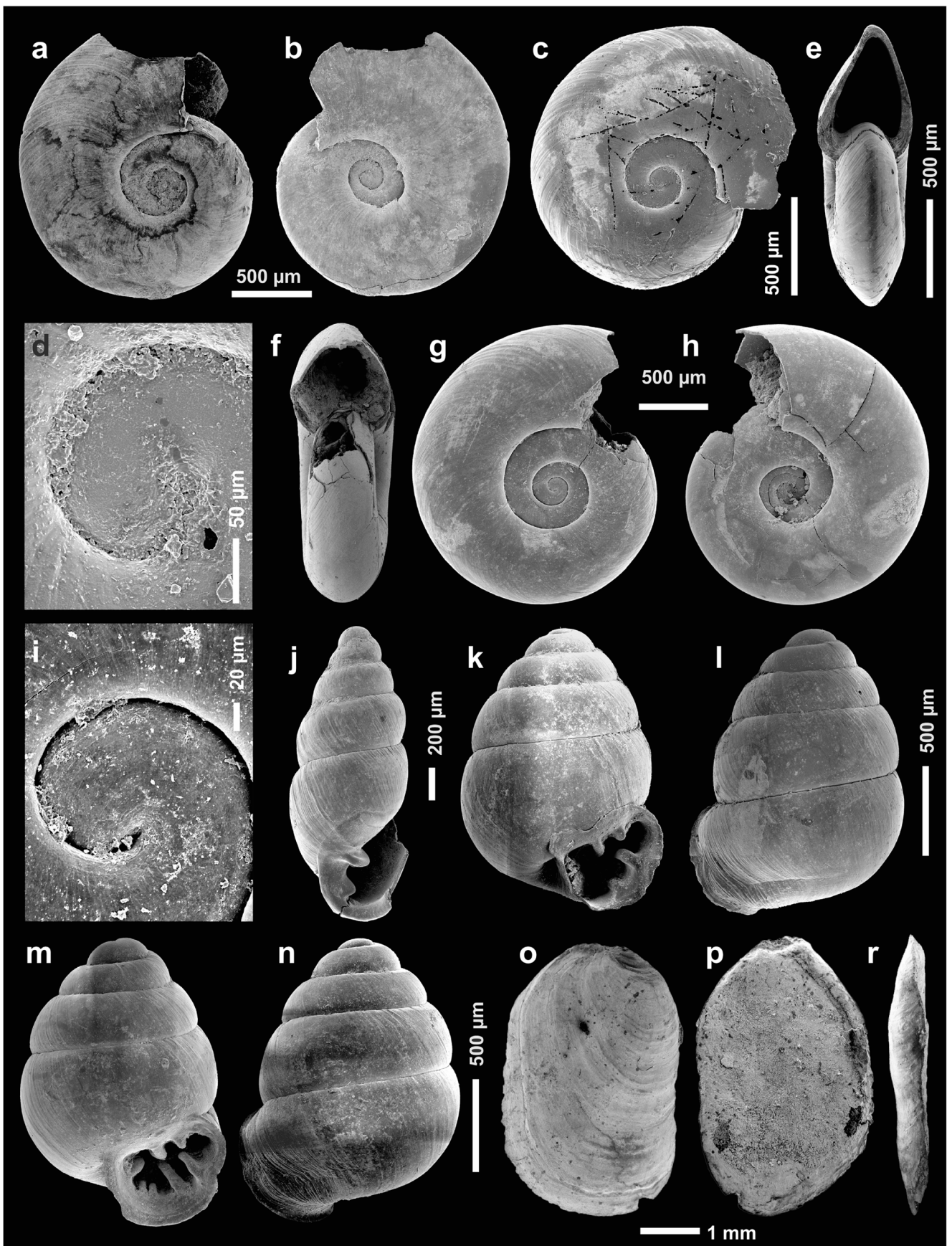
2018 *Carychium nouleti* Bourguignat, 1857—Harzhauser and Neubauer, p. 86–87, fig. 4G–I.

Material: Fourteen specimens from sample BU1708/5 (NHMW 2018/0101/0103, NHMW 2018/0101/0104), 2 specimens from sample BU1708/1 (NHMW 2018/0101/0102), 22 specimens from sample BU1708/2 (NHMW 2018/0101/0100, NHMW 2018/0101/0101), 1 specimen from sample BU0907/M2 (NHMW 2018/0101/0129) and 1 specimen from sample BU1708/1-5 (NHMW 2018/0101/0043).

Dimensions: NHMW 2018/0101/0043: diameter 0.8 mm, height 1.8 mm (Fig. 9j).

Remarks: A single incomplete specimen is available, showing a very slender shell with high slender last whorl, prominent prosocline axial growth lines, which are accentuated along the adapical suture, and narrow aperture with strong parietal lamella and slightly weaker columellar lamella. This morphology agrees fully to *Carychium nouleti* as described by Neubauer et al. (2017) and Harzhauser and Neubauer (2018). The morphologically similar middle to late Miocene *Carychium sandbergeri* Handmann, 1887 differs in its even more slender outline (see Harzhauser and Binder 2004). The status of *C. nouleti* was discussed in great detail by Neubauer et al. (2017).

Distribution: Neubauer et al. (2017) listed occurrences from Sansan in France (late Langhian), from Sarmatian deposits of Hollabrunn and Hautzendorf in Austria (Schütt 1967; Reischütz 2000), Nowa Wieś Królewska near Opole (Strauch 1977), the Bakony Mts. in Hungary (Kóckay 2006) and Zwierzyniec in Poland (Stworzewicz et al. 2013). A Turkish record was reported from the middle Miocene of Çifteçesme near Ayvalı by Schütt (1994). Recently, the species was also described from the late early Miocene of Bavaria (Salvador et al. 2016) and Austria (Binder 2004) and the late middle Miocene (Sarmatian) of Styria (Doubrava et al. 2018).



◀ **Fig. 9** *Gyraulus*, *Carychium*, *Vertigo* and Agriolimacidae species: **a–e** *Gyraulus dalmaticus* (Brusina, 1884); **a, b** BU0907/M8 (NHMW 2018/0101/0039); **c, d** BU0907/M8 (NHMW 2018/0101/0040); **d** protoconch; **e** BU0907/M8 (NHMW 2018/0101/0041); **f–i** *Gyraulus pulici* (Brusina, 1897), BU1708/1-5 (NHMW 2018/0101/0042); **i** protoconch; **j** *Carychium nouleti* Bourguignat, 1857, BU1708/1-5 (NHMW 2018/0101/0043); **k, l** *Vertigo callosa* (Reuss, 1849), BU1708/1-5 (NHMW 2018/0101/0044); **m–n** *Vertigo diversidens* (Sandberger, 1872), BU1708/1-5 (NHMW 2018/0101/0045); **o–r** Agriolimacidae gen. et sp. indet., BU1708/1 (NHMW 2018/0101/0062)

Order Stylommatophora Schmidt, 1855
Suborder Orthuretha Pilsbry, 1900
Family Vertiginidae Fitzinger, 1833
Subfamily Vertigininae Fitzinger, 1833
Genus *Vertigo* Müller, 1774

Type species: *Vertigo pusilla* Müller, 1774; by monotypy.
Recent, Europe.

Vertigo callosa (Reuss, 1849)
(Fig. 9k, l)

*1849 *V.[ertigo] callosa* m.—Reuss, p. 30, pl. 3, fig. 7.
1999 *Vertigo callosa* (Reuss, 1849)—Stworzewicz, p. 137, figs. 6, 7.
2014a *Vertigo callosa* (Reuss 1849)—Harzhauser et al., p. 23, pl. 8, figs. 1–2, 15 (cum syn.).
2014b *Vertigo callosa* (Reuss in Reuss and Meyer, 1849)—Harzhauser et al., p. 853, fig. 8G–H (cum syn.).

Material: One specimen from sample BU1708/1-5 (NHMW 2018/0101/0044).

Dimensions: Diameter 1.2 mm, height 1.65 mm (Fig. 9k, l).

Remarks: A single well-preserved specimen is available showing a stout, solid shell of four moderately convex teleoconch whorls with cyrtocoenoid spire; sculpture consisting of densely spaced prosocline growth lines. The aperture bears two prominent parietal lamellae and two palatal lamellae with a stronger lower one. Only the columellar lamella—if present—is obscured by sediment. Assuming that the columellar lamella is present, the specimen agrees well with specimens of *Vertigo callosa* described by Stworzewicz (1999) from the early Miocene of Bełchatów (Poland) and by Harzhauser et al. (2014a, b) from the Langhian of the Rein Basin in Styria and the Burdigalian of Tuchořice (Czech Republic).

