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# Middle Miocene Otoliths of Freshwater Fishes from the Vračević Lake (Serbian Lake System)

Katarina Bradić-Milinović<sup>1</sup>, Ljupko Rundić<sup>2</sup> & Werner Schwarzhans<sup>3</sup>

**Abstract.** The Serbian Lake System (SLS) is a key area for early to middle Miocene freshwater environments in southeastern Europe. Here, we describe a rich fossil association of freshwater fish otoliths of late Badenian to early Sarmatian (Serravallian, MN 7+8 zone) age. The studied material was collected from several small outcrops along the Grabovac stream near Vračević. The Vračević locations are part of the Valjevo-Mionica Basin (VMB). We identified nine different species, including two in open nomenclature and three new to science: Aphanius jeani, Aphanolebias bettinae n.sp., Klincigobius andjelkovicae, Klincigobus haraldahnelti n. sp., Klincigobius serbiensis, Klincigobius sp., Ponticola sp., Toxopyge campylus, Toxopyge vracevicensis n.sp. We found that the composition of this fish fauna correlates well with the slightly older fauna from the early to middle Miocene of Klinci. Both localities were most likely part of a continuous environment during the existence of the Valjevo–Mionica Basin. The composition of the community of freshwater gobies from the early to early middle Miocene of southeastern Europe indicates the presence of a "lost" Miocene freshwater goby fish fauna that existed prior to and was unrelated to the Ponto-Caspian fish fauna that prevails today. The new data may prove to be helpful in reconstructing the paleogeographical evolution of the Valjevo-Mionica Basin in detail.

#### **Key words:**

Middle Miocene, otoliths, Vračević, Valjevo-Mionica Basin, Serbian Lake System

Апстракт. Српски језерски систем (SLS) је кључно подручје истраживања слатководне животне средине у ЈИ Европи за време старијег и средњег миоцена. Овде описујемо богату фосилну асоцијацију рибљих отолита од касног бадена до раног сармата (серавалијан, МN 7+8 зона). Проучавани материјал је прикупљен на локалитетима у близини Врачевића, на неколико малих изданака уз поток Грабовац. Локалитет Врачевић је део Ваљевско-мионичког басена (ВМБ). Идентификовали смо девет различитих врста, од којих су две у отвореној номенклатури и три нове у науци: Aphanius jeani, Aphanolebias bettinae n.sp., Klincigobius andjelkovicae, Klincigobius haraldahnelti n.sp., Klincigobius serbiensis, Klincigobius sp., Ponticola sp., Toxopyge campylus, Toxopyge vracevicensis n.sp. Утврдили смо да је састав ове фауне риба у доброј корелацији са нешто старијом фауном

<sup>&</sup>lt;sup>1</sup> Geological Survey of Serbia, Roviniska 12, 11 000 Belgrade, Serbia. E-mail: katarina.bradicmilinovic@gzs.gov.rs

<sup>&</sup>lt;sup>2</sup> University of Belgrade, Faculty of Mining and Geology, Department of Regional Geology, Kamenička 6, 11000 Belgrade, Serbia. E-mail: ljupko.rundic@rgf.bg.ac.rs

<sup>&</sup>lt;sup>3</sup> Natural History Museum of Denmark, Zoological Museum, Universitetsparken 15, 2100 København, Denmark. E-mail: wwschwarz@aol.com.

#### Кључне речи:

средњи миоцен, отолити, Врачевић, Ваљевско-тионички басен, Српски језерски систем раног до средњег миоцена локалитета Клинци. Оба локалитета су вероватно била међусобно повезана током постојања Ваљевско-мионичког басена (VMB). Заједница слатководних гобида од доњег до старије-средњег миоцена југоисточне Европе документује присуство "нестале миоценске фауне слатководних риба- гобида", која је постојала раније и није била повезана са данас преовлађујућом понтокаспијском фауном риба. Нови подаци пружају важне информације за детаљну реконструкцију палеогеографске еволуције Ваљевско-мионичког басена.

#### Introduction

The sediments of the Neogene continental lacustrine systems of the states of the former Yugoslavia have been a subject of research interest among geologists and paleontologists for more than a century. Intramontane basins in Croatia, Bosnia and Herzegovina, and Serbia contained various long-lived freshwater lakes during the late Oligocene and early to middle Miocene (e.g., Harzhauser & Mandic, 2008; Mandic et al., 2010, 2019; Neubauer et al., 2011, 2013, 2015a, b, 2016 and references therein). Generally, two large freshwater systems are recognized: the Dinaride Lake System (DLS) and a younger one, the Serbian Lake System (SLS) (KRSTIĆ et al., 2003, 2007; DE LEEUW et al., 2010; MANDIC et al., 2010, 2012; SANT et al., 2018a, b; NEUBAUER et al., 2020). These two lake systems were first recognized by S. Brusina (1845–1908), a prominent zoologist and paleontologist from Zagreb. Today, a century and half later, the aforementioned authors have built on Brusina's pioneering work and unearthed more details concerning the "great mosaic" of ancient lake systems. During the last 10 years, the DLS has been studied using different approaches. In addition to conventional methods, such as those of biostratigraphy, paleontology, sedimentology, and tectonics, independent chronostratigraphic techniques, such as magnetostratigraphy and radiometric age control, have also been applied (e.g., DE LEEUW et al., 2010; Mandic et al., 2012). This modern integrated approach has led to a more precise determination of the geologic age and an improved understanding of the tectonics that determined the origins of the lakes, the provenance of the sedimentary input, local and regional environmental settings, climate variations, and a variety of biotic and abiotic features, including the level of endemism (De Leeuw et al., 2010, 2011; Mandic et al., 2010, 2012, 2019; Sant et al., 2018a, b). During the last decade, significant attention has also been paid to the system of paleolakes that extended across a wide area of Serbia, the SLS (Neubauer et al., 2016, 2020; Simić et al., 2017; SANT et al., 2018a; MARIĆ et al., 2019; BRADIĆ-MILINOVIĆ et al., 2019). Generally, most published data indicate that the SLS is of middle Miocene age (e.g., Krstić et al., 2012). Krstić et al. (2012) also suggested the presence of a single large lake extending from Belgrade via Northern Macedonia to Greece. Conversely, SANT et al. (2018a) came to the view that a system of lakes stretched over Serbia (i.e., the SLS). Radiometric age dating has provided evidence of the existence of early Miocene (16.9 Ma) lakes in eastern Serbia, resulting in a further modification of the scenario and of the relation between the DLS and SLS with respect to their spatial and temporal overlap (Rundić et al., 2019). It became possible to compare the fossil diversity and evolution of different biota (mostly mollusks) in the SLS with that from the DLS, although most inhabitants of the SLS are considered endemic (Neubauer et al., 2020). These investigations indicate that the SLS was "a stepping stone for many of the mollusk lineages" found in the late Miocene Lake Pannon (NEUBAUER et al., 2020).