Distribution: *Vertigo callosa* is a widespread early and middle Miocene species throughout central and southeastern Europe, documented from the early Miocene of France, Germany and Czech Republic (Stworzewicz 1999; Kóckay 2006; Harzhauser et al. 2014b). During the late early and early middle Miocene, it is widespread in southern Germany (Finger 1998; Salvador 2013; Salvador et al. 2017). It is also

documented from the Badenian and Sarmatian of Austria and Hungary (Schütt 1967; Reischütz 2000; Kóckay 2006). Its easternmost records come from the Sarmatian of Ukraine (Gozhik and Prysajzhnjuk 1978) and the middle Miocene of the Caucasus region (Steklov 1966). Its last occurrences are known from the late Miocene of Austria and Hungary from the hinterland of Lake Pannon (Lueger 1981; Harzhauser and Binder 2004).

Vertigo diversidens (Sandberger, 1872)
(Fig. 9m, n)

*1872 [*Pupa*] *diversidens* Sandb.—Sandberger, plate captions, pl. 29, figs. 23–23a.
1875 *Pupa (Vertigo) diversidens* Sandberger—Sandberger, p. 549.
1919 *Vertigo (Alaea) callosa diversidens* Sandberger—Gottschick and Wenz, p. 15, pl. 1, fig. 31.
1919 *Vertigo (Alaea) callosa steinheimensis* n. var.—Gottschick and Wenz, p. 15, pl. 1, figs. 32–33.
1919 *Vertigo (Alaea) callosa perarmata* n. var.—Gottschick and Wenz, p. 15, pl. 1, figs. 34–35.
1998 *Vertigo callosa steinheimensis*—Finger, p. 44, pl. 9, fig. D.
1998 *Vertigo callosa diversidens*—Finger, p. 44, pl. 9, fig. E.
1998 *Vertigo callosa perarmata*—Finger, p. 44, pl. 9, fig. F.
1999 *Vertigo diversidens* (Sandberger, 1874)—Stworzewicz, p. 138, fig. 8 (cum syn.).
2000 *Vertigo (Vertigo) diversidens* Sandberger, 1874—Fischer, p. 143, fig. 20.

Material: One specimen from sample BU1708/1-5 (NHMW 2018/0101/0045).

Dimensions: diameter 1.2 mm, height 1.55 mm (Fig. 9m, n).

Description: Stout ovoid shell of 4.5 moderately convex whorls. Low protoconch with delicate, wrinkled microsculpture. Teleoconch whorls with distinct, prosocline growth lines; suture impressed. Last whorl accounting for about 60% of total height; base regularly convex. Aperture broad U-shaped with weakly reinforced peristome; inner lip narrowly reflected. Weakly concave columella with prominent columellar lamella: two prominent, parallel parietal lamellae of nearly equal strength opposed by two longer, parallel palatal lamellae. Delicate suprapalatal denticle well behind peristome. Bifid basal lamella. Umbilicus narrow. Outer surface of last whorl with two depressions corresponding to palatal lamellae.

Remarks: The tendency to develop a deeply split basal lamella characterises *Vertigo diversidens* (Gottschick and Wenz, 1919). This species was revised by Stworzewicz (1999), who documented a considerable variability concerning number and strength of the denticles. This variability gave rise for

the introduction of two varieties by Gottschick and Wenz (1919), all based on material from the same locality (Steinheim, Germany). We follow Stworzewicz (1999), who considered these varieties synonyms of *V. diversidens*.

Distribution: *Vertigo diversidens* was described from the middle Miocene of Sansan (France) and Steinheim (Germany). The oldest occurrence was reported from the late early Miocene of Bełchatów (Beł-B) in Poland (Stworzewicz 1999).

Infraorder Stylommatophora Schmidt, 1855
 Superfamily Helicoidea Rafinesque, 1815
 Family Helicidae Rafinesque, 1815
 Subfamily Ariantinae Mörch, 1864
 Genus *Paradrobacia* Nordsieck, 2014

Type species: *Josephinella thiedei* Schlickum and Strauch, 1972; by original designation. Pliocene, Germany.

Paradrobacia hrvatovici Harzhauser, Mandic and Neubauer in Harzhauser et al., 2018.

*2018 (in press, this issue) *Paradrobacia hrvatovici*
 Harzhauser, Mandic and Neubauer n. sp.—Harzhauser et al., p. 4, fig. 2a–i.

Material: Five specimens from sample BU1708/5 (NHMW 2018/0101/0003, NHMW 2018/0101/0004, NHMW 2018/0101/0134, NHMW 2018/0101/0135), 12 specimens from sample BU1708/1 (NHMW 2018/0101/0001, NHMW 2018/0101/0002, NHMW 2018/0101/0130), 2 specimens from sample BU1708/4 (NHMW 2018/0101/0133) and 1 silicone cast from sample BU1708/1-5 (NHMW 2018/0101/0005).

Remarks: This species is characterised by its medium-sized shell with depressed spire, weakly convex spire whorls, blunt angulation on last whorl and moderately convex base; sculpture consisting of prominent, densely spaced, prosocyr axial ribs. See Harzhauser et al. (in press, this issue) for a detailed description and discussion.

Distribution: Restricted to the type locality (Gračanica coal pit—Bugojno Basin).

Unassigned “subclade” Limacoidea
 Family Agriolimacidae Wagner, 1935
 Agriolimacidae gen. et sp. indet.
 (Fig. 9o–r)

Material: One shell from BU1708/1.

Dimensions: NHMW 2018/0101/0062 (Fig. 9o–r): length 3.1 mm, height 4.7 mm and thickness 0.7 mm.

Remarks: The single vestigial shell is tentatively placed in the family Agriolimacidae based on its subparallel margins and the moderately displaced nucleus, as described by Reuse (1983) and Frank (2006). No shells of Limacidea, Milacidae or Agriolimacidae have been described so far from the DLS, which might rather be the result of a sampling bias.

Class Bivalvia Linnaeus, 1758
 Subclass Heterodonta Neumayr, 1883a
 Infraclass Euheterodonta Giribet and Distel, 2003
 Superorder Imparidentia Bieler, Mikkelsen and Giribet in Bieler et al., 2014
 Order Myida Stoliczka, 1870
 Superfamily Dreissenoida Gray in Turton, 1840
 Family Dreissenidae Gray in Turton, 1840
 Subfamily *Congerinae* Mandic and Harzhauser in Neubauer, Mandic and Harzhauser, 2016a
 Genus *Illyricocongeria* Mandic in Neubauer, Mandic and Harzhauser, 2016a

Type species: *Congeria aletici* Brusina, 1907. Middle Miocene, Langhian; Dinarides Lake System (S Croatia, SW Bosnia and Herzegovina)

Illyricocongeria forcakovici nov. sp.
 (Figs. 10a–s and 11a–l)

Holotype: NHMW 2018/0101/0009: $L = 16.5$ mm, $H = 16.5$ mm, $C = 4.5$ mm, $La = 1.6$ mm, $Lt = 4$ mm, $Adp = 90^\circ$, $Ada = 90^\circ$ (RV from BU0907/M5; Fig. 10e–g).

Paratypes: Paratype 1—NHMW 2018/0101/0008: $L = 20.5$ mm, $H = 22.0$ mm, $C = 6.3$ mm, $La = 0.8$ mm, $Lt = 7$ mm, $Adp = 105^\circ$, $Ada = 66^\circ$ (LV from sample BU0708/368; Fig. 10a–d); paratype 2—NHMW 2018/0101/00010: $L = 28.4$ mm, $H = 29.6$ mm, $C = 6.1$ mm, $La = 2.5$ mm, $Adp = 98^\circ$, $Ada = 73^\circ$ (LV from sample BU0907/M5; Fig. 10h); paratype 3—NHMW 2018/0101/00011: $L = 23.4$ mm, $H = 21.5$ mm, $La = 3.5$ mm, $Adp = 105^\circ$, $Ada = 99^\circ$ (AV from sample BU0907/M5; Fig. 10i).

Type locality: Gračanica coal pit SE of Bugojno in central Bosnia and Herzegovina (coordinates: 43.99754° N, 17.51880° E, WGS84).

Type stratum: Unit 21 (Fig. 2), Langhian, middle Miocene.
Derivation of name: In honour of Dževad Forčaković, chief geologist at the Gračanica coal mine company, for his valuable support enabling the present studies.