Here, we expand on our earlier studies of the fish remains (otoliths and articulated skeletons with otoliths in situ) from lacustrine basins of western Serbia in the Valjevo–Mionica area (BRADIĆ-MILINOVIĆ et al., 2018, 2019). For the first time, we present details concerning the taxonomy and paleoecology of the fresh-

water fishes by means of otoliths from the Vračević paleo-lake and analyze the possible stratigraphic positions of the respective sediments. We found a total of 295 otolith specimens, from which we identify nine freshwater fish species in the sediments of the Vračević paleo-lake, two pertaining to the Cyprinodontidae and seven to the Gobiidae. The composition of the fauna shows some congruence between the Vračević paleo-lake and neighboring Valjevo paleo-lake but also certain differences, which may indicate a difference in time between the two basins.

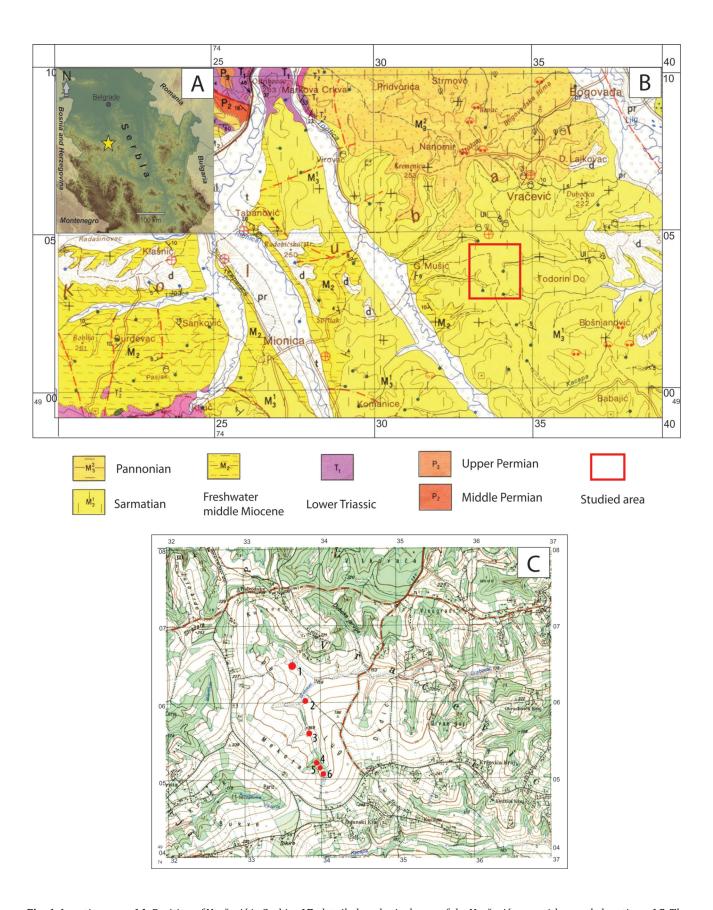
## **Geological Setting**

The Vračević village, which lies north of Mionica in western Serbia, is situated within the large Valjevo-Mionica Basin (VMB; Fig. 1A). The Dinaride basin belongs to a series of Miocene intramontane basins that are distributed across Serbia (Simić et al., 2017; Bradić-Milinović et al., 2018, 2019). It covers an area of 350 km<sup>2</sup> and represents the western part of the Valjevo-Mionica-Belanovica Graben (MAROVIĆ et al., 2007). This two-part graben (Valjevo-Mionica is in the western part and Belanovica in the east) was formed during the Ottnangian-Karpatian and the early Middle Miocene (early Badenian); it became inverted and subject to moderate or weak uplifting in the Quaternary (MAROVIĆ et al., 2007). Based on previous studies as well as data obtained from new drillings, a few cycles of sedimentary rocks and volcano-clastites (ranging from lacustrine to reduced marine and brackish sediments) may reach thicknesses of up to 1,000 m in the center of the basin (e.g., Obradović & Vasić, 2007). The western part of the VMB (Valjevo area) is filled with a succession of lacustrine early Miocene sediments that commonly contain oil shales at the base with tuff intercalations and otherwise consist of sandstone and mudstone to limestone with gravel. Quaternary alluvial and diluvial-proluvial deposits are widely distributed at the surface of the basin area (BRA-DIĆ-MILINOVIĆ et al., 2019 and references therein). The VMB was largely formed on the Jadar block (JB), which represents a northern part of the Jadar-Kopaonik thrust sheet derived from the most distal Adriatic passive margin (SCHMID et al., 2008;

NEUBAUER et al., 2016; BRADIĆ-MILINOVIĆ et al., 2019). The JB is composed of Devonian and Carboniferous predominantly shallow-marine carbonates and a flysch series overlain by Permian and Triassic shallow-marine carbonates that were obducted in the Jurassic by ophiolites of the Western Vardar Ocean (Schmid et al., 2008). The eastern part of the VMB between the Toplica and Ljig Rivers (Vračević, Mionica area) is characterized by restricted marine and lacustrine deposits of Sarmatian and Pannonian age (middle and late Miocene; Fig. 1B).

Lithostratigraphically, the above-mentioned sediments correspond to the Vračević Formation (Jova-NOVIĆ et al., 1994; OBRADOVIĆ & VASIĆ, 2007; LAZAREVIĆ et al., 2013; Rundić, 2017; Bradić-Milinović et al., 2019; Fig. 2). According to most earlier studies, there is no transition between the lower Miocene lacustrine sediments and the middle Miocene marinebrackish ones (e.g., Jovanović et al., 1994). In other words, the Sarmatian restricted-marine sediments are transgressive and unconformable overlay the lower-middle Miocene lacustrine sediments (JOVA-NOVIĆ & DOLIĆ, 1994; DOLIĆ, 1995; LAZAREVIĆ et al., 2013). In addition, there is an ongoing debate concerning the interrelationships among the VMB lacustrine basins in time and space. Much more detailed and varied stratigraphic methods and radiometric age control are required to clarify this issue. The Vračević (Mionica) area is an east-west striking elongated small basin (ca. 70 km long and 15 km wide) formed in the middle Miocene during the maximum extension phase of the southeastern Pannonian Basin (Matenco & Radivojević, 2012; Rundić, 2017; Rundić et al., 2019) that coincided with the Middle Miocene Climatic Optimum (MMCO; MANDIC et al., 2010, 2012; NEUBAUER et al., 2015a, b). The Vračević Basin represented an isolated lacustrine basin that was occasionally flooded from the north by Paratethyan marine-brackish waters during the early to middle Miocene and subsequently by Lake Pannon caspibrackish waters (similar to the water mineralization in the contemporary Caspian Lake).

Paleontological research has been conducted for more than 70 years near Vračević. Among the first researchers, Laskarev (1948) identified remains of *Deinotherium giganteum* from the upper part of the Grabovac Stream. A few years later, Stevanović



**Fig. 1.** Location map. **1A**. Position of Vračević in Serbia; **1B**. detailed geological map of the Vračević area with sample locations. **1C**. The red circles with numbers mark outcrop positions mentioned in the text.