Additional material: Eight specimens from sample BU0708/364 (NHMW 2018/0101/0108), 10 specimens from sample BU0907/M8 (NHMW 2018/0101/0110, NHMW 2018/0101/0111), 6 specimens from sample BU0907/B30M (NHMW 2018/0101/0109), 26 specimens from sample BU0804/Mtop (NHMW 2018/0101/0112, NHMW 2018/0101/0113, NHMW 2018/0101/0115), 30 specimens from sample

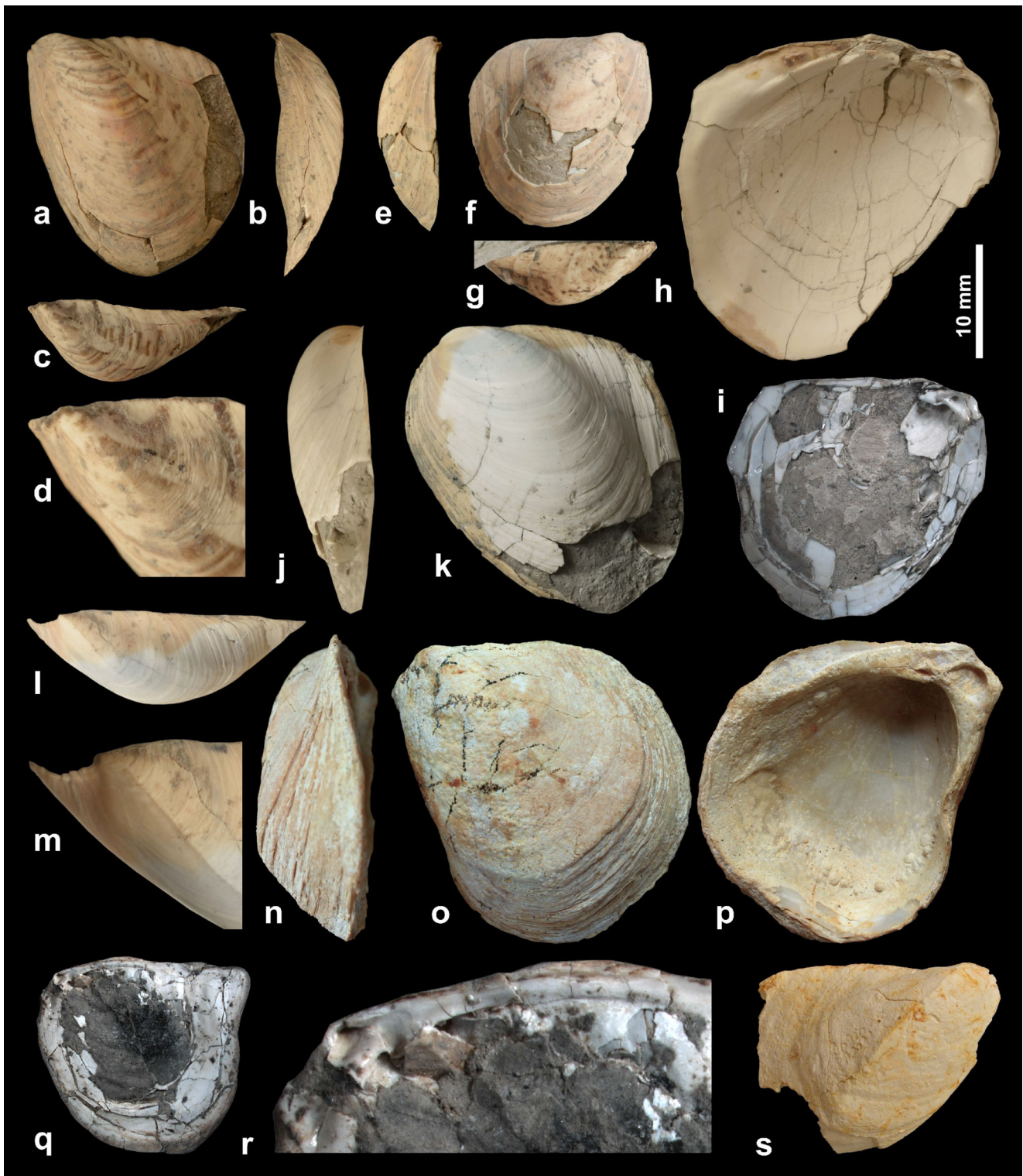


Fig. 10 *Illyricocongeria forcakovici* nov. sp.: **a–d** Paratype 1, LV, BU0708/368 (NHMW 2018/0101/0008); **b** anterior view; **c** dorsal view; **d** detail of the proximal exterior shell in dorsal view showing suppressed umbonal carina; **e–g** holotype, RV, BU0907/M5 (NHMW 2018/0101/0009); **g** dorsal view; **h** paratype 2, LV, BU0907/M5 (NHMW 2018/0101/0010); **i** paratype 3, AV demonstrating the typical preservation at sampled site, BU0907/M5 (NHMW 2018/0101/0011); **j–m** morphotype characterised by a protruded anterior shell side and an elongated umbonal thread, LV, BU0907/5d (NHMW 2018/0101/0012); **j** posterior view; **l** dorsal view; **m** detail of the proximal exterior shell in

dorsal view showing the umbonal thread; **n–p** morphotype characterised by thickened shell wall and reduced anterior shell side, LV, BU1610/LS (NHMW 2018/0101/0013); **n** posterior view; **p** interior view showing hypertrophied hinge elements; **q, r** morphotype with a keel and a pointed antero-dorsal tip, fragmented AS, BU0907/M9 (NHMW 2018/0101/0016); **q** left exterior view showing parts of interior RV and exterior LV; **r** detail of the proximal shell showing the RV hinge and a fragment of the LV with a diagonal thread; **s** morphotype with a prominent, ridge-like umbonal thread, RV missing the ventral part, BU1610/LS (NHMW 2018/0101/0015)

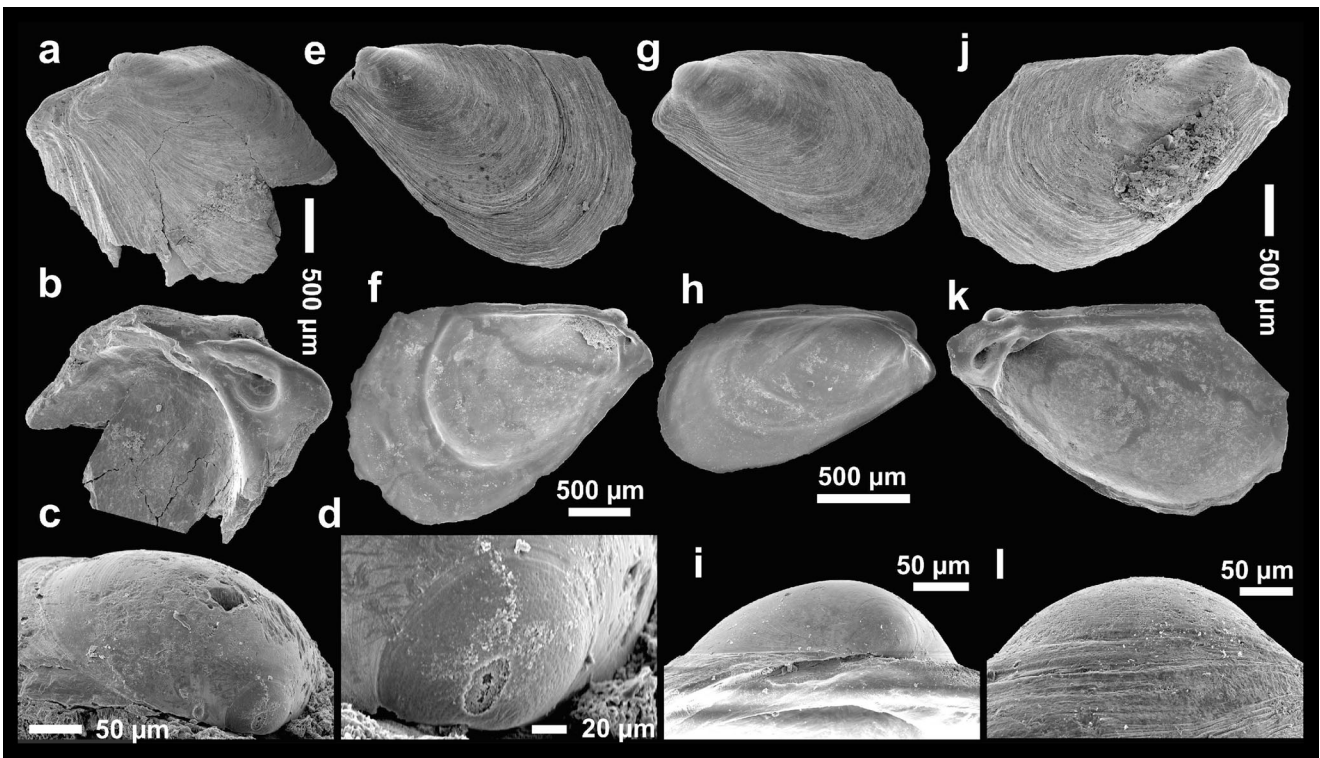


Fig. 11 SEM photographs of juvenile *Illyricocongeria forcakovici* nov. sp.: **a–d** fragmented LV, BU0907/M4 (NHMW 2018/0101/0046); **c** prodissoconch I and II; **d** prodissoconch I; **e, f** RV, BU0907/M4

(NHMW 2018/0101/0047); **g–i** LV, BU0907/M4 (NHMW 2018/0101/0048); **i** prodissoconch I and II dorsal view; **j–l** fragmented RV, BU0907/M4 (NHMW 2018/0101/0049); **l** prodissoconch II ventral view

BU1610/LS (NHMW 2018/0101/0013, NHMW 2018/0101/0015, NHMW 2018/0101/0107), 60 specimens from sample BU0907/M9 (NHMW 2018/0101/0016, NHMW 2018/0101/0116), 12 specimens from sample BU0907/M9d (NHMW 2018/0101/0106), 27 specimens from sample BU0907/M5 (NHMW 2018/0101/0009, NHMW 2018/0101/0010, NHMW 2018/0101/0011, NHMW 2018/0101/0125), 11 specimens from sample BU0907/M5d (NHMW 2018/0101/0012, NHMW 2018/0101/0124), 15 specimens from sample BU0708/368 (NHMW 2018/0101/0120), 63 specimens from sample BU0907/M4 (NHMW 2018/0101/0046, NHMW 2018/0101/0047, NHMW 2018/0101/0048, NHMW 2018/0101/0049, NHMW 2018/0101/0122, NHMW 2018/0101/0123), 47 specimens from sample BU0708/362 (NHMW 2018/0101/0119) and 21 specimens from sample BU0708/361 (NHMW 2018/0101/0121).

Dimensions: NHMW 2018/0101/00012: $L = 25.8$ mm, $H = 25.5$ mm, $C = 7.7$ mm, $La = 4.0$ mm, $Lt = 8$ mm, $Adp = 114^\circ$, $Ada = 53^\circ$ (LV from sample BU0907/M5d; Fig. 10j–m); NHMW 2018/0101/00013: $L = 26.7$ mm, $H = 27.2$ mm, $C = 9.1$ mm, $La = 2.5$ mm, $Adp = 103.5^\circ$, $Ada = 74^\circ$, $Ts = 2$ mm (LV from sample BU1610/LS; Fig. 10n–p); NHMW 2018/0101/0016: $L = 17.0$ mm, $H = 15.8$ mm, $La = 1.9$ mm, $Adp = 73^\circ$, $Ada = 60^\circ$ (AV from sample BU0907/M9; Fig. 10q–s).

Diagnosis: Modioliform, moderately sized, diagonally arched *Illyricocongeria* with well-developed anterior shell area, narrow straight or pointed anterior and widely rounded posterior margin, marked by a high morphological variation of outline, umbonal thread prominence and shell wall thickness.

Description: Shell modioliform, approximately as high as long, moderate in size, reaching up to 30 mm height. Outline inequilateral, pointed anterodorsally, rounded elsewhere. Anterior shell portion present but short, attaining maximally 15% of shell length. In lateral view, dorsal margin straightened to broadly convex. Posterior margin subvertical or slightly distally inclined; ventral margin strongly convex and pointed; anteroventral margin straightened and inclined posteriorly by $\sim 60\text{--}70^\circ$. The anterior margin straight or broadly convex and subvertical, rarely pointed (Fig. 10n–p).

Umbo prosogyrate and pointed. Beak inflated, projecting over dorsal margin. Shell convexity attains about 30% of shell height, with point of maximum convexity slightly shifted towards dorsal margin. Maximum convexity area forms diagonal ridge, which is broadly convex in cross-section, moderately to strongly inflated proximally and flattened distally; positioned more or less in the central shell part. Umbonal part of diagonal ridge, up to 8 mm of growth, more or less angular

and bears minute umbonal thread. Posterodorsal shell area concave providing shell part a wing-like appearance. Anteroventral shell part flattened and distally dipping.

Shell surface smooth and shiny, sometimes with colour pattern preserved, made by dark brown concentric bands, interrupted posterodorsally by colourless radial band. In oblique light, irregular growth lines and shallow concentric ledges are visible on shell surface, getting more prominent towards shell margin. Concentric ledges are marked by incisions of dorsal margin.

Hinge comprises small rounded apical septum placed anteriorly from umbo. Small apophysis positioned slightly beneath or at level of hinge plate, behind septum. Septum only slightly projecting, being largely integrated into shell wall. Prominent, convex-up or straightened nymph present in posterior shell part. It is slightly posteriorly inclined and well distanced from dorsal margin. Shell wall thin to moderately thick, except for latter specimen. Shell interior shows undulated surface with tubercles and irregular radiate threads. Mantle line integripalliate. Posterior adductor scar large irregularly vertically elongated, byssal retractor scar above it is small.

Remarks: The study collection shows an extraordinary high level of morphological variation in the present species. This variation relates to (1) the prominence and length of the umbonal thread, (2) the shape of the outline and (3) the thickness of the shell wall. (1) The umbonal thread (= “longitudinal ledge” in Neubauer et al. 2016a) is mostly well visible by the naked eye under oblique light; however, in some specimens, it is hardly visible (Fig. 10g), whereas in others, it is conspicuously prominent (Fig. 10s). In most cases, it is only few millimeters long, but in the latter specimen, it attains 15 mm and additionally displays a blunt ridge at its prolongation. Conspicuously, a trend of increasing prominence in the umbonal thread towards stratigraphically younger strata was observed. Still, because of increasingly worse preservation upwards, this trend could not be studied in detail. (2) Most of the outline variation is concentrated to the anterior margin, which is more or less protruded forward and might be pointed (Fig. 10o), straightened (Fig. 10a and f) or broadly rounded (Fig. 10k). Additionally, the contact of dorsal and posterior margins is mostly rounded (Fig. 10a, f, k and o), sometimes obtuse angular (Fig. 10h and i) and only in one case acute angular (Fig. 10q). (3) The shell wall is usually moderate to thin. In sample BU1610/LS, specimens tend to increase the shell thickness (Fig. 10p) and sculpture prominence (Fig. 10s) which might be an adaptation to higher water energy due to intermittent shallow littoral conditions and/or increasing water mineralisation upward in the section.

Such variation in DLS dreissenids has been already described by Kochansky-Devidé and Slišković (1978), who defined a great number of transitional phenotypes for several species. The authors explained this variation by a gradual

morphological evolution within phyletic lineages. The stratigraphic succession obtained for some of the species described by previous authors, such as *I. drvarensis*, *I. frici* and *I. aletici*, supports this hypothesis (de Leeuw et al. 2010; Mandić et al. 2011).

The present species is most similar to *I. moirae* Mandić in Neubauer et al. (2016a) from the Drniš Basin, differing from the latter by a larger anterior shell area, generally wider outline, and a larger size. Specimens from the upper part of the section, such as the specimen illustrated on Fig. 10s, resemble by a prominently developed umbonal ridge *Illyricocongeria dalmatica* (Brusina, 1884). According to Kochansky-Devidé and Slišković (1978), the latter species predates phylogenetically *I. drvarensis* (Toula, 1913) in a lineage characterised by a progressive shortening and weakening of the umbonal ridge, thus contrasting the trend observed at Gračanica. Furthermore, *I. dalmatica* differs by the mostly broader ventral margin producing a more rounded general outline. *Illyricocongeria brevicosta* Kochansky-Devidé and Slišković, 1981 from the late Miocene of the Livno Basin, showing a similar modioliform shape and a short but prominent umbonal thread, is smaller and more slender in outline. *Illyricocongeria fuchsi* (Pilar, 1873) from the Karlovac-Glina Basin shows a reduced and mostly pointed anterior margin and a broadly arched bulbous proximal shell portion. *Illyricocongeria obliqua* (Kochansky-Devidé and Slišković, 1981) and *I. bosniaca* (Katzner, 1913) from northern Bosnia and Herzegovina have always reduced or absent umbonal threads and subtrapezoidal or subrhomboidal outlines.