Epo S	ch / tage	General	Regional	Thickness	Lithology	Lithostratigraphy & rocks	Environment
Ш	Upper	Tortonian	Pannonian	0 m	\ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \	Bogovađa Fm. (sand, gravel, silt, clay)	Lacustrine, terrigenous
O - W	Middle	Serravallian	Badenian - Sarmatian	400m		Vračević Fm. (marl, silt, clay, sand, tuff interbeds)	Lacustrine, marine-brackish

Fig. 2. Stratigraphic summary column of the Vračević area and the Vračević Formation. ICS stages according to the ICS Chart v2021/5 (https://stratigraphy.org/chart).

(1953a, b) published first reports concerning marine-brackish, terrestrial, and freshwater mollusks from this area. During a detailed field campaign and geological mapping survey, Filipović et al. (1978) gathered a great amount of new data from the surface and drillings and reported that the basin fill contained marine-brackish and freshwater Sarmatian deposits overlain by Pannonian brackish and freshwater lacustrine deposits. However, over the last 20 years, further detailed paleontological studies have been conducted in a wider area of Vračević; such studies have resulted in a identification of various other fossil remains, including, for example, those of reptiles (Jovanović et al., 2002; Jovanović & Đurić, 2005, 2016), small terrestrial mammals collected from the freshwater sediments of Vračević (MARKOVIĆ, 2003), freshwater mollusks (PRYSJAZHNJUK et al., 2000; Ko-VALENKO, 2004; PRISYAZHNYUK & RUDYUK, 2005), and terrestrial gastropods (Neubauer et al., 2016). Recently, a shallow well drilled at a hill close to the Grabovac Stream yielded marine-brackish Sarmatian and brackish Pannonian sediments (BRADIĆ-MILINOVIĆ et al., 2018). According to these studies and a synthesis published by Jovanović & Đurić (2016), the Sarmatian lacustrine sediments exhibit lateral alternation with restricted marine sediments.

In our study of otoliths from the Vračević Formation, we found exclusively freshwater fish taxa, which were obtained from lacustrine sediments. According to recent publications (Neubauer et al.,

2016; Marković, 2003; Bradić-Milinović et al., 2018), the stratigraphic position of these lacustrine sediments is controversial; this topic is discussed in more detail in the Results section of the present study. In our view, the assessment of the stratigraphic position requires a comprehensive multidisciplinary approach.

#### **Material and Methods**

One part of the studied materials stems from an old collection housed at the Natural History Museum of Belgrade (NHMB) under the inventory number 107/15. The other, larger portion was collected from several small outcrops along the Grabovac Stream near the village of Vračević and is also catalogued at the NHMB under the following inventory numbers: NP-240, NP-332, NP-340, NP-239, NP-333, NP-334, NP-342, NP-335, NP-336, NP-337, NP-338, NP-339, NP-344, NP-346, NP-347, NP-348, NP-349, NP-350, and NP-351. The field study and sampling were conducted in November 2019 (by KBM and LJR). In the study area, a small dry valley with a slow-flowing stream is situated between 138–220 m a.s.l. Six small outcrop sections (up to 2.5 m high) revealed predominantly fine-grained clastic freshwater deposits (Fig. 3). The first outcrop downstream on the northernmost part of the Grabovac Stream (i.e., on a small tributary to the right of the Grabovac Stream - 74 33 680, 49 07 158) contains only the upper part of the stratigraphic section. Further downstream, deeper parts of the section are exposed along the right bank of the stream (Point 2 - 74 33 780, 49 05 789; Point 3 - 74 33 823, 49 05 662; Point 4 – 74 33 997, 49 05 239; Point 5 - 74 34 066, 49 05 113). The last location (point 6 – 74 34 065, 49 05 098) is situated near the mouth of the stream. This location is at 167 m a.s.l. The well-exposed sections (points 4, 5, and 6) were found to the south at a small confluence of the southern dry tributaries with the stream. At point 2, where the majority of the otoliths were found, the four main horizons were separately sampled (Fig. 3; Vr. 2.1-Vr. 2.4). Detailed sampling was also performed at point 4, where three horizons were exposed (Vr. 4.1–Vr. 4.3). Other points (1 and 3) contained only one (point 1) or two (point 3) horizons. At all sites, bulk sediment

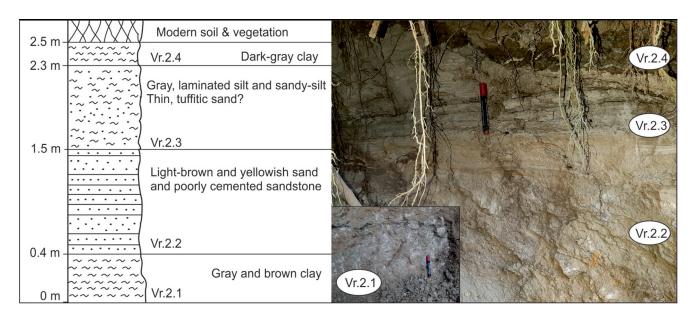


Fig. 3. Example of a local sedimentary succession (Vr.2.1-Vr.2.4) up to 2.5 m thick. (Point 2, Grabovac stream, Vračević)

samples were taken for differents paleontological, palynological, and sedimentological purposes, as each site contains remains of fossil fauna and flora (the size of each sample was about 1 kg).

All samples were processed at the Laboratory of the Geological Survey of Serbia. The photographs were taken with a digital camera mounted on a Wild M400 photomacroscope and remotely controlled from a computer. Individual photographs at different fields of depth were taken of each object and subsequently digitally stacked to produce consistently focused photographs using HeliconSoft's HeliconFocus software. The resulting photographs were enhanced for contrast, exposure, or retouching in Adobe Photoshop, as far as doing so did not affect the morphological image of the otolith.

The abbreviations used are as follows: OL = otolith length; OH = otolith height; OT = otolith thickness; SuL = sulcus length; OsL = ostium length; CaL = caudal length.

## Systematic Paleontology

Order Cyprinodontiformes Rosen, 1964 Family Valenciidae Parenti, 1981 Genus *Aphanius* Nardo, 1827

# Aphanius jeani Reichenbacher & Kowalke, 2009 Fig. 4.1-6

2009 Aphanius jeani - Reichenbacher & Kowalke: fig. 4a-l.

**Material**. 10 specimens in total: 8 specimens, NHMB-NP 240 (point 2, material collected 2002); 2 specimens, NHMB-NP 350 (point 4, material collected 2019).