Distribution: Known only from the type locality.

Order Sphaeriida Lemer, Bieler and Giribet, 2019
 Superfamily Sphaerioidea Deshayes, 1855 (1820)
 Family Sphaeriidae Deshayes, 1855 (1820)
 Subfamily Pisidiinae Gray, 1857
 Genus *Pisidium* Pfeiffer, 1821

Type species: *Tellina amnica* Müller, 1774; Recent, Northern Hemisphere; type by subsequent designation by Gray (1847).

Pisidium bellardii Brusina, 1884
 (Fig. 12a–g)

*1884 *Pisidium Bellardii* Brusina—Brusina, p. 48.
 1897 *Pisidium Bellardii* Brus.—Brusina, p. 36, pl. 21,
 figs. 43–45.
 2013b *Pisidium bellardii* Brusina, 1884—Neubauer et al.,
 p. 55, fig. 11A–D (cum syn.).

Material: Five specimens from sample BU0708/364 (NHMW

2018/0101/0108), 4 specimens from sample BU1610/LS (NHMW 2018/0101/0017, NHMW 2018/0101/0018, NHMW 2018/0101/0020, NHMW 2018/0101/0105), 10 specimens from sample BU0907/M9 (NHMW 2018/0101/0016, NHMW 2018/0101/0116), 8 specimens from sample BU0907/M9d (NHMW 2018/0101/0106), 101 specimens from sample BU0907/M7 (NHMW 2018/0101/0019, NHMW 2018/0101/0117), 25 specimens from sample BU0907/M6 (NHMW 2018/0101/0118), 1 specimen from sample BU0907/M5 (NHMW 2018/0101/0125), 1 specimen from sample BU0708/368 (NHMW 2018/0101/0120) and 1 specimen from sample BU0907/M1 (NHMW 2018/0101/0127).

Dimensions: NHMW 2018/0101/0017: $L = 1.9$ mm, $H = 1.6$ mm (LV from sample BU1610/LS; Fig. 12a, b); NHMW 2018/0101/0020: $L = 1.76$ mm, $H = 1.45$ mm (RV from sample BU1610/LS, Fig. 12f, g); NHMW 2018/0101/0018: $L = 1.64$ mm, $H = 1.33$ mm, $C = 0.52$ (LV from sample BU1610/LS; Fig. 12c, d); NHMW 2018/0101/0019: $L = 2.47$ mm, $H = 1.96$ mm (LV embedded to sediment from unit 29—sample BU0907/M7; Fig. 12e).

Description: Minute shell with oval to subtriangular outline, longer than high, with anterior side about 1.5 times longer than posterior side. Convexity attains about 40% of shell height. Margin outline anteriorly narrowly convex and pointed, posteriorly broad convex and straightened, ventrally broadly convex. Dorsal margin with straightened flanks meeting at very obtuse angle at slightly dorsally pointed umbo. Umbonal area broadly

inflated, slightly projecting over dorsal margin, anterodorsal area steep, concave, slightly pointed and wing-like projecting. Shell thin and translucent showing exteriorly fine growth lines and at distal half few weak growth ledges at regular distances. Interior surface with comarginal integripalliate mantle line, positioned at ~ 85% of height. Adductor muscle scars moderately in size, subvertically elongated, anterior one broader than posterior one. Hinge broadly bended and relatively narrow, only anteriorly slightly broadened. In LV with inverse broadly V-shaped C2 and straightened, posteriorly inclined C4, slender PII and AII. RV shows minute inverse U-shaped C3, massive AI, reduced AIII, slender PI and minute PIII. All teeth except for AIII and PIII strongly projecting.

Remarks: The specimens coincide with material of *Pisidium bellardii* Brusina, 1884, described previously by Neubauer et al. (2016a) concerning size, hinge structure, regular growth lines and the thin shell wall. The minor difference in the largely subtriangular outline due to a straight, broader convex to sub-rectangular posterior shell margin can be related to phenotypic variability. This variability also involves a broadly inflated umbonal area in few larger specimens. *Pisidium vukovici* Neubauer et al., 2013b from the Gacko Basin is much narrower and shows a thickened shell and a massive hinge.

Pisidium bellardii Brusina, 1884, originally described from Miočić (Drniš Basin, early Langhian) and Ruduša (Sinj

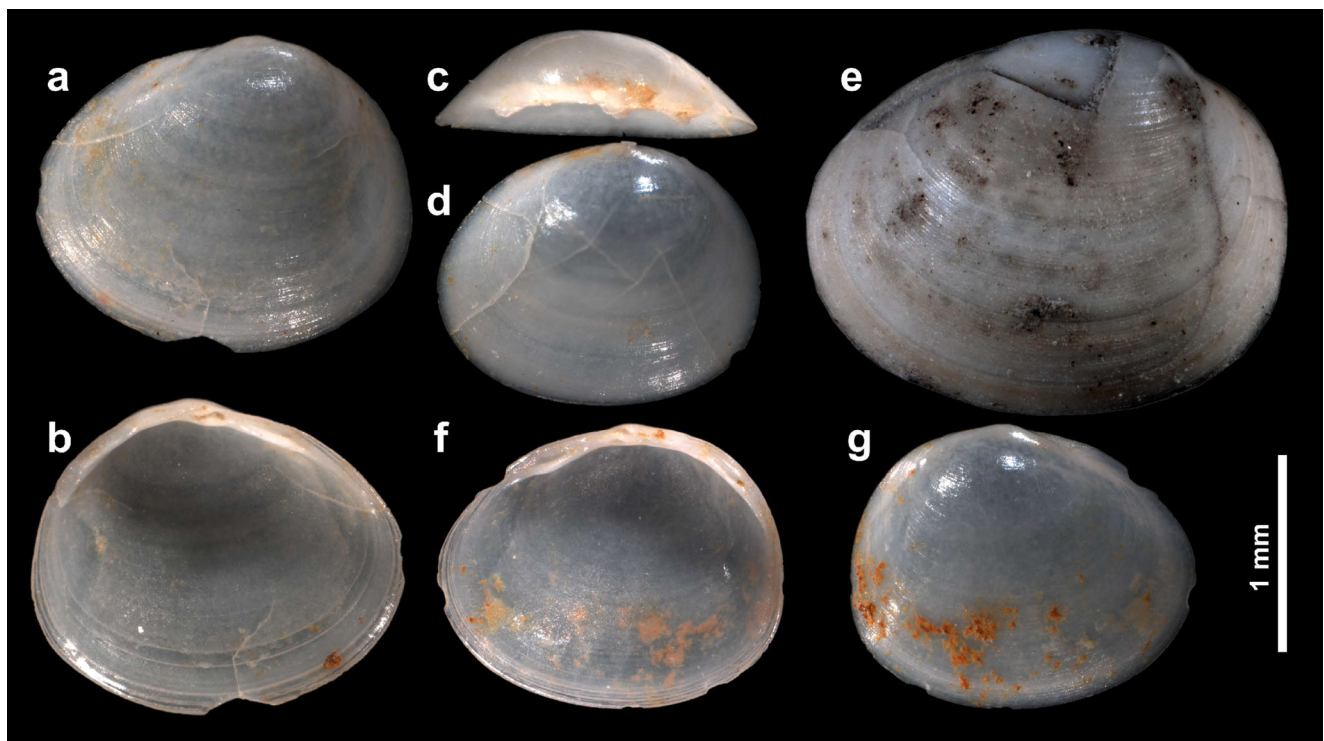


Fig. 12 *Pisidium bellardii* Brusina, 1884: **a, b** LV, BU1610/LS (NHMW 2018/0101/0017); **c, d** LV, BU1610/LS (NHMW 2018/0101/0018); **e** dorsal view; **e** LV, BU0907/M7 (NHMW 2018/0101/0019); **f, g** RV, BU1610/LS (NHMW 2018/0101/0020)