**Discussion.** Aphanius jeani was described by REICHENBACHER & KOWALKE (2009) from the uppermost Astaracian of the Duero Basin in northwestern Spain, mammal zone MN 7-8, which corresponds to the late Badenian and Sarmatian s.s. of the Central Paratethys. While the stratigraphic timing thus corresponds well with the presumed age of the sediments in Vračević, the rather wide geographic range, which extends from Spain to Serbia, is surprising. Reichenbacher & Kowalke found the symmetrical and high triangular shape with a very low OL:OH index of about 1.0 as the most diagnostic feature to distinguish A. jeani from all other extant or fossil species of Aphanius. All but two specimens from Vračević are well within this range, with OL:OH ratios of 0.93 to 1.02. The largest specimen (Fig. 4.1), however, which is of 1.47 mm in length, is slightly less high-bodied, with an OL:OH ratio of 1.12, while the second largest specimen is of 1.32

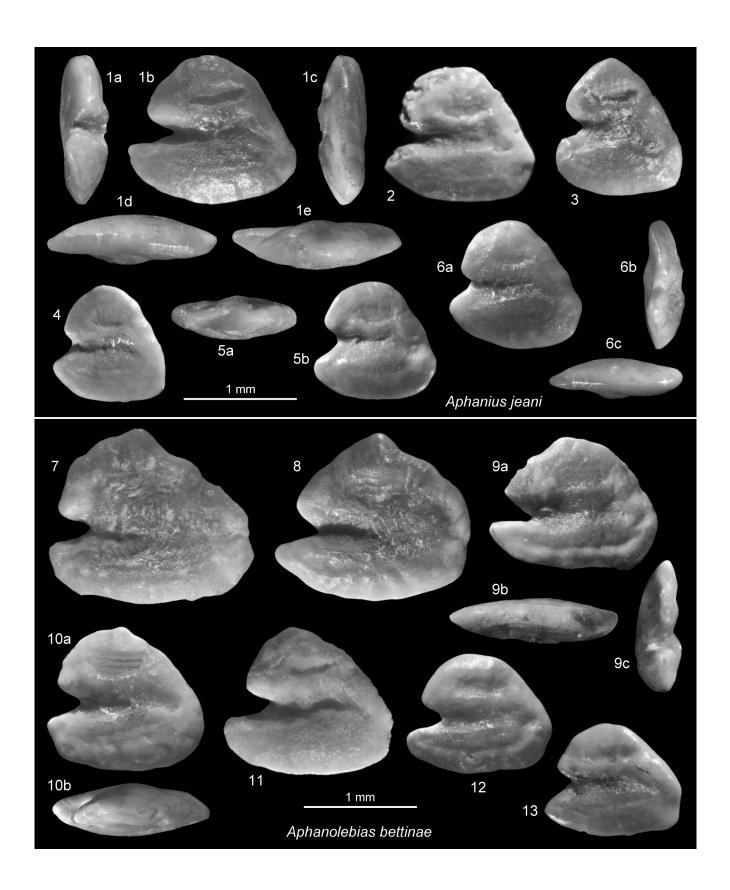


Fig. 4. Cyprinodontid otoliths from Vračević; 1–6. Aphanius jeani Reichenbacher & Kowalke, 2009, NHMB-NP 240; 7–13. Aphanolebias bettinae n. sp., holotype (9), NHMB-NP 340; paratypes (7-8, 10-13), NHMB-NP 332.

mm in length (Fig. 4.2), with an OL:OH ratio of 1.1. However, the largest specimen figured by Reichenbacher & Kowalke (2009; Fig. 4h) is about 0.93 mm in length (measured from their photograph) and also has an OL:OH ratio of about 1.1. We therefore consider the slight increase of the OL:OH ratio with size observed in specimens from both Spain and Serbia as representing an ontogenetic effect.

Genus Aphanolebias Reichenbacher & Gaudant, 2003

# Aphanolebias bettinae n. sp. Fig. 4.7–13

**Material**. 26 specimens in total: 24 specimens from point 2 – NHMB-NP 332 (13 specimens from 2002 and 11 specimens from 2015) and 2 specimens from point 5 – NHMB-NP 351 (2019). Holotype: NHMB-NP 340 (point 2, 2002).

**Holotype**. Fig. 4.9; paratypes: Fig. 4.7–8, 3.10–13; additional material: 17 specimens.

**Etymology**. Named in honor of Bettina Reichenbacher (Munich) in recognition of her outstanding contribution to the understanding of fossil cyprinodontid fishes and her advice regarding the recognition of these otoliths.

**Diagnosis**. Otoliths triangular in shape with a short rostrum, deep and sharp excisura, rounded posterior rim, and forward-positioned middorsal angle. Ratio OL:OH = 1.12–1.28. Space below ostium narrow.

**Description**. Relatively large otoliths for a cyprinodontid with an observed maximum size of 1.8 mm length (holotype 1.5 mm). Otolith outline triangular with a sharp rostrum, a rounded inferior posterior tip, and a variably developed sharp or rounded slightly forward-positioned middorsal angle. OL:OH = 1.12–1.28; OH:OT = 2.7–3.0. Rostrum relatively slender, pointed, 19–26% of OL. Excisura deep and sharp; antirostrum blunter than rostrum and somewhat shorter, 12–16% of OL. Predorsal rim steeper than postdorsal rim, the latter often slightly curved; ventral rim shallow, moderately curved. All rims smooth or slightly and irregularly undulating.

Inner face slightly convex with an inframedian to axially positioned sulcus. Distinction of ostium and cauda gradual, but ostium distinctly longer than cauda and usually deeper. Ostium length to cauda length

ranges from about 1.8 to 2.3. Caudal shallowing with fading margins in largest specimens (Fig. 4.7 and 4.8). Otherwise, cauda slightly flexed with a downward directed tapering termination. Dorsal depression small; ventral furrow distinct, running at center of ventral field. Space of ventral field below ostium relatively narrow. Outer face slightly convex, about as much as inner face, and smooth or irregularly ornamented.

**Discussion**. According to Reichenbacher & Kowal-KE (2009), the shallow ventral rim with the narrow space of the ventral field below the ostium are the most diagnostic characters to define otoliths of the fossil genus Aphanolebias. Thus far, four species have been described pertaining to Aphanolebias (see Reichenbacher et al., 2018) from the early Miocene to the late middle Miocene. The latest stratigraphic record is that of A. sarmaticus Reichen-BACHER, FILIPESCU & MICLEA (2018) from the Sarmatian s.s. from the Apuseni Mountains in Romania. Aphaniolebias bettinae differs from the roughly timeequivalent A. sarmaticus in the higher dorsal rim with a forward-positioned middorsal angle, the deep and sharp excisura combined with the relatively long rostrum and antirostrum, and the ostium being distinctly longer than the cauda. In addition, the fading of the caudal sulcus margin in large specimens has not been observed in any other fossil cyprinodontid otoliths.

Order Gobiiformes Thacker, 2009
Family Gobiidae Cuvier, 1816
Genus *Klincigobius* Bradić-Milinović, Ahnelt & Schwarzhans 2019

## Klincigobius and jelkovicae Bradić-Milinović, Ahnelt & Schwarzhans, 2019

Fig. 5.1-8

2019 *Klincigobius andjelkovicae* – Bradić-Milinović, Ahnelt & Schwarzhans, fig. 6.

**Material**. 60 specimens, NHMB-NP 239 (point 2, 2015).

**Discussion**. This species was described based on articulated skeletons with otoliths in situ from the early Miocene of Klinci (VMB), Serbia (BRADIĆ-MILINOVIĆ et al., 2019). The otoliths of *K. andjelkovi*-

cae are characterized by a prominent preventral projection and a slightly less prolonged but still distinctive postdorsal projection. The sulcus is large and wide with a variably developed and sometimes indistinct or indiscernible subcaudal iugum positioned below the anterior part of the cauda. The ventral furrow is very distinct and deep and regularly curved, clipping the anterior and posterior ventral angles; it begins below the tip of the ostium and terminates at about the tip of the cauda.

Otoliths of *K. andjelkovicae* resemble *K. serbiensis* in many aspects, including the large, wide, and deep sulcus; the shape of the ventral furrow; and the sometimes indistinct, small subcaudal iugum positioned below the anterior part of the cauda. Given a relatively strong degree of variability, *K. andjelkovicae* is best distinguished from *K. serbiensis* in the more slender shape of the otolith, caused primarily by the prominent preventral and postdorsal projections (OL:OH = 1.25–1.40 vs. 1.05–1.20) and the depressed or rounded predorsal region (vs. angular and usually distinct). Furthermore, the postdorsal projection is distinctly more strongly bent outwards in *K. serbiensis* than in *K. andjelkovicae*.

# Klincigobius aff. andjelkovicae Bradić-Milinović, Ahnelt & Schwarzhans, 2019

Fig. 5.9-10

**Material**. 11 specimens, NHMB-NP 333 (point 2, 2015).

**Discussion.** A small number of specimens differs from the typical morphological pattern of *K. andjelkovicae* otoliths in that they show a less depressed, albeit rounded, predorsal angle and shorter preventral and postdorsal projections. They may represent extreme forms of variability of *K. andjelkovicae* or another, closely related species. We therefore allocate them tentatively to *K. andjelkovicae*, while additional specimens would probably rectify the identification.

# Klincigobius haraldahnelti n. sp.

Fig. 5.11-20

**Material**. 81 specimens in total: 80 specimens from point 2 – NHMB-NP 334 (2015) and one spec-

imen from point 4 – NHMB-NP 349 (2019). Holotype: NHMB-NP 342 (point 2, 2015).

**Holotype**. Fig. 5.14; paratypes: Fig. 5.11–5.13, 5.15–5.20; additional material: 44 specimens.

**Etymology**. Named in honor of Harald Ahnelt (Vienna) in recognition of his outstanding contribution to the understanding of extant and fossil Ponto-Caspian gobiid fishes.

**Diagnosis**. Otoliths with a depressed rounded predorsal region and a greatly elevated broad postdorsal region without significant postdorsal projection. OL:OH = 1.03–1.22. Preventral projection moderately developed. Sulcus deep, wide, with small, sometimes indistinct subcaudal iugum below anterior part of cauda. Ventral furrow deep, regularly curved, clipping anterior and posterior ventral angles, not extending beyond tip of sulcus.

**Description**. Small subtriangular otoliths up to about 1.7 mm in length. OL:OH = 1.03–1.22, increasing with size; OH:OT = 3.0–3.4. Dorsal rim distinctly asymmetrical; its anterior region is depressed or broadly rounded, while its posterior region is distinctly elevated and set-off from the anterior region by a notch slightly behind middle of otolith and does not or only slightly extends into the postdorsal projection. Rounded postventral angle usually projects further out than postdorsal angle. Preventral projection moderately developed, but usually distinct. Ventral rim shallow, horizontal, smooth. All rims smooth except postdorsal portion, which is irregularly ornamented.

Inner face almost flat with wide, centrally positioned, and deep sulcus. Dorsal rim of sulcus usually regularly bent without prominent ostial lobe. Ostium more strongly inclined than cauda; entire sulcus inclination 13–23°, inclination of ostium 25–36°. Colliculum poorly defined and indistinct. Subcaudal iugum small, below anterior part of cauda, often indistinct. Dorsal depression indistinct, narrow; dorsal field anteriorly narrowed. Ventral field relatively wide with distinct, deep, and gently and regularly curved ventral furrow running from anterior tip to posterior tip of sulcus and clipping anterior and posterior ventral corners. Outer face slightly convex and smooth.

**Discussion.** *Klincigobius haraldahnelti* is best defined by the distinctive elevation of the posterior region of the dorsal rim, relatively compressed

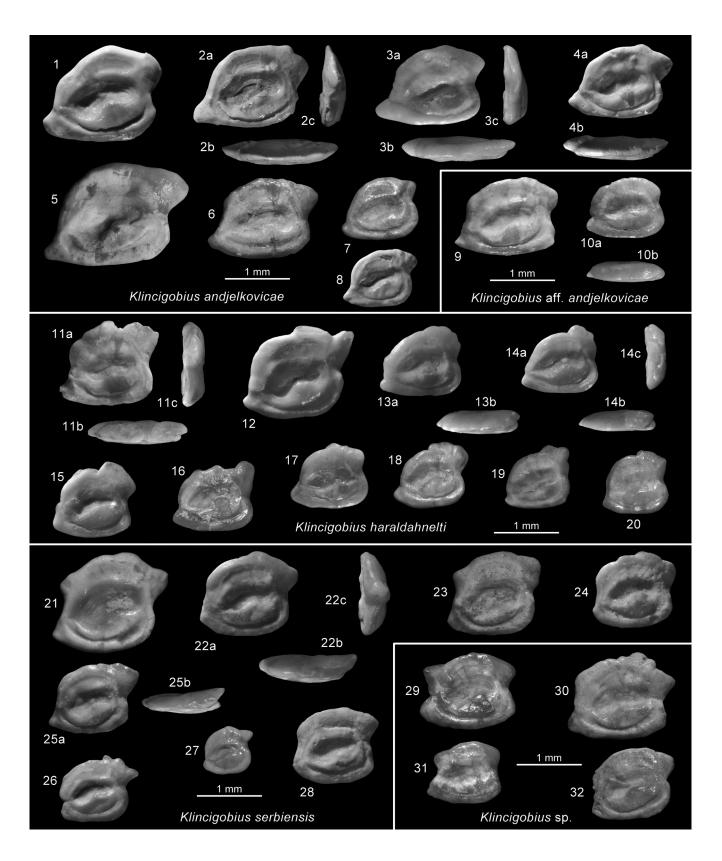


Fig. 5. Otoliths of Klincigobius from Vračević; 1–8. Klincigobius andjelkovicae Bradić-Milinović, Ahnelt & Schwarzhans 2019, NHMB-NP 239; 9–10. Klincigobius aff. andjelkovicae Bradić-Milinović, Ahnelt & Schwarzhans 2019, NHMB-NP 333; 11–20. Klincigobius haraldahnelti n. sp., holotype (14), NHMB-NP 342; paratypes (11-13, 15-20), NHMB-NP 334; 21–28. Klincigobius serbiensis (Gaudant, 1998), NHMB-NP 335; 29-32) Klincigobius sp., NHMB-NP 336.

shape, and low OL:OH ratio of 1.03 to 1.22. It further differs from *K. andjelkovicae* in the lack of a significant postdorsal projection and from *K. serbiensis* in the depressed and rounded predorsal angle.

## Klincigobius serbiensis (GAUDANT, 1998) Fig. 5.21-28

1998 Gobius serbiensis – Gaudant, p. 108, Fig. 2
2019 Klincigobius serbiensis (Gaudant, 1998) – Bradić-Milinović, Ahnelt & Schwarzhans, figs. 3,4, 5, tab. 1

**Material.** 50 specimens in total: 49 specimens from point 2 (2015) – NHMB-NP 335 and one specimen from point 4 (2019) – NHMB-NP 347.