Table 1 Species distribution, number of individuals, species richness and abundances (%) in the samples from the Gračanica coal pit in the Bugojno Basin

| Height (m) | Sample (BU) | Number of individuals Species richness | | Gastropods | | | | | | | | | | | | Bivalves | | | | | | | |
|------------|-------------|---|---|---------------------------|------------------------------|----------------------------------|------------------|----------------------------------|--|---------------------|-------------------------------|---------------------------|------------------------------|----------------------------|------------------------|--------------------------|-----------------------|----------------------------|-----------------------------------|--------------------------------|--|---------------------------|----|
| | | | | aquatic | | | | | | terrestrial | | | | | | | | | | | | | |
| | | | | neritids | melanopsids | hydrobiids | | bithyniids | lymnaeids | planorbids | | carychiids | vertiginids | agriolimacids | helicids | dreissenids | sphaeriids | | | | | | |
| | | | | <i>Theodoxus sirjanus</i> | <i>Melanopsis visianiana</i> | <i>Bania goehlichae</i> nov. sp. | <i>Bania</i> sp. | <i>Cyclothyrella tryoniopsis</i> | <i>Prosothenia krijgsmani</i> nov. sp. | <i>Bithynia</i> sp. | Lymnaeidae gen. et sp. indet. | <i>Ferrissia illyrica</i> | <i>Planorbarius mantelli</i> | <i>Gyraulus dalmaticus</i> | <i>Gyraulus pulici</i> | <i>Carychium nouleti</i> | <i>Vetigo callosa</i> | <i>Vertigo diversidens</i> | Agriolimacidae gen. et sp. indet. | <i>Paradrobacia hrvatovici</i> | <i>Illyricocongeria forcakovi</i> nov. sp. | <i>Pisidium bellardii</i> | |
| ~35.2 | 0708/364 | 25 | 6 | 16 | | | | 4 | 12 | | | | | 16 | | | | | | | | 32 | 20 |
| 34.8 | 0907/M8 | 1269 | 8 | 1 | 4 | 5 | | 81 | 3 | 0 | | | | 5 | | | | | | | | 1 | |
| ~34.8 | 0907/B30M | 37 | 7 | 41 | 22 | 3 | | 14 | 3 | | | | | 3 | | | | | | | | 16 | |
| " | 0804/Mtop | 93 | 7 | 33 | 30 | 2 | | 3 | 2 | | | | | 1 | | | | | | | | 28 | |
| " | 1610/LS | 162 | 8 | 7 | 65 | 1 | | 1 | 3 | | | | | 2 | | | | | | | | 19 | 2 |
| 33.9 | 0907/M9 | 77 | 4 | 1 | | | | | | | | | | 8 | | | | | | | | 78 | 13 |
| ~33.9 | 0907/M9d | 20 | 2 | | | | | | | | | | | | | | | | | | | 60 | 40 |
| 32.4 | 0907/M7 | 102 | 2 | | | | | | 1 | | | | | | | | | | | | | | 99 |
| 30.8 | 0907/M6 | 32 | 2 | | | | | | | | | | | 22 | | | | | | | | | 78 |
| 23.6 | 0907/M5 | 33 | 4 | | 3 | | | | | | | | | 3 | | | | | | | | 91 | 3 |
| ~23.6 | 0907/M5d | 11 | 1 | | | | | | | | | | | | | | | | | | | 100 | |
| " | 0708/368 | 21 | 5 | | 5 | 10 | | | | | | | | 10 | | | | | | | | 71 | 5 |
| 22.6 | 0907/M4 | 252 | 5 | | 61 | 12 | 0 | | | | | | | 2 | | | | | | | | 25 | |
| ~22.6 | 0708/362 | 1024 | 4 | | 91 | 1 | | | | | | | | 4 | | | | | | | | 5 | |
| ~21.0 | 0708/361 | 224 | 4 | | 89 | 1 | | | | | | | | 0 | | | | | | | | 9 | |
| ~19.0 | 1708/5 | 40 | 6 | | | 3 | | | | | 20 | | 10 | 20 | 35 | | | | | | | 13 | |
| 17.6 | 0907/MA | 71 | 4 | | 32 | 54 | | | | | 1 | | | 13 | | | | | | | | | |
| ~16.5 | 1708/1 | 64 | 8 | | | 17 | | | | 2 | 6 | | 27 | 25 | 3 | | | | 2 | | | 19 | |
| ~15.5 | 1708/2 | 25 | 2 | | | | | | | | | | | 12 | 88 | | | | | | | | |
| ~14.5 | 1708/3 | 49 | 5 | | | 4 | | | | | 10 | 2 | 45 | 39 | | ? | ? | | | | | | |
| ~10.0 | 1708/4 | 8 | 3 | | | | | | | | | | 25 | 50 | | | | | | | | 25 | |
| 7.6 | 0907/M3 | 16 | 4 | | | | | | | | 19 | 13 | 38 | 31 | | | | | | | | | |
| 1.6 | 0907/M2 | 8 | 3 | | | | | | | | | | 75 | 13 | 13 | | | | | | | | |
| 0.1 | 0907/M1 | 41 | 5 | | | 24 | | | | | 5 | | 5 | 63 | | | | | | | | | 2 |

Basin, early Langhian), was subsequently illustrated by Brusina (1897, figs. 43–45; NHMZ 33203-849) from Trnovača (Sinj Basin, early Langhian). The latter specimen was erroneously considered for a holotype by Milan et al. (1974).

Distribution: Endemic to DLS–middle Miocene (early Langhian): Drniš Basin (Miočić), Gacko Basin (Gračanica, Vrbica) and Sinj Basin (Ruduša, Trnovača) (Brusina 1884, 1897; Neubauer et al. 2013b, 2016a).

Discussion

Faunal composition and its distribution in the section

The mollusk fauna from the Gračanica coal pit comprises 19 species in total (Table 1). Five species are terrestrial gastropods, all restricted to the lower, coal-bearing interval of the succession (Fig. 2). Common terrestrial taxa are *Carychium nouleti* and *Paradrobacia hrvatovici*, accompanied by rare findings of two vertiginid and one agriolimacid species.

The limnic part of the fauna includes the new dreissenid species *Illyricocongeria forcakovici* and the minute sphaeriid *Pisidium bellardi*. They both tend to build monotypic shell beds in the upper, marly interval of the succession, being absent or very rare in the coal interval of the lower part of the section. Corresponding shell beds are in situ deposited in a low-energy open-lake environment and showing no traces of transport.

Twelve gastropod species occur in the limnic guild of the Gračanica mollusk fauna. Most common are *Melanopsis visianiana*, *Cyclothyrella tryoniopsis* and the planorbids *Planorbarius* cf. *mantelli* and *Gyraulus pulici*, followed by *Bania goehlichae*, *Theodoxus sinjanus* and *Gyraulus dalmaticus*. Whilst *G. dalmaticus* is restricted to the marly part of the succession, the other two planorbids are restricted to the coal-bearing interval. Lymnaeids are also confined to that interval. *Bania goehlichae* is present throughout the section, showing however an increased abundance in the coal-dominated interval. *Melanopsis visianiana* occurs for the first time in the Gračanica succession just before the ultimate coal bed and is dominating in the first bed above it and in the lateral site (BU1610/LS). *Cyclothyrella tryoniopsis* shows its first occurrence in the shell accumulation at 34.8 m of the section, being there extraordinarily abundant. This uppermost part of the section is marked additionally by the frequent presence of *M. visianiana* and *T. sinjanus*.

Muftić and Behlilović (1966) reported 17 mollusk taxa from the Gračanica coal pit succession and indicated their occurrence within the stratigraphic units. Conspicuously, the taxonomic content of the section documented in that report has no overlap with the account presented in this study. Except maybe for *Tinnyea verbasensis* (Neumayr, 1883b)

and *Orygoceras* sp., showing unique morphological features that allow straightforward identification, all other species clearly represent erroneous identifications. This result demonstrates the relevance of a careful taxonomic analysis to allow for reliable comparison and correlations. As an example, Muftić and Behlilović (1966) misidentified four taxa with late Miocene to early Pliocene species endemic to Lake Pannon (*Melanopsis cognata* Brusina, 1878; *Melanopsis pygmaea* Hörnes, 1856; *Sphaerium ozegovici* Brusina, 1897; and *Radix grammica* (Brusina, 1874)), which has severe implications for biostratigraphic correlation as well as the reconstruction of the fauna's palaeobiogeographic relationships. Likewise, their erroneous identification of *Illyricocongeria frici* (Brusina, 1904), an important biostratigraphic marker species in the DLS, in the topmost section, would constrain its age to ~15.5 Ma (Mandic et al. 2016; see next chapter).

Palaeoenvironmental evolution of the Lake Bugojno

The distribution of mollusk species and their abundances reflect the changes of depositional environments in the section (Table 1, Fig. 2). Hence, the coal deposition in the lower part of the section, marking the vicinity of terrestrial environments, bears common terrestrial gastropods, which disappear with the uppermost coal layer. That interval is dominated by limnic mollusks, implying a persistent wetland environment throughout the unit. A general shift of the mollusk assemblages towards younger strata indicates a distinct environmental change within the coal-bearing interval. Hence, the samples covering the lower 15 m of the interval show increased planorbid abundance with a minimum of 69% contribution. The samples from the upper part of the interval show in contrast fewer planorbid snails, compensated by an increased abundance of terrestrial (*C. nouleti*) and/or limnic caenogastropod (*B. goehlichae* and *M. visianiana*) species, associated with a general increase of species richness. This change in the mollusk composition correlates well with the gradual shift of the depositional environment between 10 and 15 m of the interval, marked by the disappearance of trunk remains and the decrease of organic components in the marly interbeds between the coal seams. That shift marks a transition from swamp towards palustrine conditions, reflecting a lake level rise that caused a gradual flooding of the terrestrial environments around the lake.

On top of the last coal seam, the assemblage goes through a distinct shift towards a littoral mollusk assemblage. Unit 20 is dominated by *M. visianiana*, followed by the dreissenid bivalve *I. forcakovici*. Mollusk shells are accumulated at the base of the foresets marking the installation of a deltaic depositional setting (Mandic et al. 2016). The following unit 21 points to a sudden increase of the relative lake level and the establishment of perennial lake conditions. Besides dominating dreissenid bivalves, scattered planorbid, hydrobiid and

melanopsid specimens are present pointing to low-energy littoral conditions established at some distance from the coast. The lack of littoral gastropods in unit 23 suggests a further lake level rise. No mollusks were found in the following unit 24. The deposition of laminated marly sediments rich in dispersed organic matter suggests oxygen-depleted deeper-water conditions (Mandic et al. 2011; Sant et al. 2018a, b).

Mollusks reappear at ~ 30 m (unit 28). From here upwards, a gradual shallowing is indicated by shifts in the mollusk composition. Units 28 and 29 are marked by almost monotypic assemblages of the minute sphaeriid *Pisidium bellardii*. This species reminds of the Recent *P. casertanum* (Poli, 1791) representing one of the world's most widely distributed non-marine mollusks (Brusina 1884; Welter-Schultes 2012). It is a pioneering species present in a wide spectrum of clear, low-energy, freshwater environments ranging from ephemeral ponds to benthic zones of deep lakes (Burky et al. 1981; Welter-Schultes 2012; Běspalaya et al. 2015). Perhaps, the dominance of *P. bellardii* in units 28 and 29 can be explained by the deeper-water conditions adverse to other mollusk species. Additionally, the gastropods *Gyraulus dalmaticus* and *Prososthenia krijgsmani* are present in low numbers and were likely transported from the littoral zone (Neubauer et al. 2011, 2013b). Further lake level fall is suggested by reoccurring dreissenid bivalves indicating the reoccurrence of littoral facies in unit 30. Sublittoral conditions are indicated by the still abundant *P. bellardii*.

At section height ~ 35 m, species richness is at its maximum. The exclusively limnic littoral mollusk assemblages are accumulated in up to 30 cm thick coquinas in clayey to sandy matrix and may show internal cross-beds. Coquinas are dominated by littoral markers *M. visianiana*, *T. sinjanus*, *I. forcakovici* and *C. tryoniopsis* (Neubauer et al. 2011, 2013b). The latter is a morphologically very characteristic species that shows its first occurrence in this level. Although the lateral site (BU1610/LS) represents a small, isolated outcrop, the identical coquina type and the same taxonomic composition, including the presence of *C. tryoniopsis*, allow a correlation with the present level. Sample BU0708/364 showing also the presence of *C. tryoniopsis* along with abundant *P. bellardii* and the conspicuously carinate *Illyricongergeria moirae* is tentatively correlated with the upper part of unit 30. It represents probably a short-term environmental deepening. Directly above, a fossil-barren clayey to sandy coarsening-upward succession starts. The upwards increase of terrestrial input along with the ripple bedding suggests a return to a shallow-water depositional environment.

Biostratigraphic and palaeobiogeographic implications

The lacustrine part of the mollusk fauna described herein comprises 14 species (Table 2). Conspicuously, roughly similar levels of species richness were reported for representative sections in other DLS basins. In particular, 17 lacustrine species

were found at Gračanica in the Gacko Basin, 19 at Lučane in the Sinj Basin, 16 at Džepi in the Konjic Basin and 18 at Fatelj in the Kupres Basin (Neubauer et al. 2011, 2013a, b, 2016b). Yet, these five localities comprise even 65 species, many of which are endemic to those basins. The studied fauna shares only three species (*Ferrissia illyrica*, *G. pulici*, *P. bellardii*) with Gračanica/Gacko, two with Lučane (*T. sinjanus*, *F. illyrica*) and one species with Fatelj and Džepi (*C. tryoniopsis*) (Table 2). This low similarity is very conspicuous because, with the exception of Fatelj, the overall sedimentary successions are very similar, representing alternations of lacustrine deposits and coal. The Bugojno fauna shares more species with the Miočić site in the Drniš Basin (*T. sinjanus*, *M. visianiana*, *C. tryoniopsis*, *G. dalmaticus*, *F. illyrica*, *P. bellardii* and tentatively *Planorbarius mantelli*). With 41 lacustrine species, the Miočić fauna is much more diverse, reflecting possibly a collection and/or preservation bias (Neubauer et al. 2016a).

The overall low similarity between the present fauna and those of other DLS basins (Table 2, Fig. 1b) may point to restricted faunal exchange between the basins and/or different ages of the faunas. Additionally, environmental filtering or speciation interactions (such as high competition) might have impeded the establishment of immigrating taxa (Hauffe et al. 2016). For the extant ancient Lake Ohrid, situated at the border between Albania and North Macedonia, these authors showed the importance of dispersal limitations shaping its endemic gastropod community. Environmental filtering and biotic interaction have still significant but much lower impact (Hauffe et al. 2016). Given its setting as a long-lived, deep, intramontane lake with high endemic diversity (Albrecht and Wilke 2008), Lake Ohrid may serve as an analogue to the DLS faunas and Lake Bugojno in particular. The topographic relief of the Dinarides Mountains, likely with largely isolated watersheds, probably inhibited immigration and promoted intralacustrine radiation, yielding the unique endemic diversity we encounter in the fossil record today. However, our knowledge is still fairly patchy and based on few sections only, and the faunas of many DLS basins are still unknown. More data on their diversity and distribution are needed to clarify the development of the DLS fauna and its evolution as biodiversity hotspot in the Miocene.

An alternative interpretation to explain the dissimilarity between the faunal compositions of DLS basins involves stratigraphic differences (Fig. 13). Lately, great improvements have been made in dating the deposits of the DLS (Jiménez-Moreno et al. 2009; de Leeuw et al. 2010, 2011, 2012; Mandic et al. 2011, 2012a; Sant et al. 2018a). Several species of the dreissenid genus *Illyricongergeria* have proved useful marker species. For example, the occurrence of *Illyricongergeria aletici* at Lučane has been dated by integrative stratigraphic studies to the time interval of ca. 15.4–15.0 Ma, which allowed biostratigraphic

Table 2 Distribution of species from the Gračanica coal pit (Bugojno Basin) in selected DLS basins and outside the DLS

| Species | Drniš Basin | Sinj Basin | Gacko Basin | Kupres Basin | Konjic Basin | Outside DLS |
|--|-------------|------------|-------------|--------------|--------------|-------------|
| <i>Theodoxus sinjanus</i> (Brusina, 1876) | x | x | | | | |
| <i>Melanopsis visianiana</i> Brusina, 1874 | x | x | | | | |
| <i>Bithynia</i> sp. | | | | | | |
| <i>Cyclothyrella tryoniopsis</i> (Brusina, 1874) | x | x | | x | x | |
| <i>Prososthenia krijgsmani</i> nov. sp. | | | | | | |
| <i>Bania goehlichae</i> nov. sp. | | | | | | |
| <i>Bania</i> sp. | | | | | | |
| Lymnaeidae gen. et sp. indet. | | | | | | |
| <i>Ferrissia illyrica</i> (Neumayr, 1880) | x | x | x | | | |
| <i>Gyraulus dalmaticus</i> (Brusina, 1884) | x | x | | | | |
| <i>Gyraulus pulici</i> (Brusina, 1897) | | | x | | | |
| <i>Planorbarius mantelli</i> (Dunker, 1848) | x | | | | | x |
| <i>Carychium nouleti</i> Bourguignat, 1857 | | | | | | x |
| <i>Vertigo diversidens</i> (Sandberger, 1872) | | | | | | x |
| <i>Vertigo callosa</i> (Reuss, 1849) | | | | | | x |
| Agriolimnacididae gen. et sp. indet. | | | | | | |
| <i>Paradrobacia hrvatovici</i> Harzhauser et al., 2018 | | | | | | |
| <i>Illyricocongeria forcakovici</i> nov. sp. | | | | | | |
| <i>Pisidium bellardii</i> Brusina, 1884 | x | x | x | | | |