**Discussion**. *Klincigobius serbiensis* is the type species of the genus *Klincigobius* (Bradić-Milinović et al., 2019). It is best recognized by the rectangular shape of the otolith, the compressed proportions (OL:OH = 1.05–1.20); the distinct, sometimes pronounced predorsal angle; the small but distinctly outward bent postdorsal projection; and the relatively short sulcus. For further specific differences, see discussion on *K. andjelkovicae* and *K. haraldahnelti*.

# Klincigobius sp.

Fig. 5.29-32

**Material**. 7 specimens, NHMB-NP 336 (point 2, 2015).

**Discussion**. A few specimens differ significantly from those of the three Klincigobius species described above. Some of them are remarkable for a distinct, projecting, and pointed predorsal angle (Fig. 5.29 and 5.31), which results in all four corners of the otolith being equally strongly developed. In other specimens, the predorsal angle is less pronounced (Fig. 5.30 and 5.32). They all show a faint furrow that ingresses into the ostium from predorsally at the position of the ostial lobe, which is most distinctly developed in the specimen depicted in Figure 5.32. The otoliths have an OL:OH ratio of 1.15-1.25, which is similar to the proportions found in *K. andjelkovicae* and higher than in the two other species. The development of the predorsal angle, however, is more similar to that status observed in K. serbiensis. Based on the currently available specimens, it is not clear whether these characteristics indicate the presence of a further *Klincigobius* species at Vračević or represent some kind of unresolved teratologic deformation.

Genus Ponticola Iljin, 1927

### Ponticola sp.

Fig. 6.1

**Material**. 1 specimen, NHMB-NP 337 (point 2, 2015).

**Discussion**. A single specimen with a characteristic parallelogram shape. Otoliths of *Ponticola* are remarkable for their sole-shaped centrally positioned sulcus (inclined about 15–20°), with a high ostial lobe and without subcaudal iugum. Our specimen has a weak and rounded preventral angle. The postdorsal angle is high and somewhat bent outwards. The single specimen could represent an undescribed *Ponticola* species, which, however, cannot be concluded based on a single specimen. It resembles the extant species *P. kessleri* (GÜNTHER, 1861; for figures, see VASILIEVA et al., 2016). In particular, *Ponticola* sp. shows a rounded postdorsal projection similar to that of *P. kessleri*.

Genus *Toxopyge* Bradić-Milinović, Ahnelt & Schwarz-Hans, 2019

# Toxopyge campylus Bradić-Milinović, Ahnelt & Schwarzhans, 2019

Fig. 6.2-10

2019 *Toxopyge campylus* – Bradić-Milinović, Ahnelt & Schwarzhans, figs. 10, 11, 12

**Material**. 35 specimens, NHMB-NP 338 (point 2, 2015).

**Discussion**. Otoliths of *T. campylus* are characterized by a trapezoidal shape with a blunt preventral angle and a reduced or very small postdorsal angle (OL:OH = 1.05-1.20; OH:OT = 2.5-3.0). The anterior rim is inclined at an angle of  $75-80^{\circ}$ , with only a narrow and shallow incision. The posterior rim is relatively straight and inclined at an angle of mostly  $75-90^{\circ}$ , with a small concavity at the level of the cau-

dal tip and sometimes a rounded and short postdorsal projection. The sulcus is relatively small (OL:SuL=2.0) and narrow; it has a low ostial lobe and is inclined at 8–15°. There is no distinct subcaudal iugum. With the many additional specimens now available, it became clear that the forward inclination of the posterior rim is a less stable character than originally assumed. Stable characters defining the genus remain the small sulcus with a low ostial lobe, the absence of a subcaudal iugum, and the compressed outline.

# **Toxopyge vracevicensis n. sp.** Fig. 6.11–14

**Material.** 14 specimens in total: 11 specimens from point 2 (2015) – NHMB-NP 339, 2 specimens from point 3 (2019) – NHMB-NP 346, and one specimen from point 4 (2019) – NHMB-NP 348. Holotype: NHMB-NP 344 (point 2, 2015).

**Holotype**. Fig. 6.11; paratypes: Fig. 6.12–6.14; additional material: 8 specimens.

**Etymology**. Named after the type locality, Vračević, Serbia.

**Diagnosis**. Otolith shape high triangular with slightly backward positioned dorsal angle. OL:OH = 1.05 – 1.15. Preventral projection distinct; postventral projection rounded; no postdorsal projection. Inner face flat; area between ventral furrow and sulcus bulged. Sulcus small, bow-shaped without ostial lobe, deep, with small colliculum. No subcaudal iugum.

**Description**. Compact and relatively small otoliths reaching sizes of about 1.2 mm in length (holotype 1.15 mm). OL:OH = 1.05-1.15; OH:OT = 2.8. Dorsal rim high; predorsal region slanting; highest point slightly behind middle; postdorsal angle reduced or slightly projecting, not extending beyond broadly rounded postventral corner. Anterior rim inclined at  $63-72^{\circ}$ , undulating, with distinct and pointed preventral projection. Posterior rim inclined at  $75-85^{\circ}$ , with small indentation at level of cauda. Ventral rim shallow, nearly flat, and horizontal. All rims irregularly undulating.

Inner face flat with slightly supramedian, deep sulcus. Sulcus narrow, bow-shaped with regularly curving dorsal rim, and without ostial lobe or subcaudal iugum. Sulcus inclination  $10-15^{\circ}$ . Colliculus

distinctly smaller than sulcus. Dorsal field with indistinct dorsal depression. Ventral field with distinct, deep, gently curved, short ventral furrow running from lower margin of ostium to lower margin of cauda. Area between ventral furrow and sulcus distinctly bulged. Outer face convex, smooth.

**Discussion**. *Toxopyge vracevicensis* shows a distinct and rather unmistakable otolith readily recognized by the combination of its triangular outline; the small, deep, bow-shaped sulcus; lack of a subcaudal iugum; and the bulged area of the inner face below the sulcus.

### **Evaluation and Discussion**

## Stratigraphic considerations

The small basins of the SLS have been the subject of numerous studies and publications over the last decades (see Simić et al., 2017; SANT et al., 2018a). Certain studies that focused on western Serbia have confirmed the existence of large economic reserves (e.g., Jadar Basin and lithium deposits) with significant importance for the national economy. Despite all the research activity and the many geologists involved, however, no consensus has yet been reached regarding the stratigraphic position of the abovementioned deposits. The VMB, which is located further to the southeast, is of less economic potential (as it only contains oil shale), and the chronostratigraphy of the Miocene of the studied sediments is also still under debate and has been the subject of considerable research activity during recent years (e.g., Jovanović & Đurić, 2016; Neubauer et al., 2015b, 2016, 2020; Bradić et al., 2018, 2019). In our opinion, the Vračević Formation represents a key area to consider when attempting to resolve the position of the different lacustrine rocks and their relationships with nearby marine-brackish sediments.

LASKAREV (1948) was the first to identify remains of *Deinotherium giganteum* from the upper part of the Grabovac Stream, which he based on six molar teeth and fragments of the lower jaw. Laskarev assumed that *Deinotherium giganteum* would occur from the lower Sarmatian to the Pannonian (the so-called Lower Congeria strata), but it is now considered to

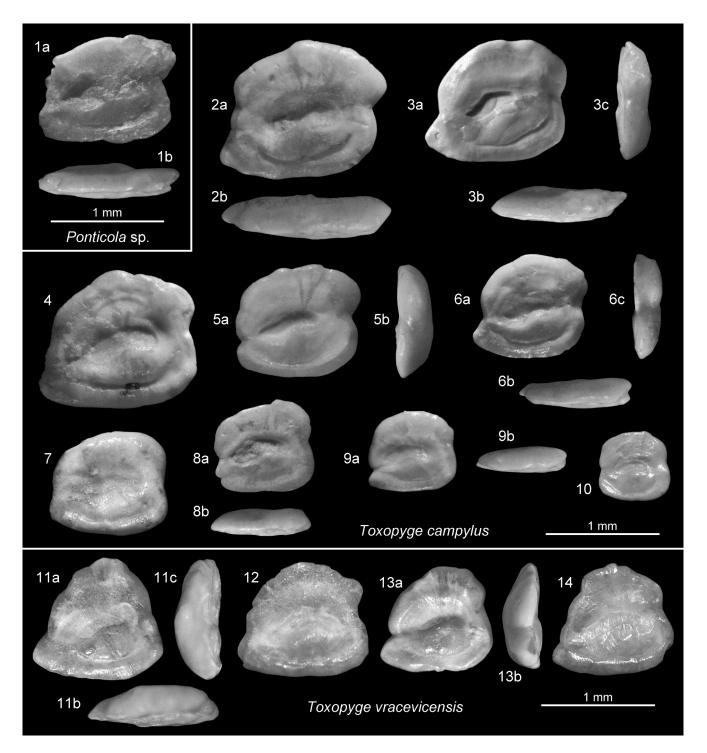


Fig. 6. Otoliths of Ponticola and Toxopyge from Vračević; 1. Ponticola sp. NHMB-NP 337; 2–10. Toxopyge campylus Bradić-Milinović, Ahnelt & Schwarzhans 2019, NHMB-NP 338; 11–14. Toxopyge vracevicensis n. sp., holotype (11), NHMB-NP 344; paratypes (12-14), NHMB-NP 339.

range from the mammal zone MN6 to MN 12 (late Langhian to late Tortonian; Gagliardi et al., 2021). Its teeth and bones were found in a meter-thick, gray sandy-mica clay, which otherwise only contained

shells of Helix shell detritus. Based on the local lithological column and the observation that the site is almost 2 km away from the Grabovac Stream and at a higher elevation (190–200 m), LASKAREV (1948) be-

lieved that the *Deinotherium*-bearing beds pertain to the Pannonian stage (i.e., the lower Congeria strata). Soon thereafter, Stevanović (1953 a, b) suggested that "the Grabovac stream is a key location" for the contact between brackish Sarmatian (clearly documented by fossil mollusks and foraminifers) and a synchronous freshwater series of marls, "fish shales", and tuffs (documented primarily by freshwater gastropods). His view was shared by Filipović et al. (1978), Prysjazhnjuk et al. (2000), Kovalenko (2004), and Prisyazhnyuk & Rudyuk (2005). The sampled locations near Vračević are also known for a rich micromammal fauna that was used for biostratigraphic correlation based on mammal zones by Marković & Pavić (2005) and MARKOVIĆ & MILIVOJEVIĆ (2010), who concluded that the fauna belongs to zone MN 7/8. MARKOVIĆ & MILIVOJEVIĆ (2010) placed the Vračević Formation in the Sarmatian s.s., but the mammal zone MN7/8 actually extends over the late Badenian and the Sarmatian s.s. (GRAD-STEIN et al., 2012).

In the assessment of the non-marine mollusks from Vračević, Neubauer et al. (2016) also concluded that they dated to the Sarmatian s.s.. However, our analysis of the fish otoliths shows a close relationship with that of Klinci, which is considered to be of late early to early middle Miocene age (Bradić-Milinović et al., 2019), and no resemblance to any of the relatively well-known Sarmatian s.s. fish associations from the Central Paratethys and its marine-brackish water transitional realms. While this difference is certainly to a significant extent due to paleoenvironmental differences, in our opinion, it points to a slightly older age than Sarmatian s.s., perhaps late Badenian.

During the fieldwork conducted in 2019, specific samples were taken for microfossil and palynological analysis. The palynological evaluation showed that the moist lower area around the paleo-lake was inhabited by grassy and shrubby plants (*Compositopollenites, Tubifloridites, Nyssa, Taxodium,* Taxodiaceae-Cupresaceae, Polypodiaceae ferns, Shizaceae) and that the somewhat drier parts were inhabited by *Carya, Engelhardti, Corylus, Betula, Myrica,* Ericaceae, and Sapotaceae. The interior region of the mainland, the coastal and hilly areas, were occupied by deciduous forests (*Quercus, Castanea, Platanus,* Juglandaceae, *Castanopsis, Rhus, Tilia*, and others), while the hilly mountainous areas were inhabited by representatives of

conifers (Pinus, Picea, Abies, Podocarpus, and Cedrus). Considering the large amounts of coniferous pollen in almost all of the prepared sample, it appears that the lake was open to the hilly mountainous environments nearby, allowing the pollen to be carried by the wind and deposited in the sediments. Furthermore, it is noticeable that the samples did not contain much organic matter, such as large plant tissues or other fragments of organic matter. The identified genera and species indicate the presence of a warm, Mediterranean-type vegetation. Their dominance is evident in relation to the completely sporadic presence of cooltemperate types found in younger Neogene sediments (middle Miocene). The plant association is interpreted to have existed in a warm, relatively humid climate, with sporadic representatives of a drier climate. This palynological association is characteristic of the MN7 zone, ranging from the upper Badenian to lower Sarmatian s.s.

We expect that future research on a greater geographical area (e.g., the small streams around Gornji Mušić) as well as radiometric dating of tuffs within this series could result in a more precise chronostratigraphic dating of the Miocene Vračević Lake.