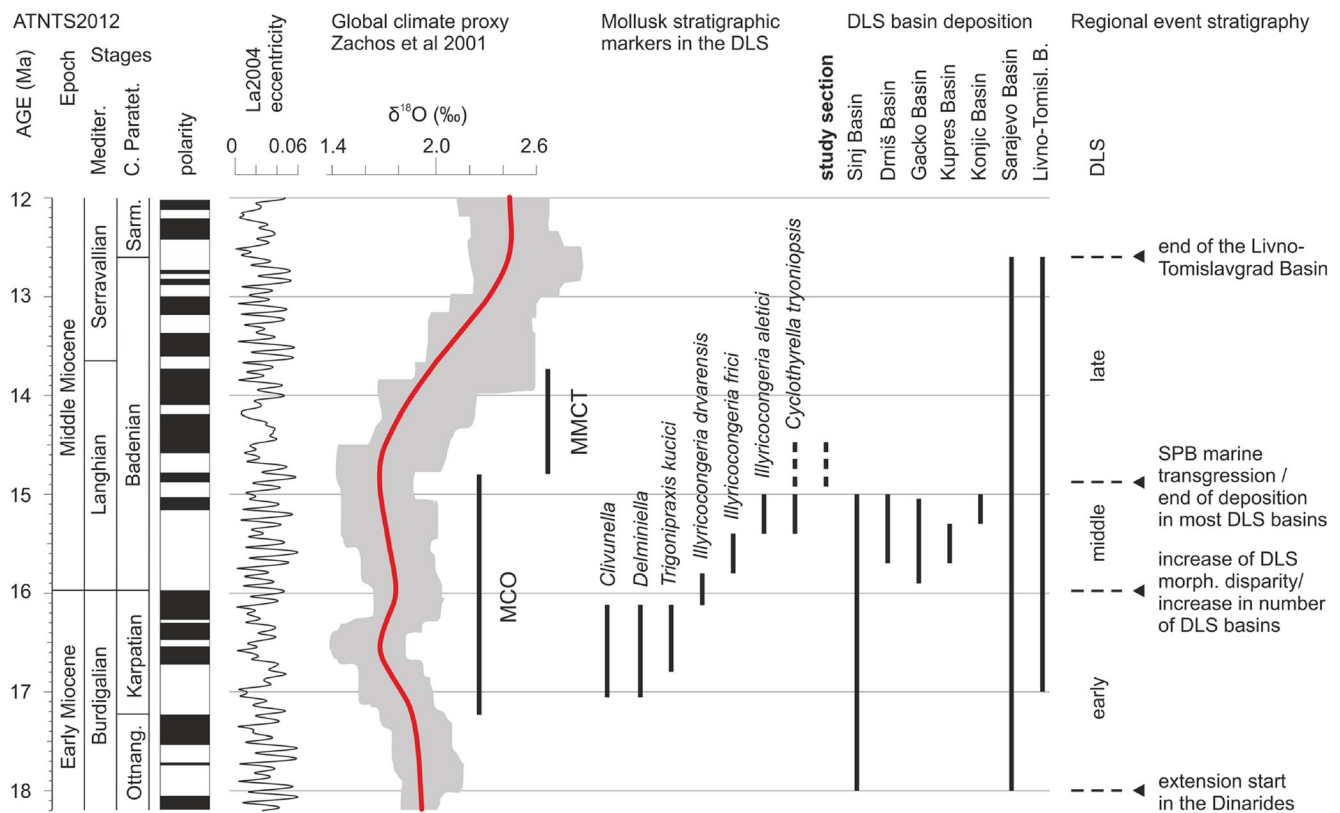


Fig. 13 Stratigraphic correlation table showing distribution of global and regional events, DLS index fossils and ages of depositional sequences inferred in previous studies as indicated in text; inferred age of the section

is indicated (MCO, Miocene Climatic Optimum; MMCT, Middle Miocene Climate Transition, Holbourn et al. 2014, 2015; ATNTS2012—Hilgen et al. 2012; La2004—Laskar et al. 2004)

correlation of the faunas retrieved at Fatelj in the Kupres Basin, Miočić in the Drniš Basin and, tentatively, Džepi in the Konjic Basin (Neubauer et al. 2013a, 2016a, b). The related species *Illyricocongeria frici* is constrained to ca. 15.8–15.4 in the Gacko Basin (Neubauer et al. 2011, 2013b; de Leeuw et al. 2010; Mandic et al. 2011). In the Bugojno Basin, however, neither the identification of *I. frici* by Muftić and Behlilović (1966) proved true, nor *I. aletici* has been found, thus, disabling a straightforward biostratigraphic correlation. The hydrobiid *C. tryoniopsis* co-occurs with *I. aletici* in the Kupres, Drniš, Konjic and Sinj basins. Both species are absent in the slightly older Gacko Basin. Thus, the presence of *C. tryoniopsis* and the absence of *I. aletici* or *I. frici* might argue for a slightly younger age of the Bugojno Basin fauna, i.e. slightly younger than ca. 15 Ma. This age coincides with the approximate time when most of the DLS basins, including the Sinj Basin, started to disintegrate (i.e. boundary of middle/late DLS phase of de Leeuw et al. 2011; Fig. 13). Nevertheless, an independent dating for the mollusk faunas is still missing for that interval.

If such a young age were supported by other stratigraphic data, the mollusk fauna from the Gračanica section in the Bugojno Basin would postdate all the presently known middle Miocene DLS mollusk assemblages. In particular, the related deposits younger than 15 Ma in two remaining DLS long-lived lakes, i.e. Livno-Tomislavgrad and Sarajevo basins, are seemingly barren of mollusks (de Leeuw et al. 2011; Sant et al. 2018a).

Summary and conclusion

The mollusk fauna recorded from the Gračanica coal pit comprises 14 limnic and 5 terrestrial species. Their distribution in the 40-m-long succession allows to detect palaeoenvironmental changes during the history of Lake Bugojno. Terrestrial species are restricted to the coal-bearing lower part of the succession representing swamp and marsh deposits. Transitional deltaic cross-beds are associated with a peak in melanopsid abundance, whereas the subsequent establishment of littoral and sublittoral conditions is marked by a dominance of dreissenid and sphaeriid bivalve species. The overlaying interval, which seems to reflect profound depositional environments of Lake Bugojno, is barren of mollusks. A short-term shallowing trend, recorded in the topmost part of the section, coincides with the occurrence of shell accumulations marked by peaks in species richness contributed by melanopsid, hydrobiid, neritid and dreissenid species.

The present taxonomic evaluation proved the species-level identifications from previous studies incorrect, resulting in a completely new understanding of the stratigraphic and palaeobiogeographic significance of the Lake

Bugojno mollusk fauna for the DLS evolution. In particular, the mollusk fauna of the Lake Bugojno shows a low level of similarity with other DLS basins, matching the general pattern of interbasinal dissimilarity among DLS faunas detected in previous taxonomic studies. Such a pattern cannot be explained by different depositional conditions as the discussed mollusk faunas derive from very similar palaeoenvironments of coal-bearing successions. At least parts of this taxonomic dissimilarity in the various DLS basins might have been caused by their isolated geographic settings, which would agree with Recent ancient-lake examples in the region (e.g. Lake Ohrid). Moreover, the presence and absence of biostratigraphic marker species suggest an age slightly younger than 15.0 Ma. Consequently, the present Lake Bugojno fauna represents presumably the youngest known middle Miocene mollusk-bearing horizon in the DLS.

Acknowledgements Our thanks go to the authorities of the Gračanica coal mine for permission to work in the pit. We are particularly grateful to Dževad Forčaković, Hamdija Puljarga and Branko Grabovac from the mine's exploration department for guiding us in the field and for providing our work in the coal pit as pleasant as possible. We appreciate the help of Medina Mandić with the field work. Thanks go also to Ursula Göhlich (NHMW) for collecting the BU1708 samples. Finally, we thank Hazim Hrvatović (Federal Geological Survey) for his continued support of our studies in Bosnia and Herzegovina. The constructive reviews by Vitaliy Anistratenko (National Academy of Sciences of Ukraine, Kiev) and by an anonymous reviewer improved an earlier draft of the manuscript.

Funding information The field work was supported by the Austrian FWF Project P18519-B17. T.A.N. was supported by an Alexander-von-Humboldt Scholarship and a DFG grant (project no. NE 2268/2-1).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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