## **Faunal Comparison and Evolution**

Setting the scene. The middle Miocene was a time of global climate change, expressed in the Miocene Climate Optimum (MCO; 17-14.7 Ma), followed by the Middle Miocene Climate Transition (MMCT; 14.2-13.8 Ma; SHEVNELL et al., 2004; HoL-BOURN et al., 2015). Global cooling events with temperature decreases in the range of 3–5°C have been dated to 13.8 Ma and 13.2 Ma (BÖHME et al., 2011, and literature cited therein). Rich fossil plant assemblages and mammal faunas have been used to establish paleoclimatic models for this time interval (UTESCHER et al., 2007; BÖHME et al., 2011; BRUCH et al., 2011; IVANOV et al., 2011). Although the paleoclimatic concepts vary in certain details, there appears to be a consensus that the Serbian terrain was characterized by a humid, warm climate with high precipitation levels and predominantly evergreen vegetation during the time of the MCO. Overall cooling and the seasonality of temperature and precipitation in-

creased in the area during the times of the MMCT, and the vegetation gradually changed to a mixed mesophytic forest environment with more deciduous elements (UTESCHER et al., 2007; BRUCH et al., 2011; IVANOV et al., 2011). However, cold winter temperatures are hypothesized to have only occurred from the Sarmatian s.s. onwards (UTESCHER et al., 2007; IVANOV et al., 2011). In the aquatic freshwater environment, Neubauer et al. (2015a) noted a first major faunal turnover in mollusks at the end of the MCO, however, their hypothesis was subsequently modified to a more gradual transitional model (Neubauer et al., 2020). An analysis of the freshwater mollusks from Vračević by Neubauer et al. (2016) pointed to the Vračević Formation having been deposited in "a standing or slow moving, probably highly vegetated, lacustrine environment."

The fish fauna from the Vračević Formation shows significant diversity in a freshwater system, as indicated by the otoliths. The fauna consists exclusively of freshwater species and is dominated by gobies (seven species) but also contains cyprinodontids (two species). Marine or brackish water faunal elements are completely lacking judging by the well-known and rich late Badenian and Sarmatian s.s. otolith associations described by, for example, BRA-TISHKO et al. (2015), SCHWARZHANS et al. (2017a-e), and REICHENBACHER et al. (2018). None of the otolithbased fish species from Vračević have been found in any of the coeval marine to brackish water environments of the Central Paratethys, and none of the marine to brackish water species of the coeval Central Paratethys were found in Vračević, with the possible exception of a single specimen of *Ponticola* sp. This lack of shared faunal elements is particularly relevant in respect to the transitional marine otolithbased fauna recently described by Reichenbacher et al. (2018) from the Sarmatian s.s. of the Apuseni region in the southeastern part of the Central Paratethys. This fauna also contained a rich goby association and a single cyprinodontid species, which are, however, all absent from Vračević.

Instead, the Vračević faunal association shows a close similarity with the older late early to early middle Miocene assemblage of Klinci (Bradić-Milinović et al., 2019). The unique combination at Klinci of well-preserved skeletons and in situ otoliths led to the de-

scription of four freshwater goby species of three different genera. Furthermore, it facilitated the recognition of a vanished early Neogene European freshwater fish fauna through the correlation of the in situ otoliths with previously described isolated otoliths from other regions (Reichenbacher & Weid-MANN, 1992; REICHENBACHER, 1993; BRADIĆ-MILINOVIĆ et al., 2019). This early Neogene European freshwater fish fauna was assumed to have disappeared during the MMCT following the MCO. In this scenario, the Klinci fauna would have been just before the turnover in the freshwater fauna. The Vračević fish fauna now contains three species already known from Klinci, namely Klincigobius andjelkovicae, K. serbiensis, and Toxopyge campylus. The fourth species in Klinci, Rhamphogobius varidens, and the genus Rhamphogobius are no longer evident at Vračević. Two new species occur in Vračević in the Klincigobius and Toxopyge lineages, namely K. haraldahnelti and T. vračevićensis (in addition to a potential further species denoted as Klincigobius sp.; Fig. 7). These findings indicate the continuation of the early Neogene European freshwater goby fauna well into the time of the MMTC (at least, in the SLS).

Another interesting aspect is the occurrence of cyprinodontid fishes at Vračević, which was not the case in the earlier Klinci fauna. The relationships of the two identified cyprinodontids are perhaps unexpected. Aphanolebias bettinae represents the last recorded species of this extinct genus, together with A. sarmaticus Reichenbacher, Filipescu & Miclea (2018) from the Sarmatian s.s. of the Apuseni region in Romania. It is remarkable that two different species of Aphaniolebias occurred at the same time in the same general area, one in a brackish environment (A. sar*maticus*) and the other in freshwater (*A. bettinae*). More surprising perhaps is the second cyrpinodontid in Vračević, Aphanius jeani Reichenbacher & Kowalke (2009), which was previously only known from timeequivalent strata of the Iberian Peninsula. These findings indicate the potential of the species to have spread across a certain marine distance, as is known to be the case for certain extant cyprinodontids (see, e.g., Valdesalici et al., 2015).

**Conclusions**. In our assessment of the fish fauna from Klinci, we concluded that it represented a European freshwater goby assemblage with lineages that

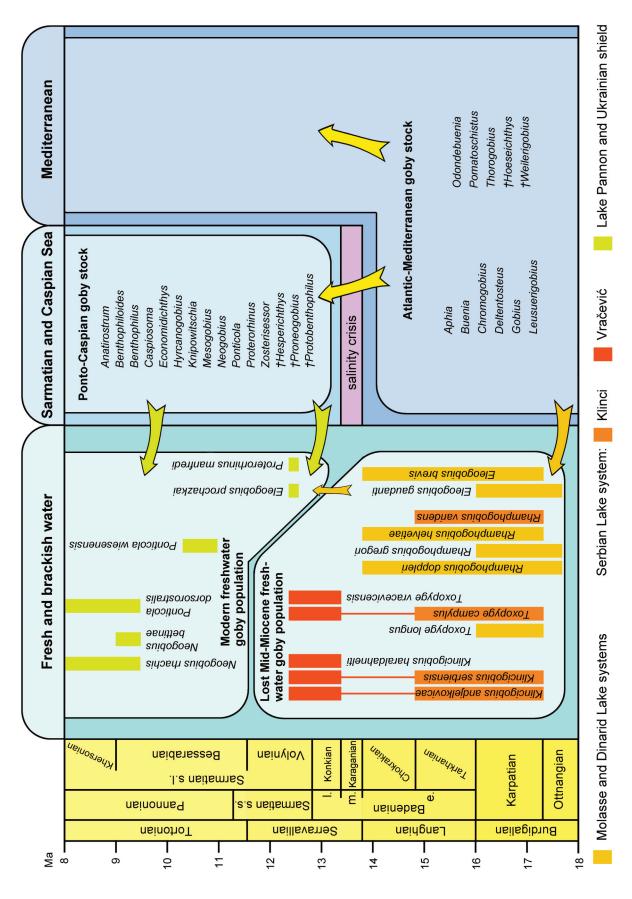


Fig. 7. The freshwater gobies from Vračević in the context of the composition of the "lost mid-Miocene freshwater goby population" depicting the species and ranges of the genera Eleogobius, Klincigobius, Rhamphogobius, and Toxopyge. Arrows indicate assumed migration routes and provenances.

became extinct after the MCO (BRADIĆ-MILINOVIĆ et al., 2019). Now, we have to consider that the faunal change in terms of freshwater fishes was probably more gradual in certain areas where climate conditions remained suitable for a continuation of those lineages, for instance in the SLS. An alternative hypothesis would be that the turnover did indeed occur later than in the marine Paratethyan environment, with the latter having been triggered by the middle Badenian salinity crisis (Bratishko et al., 2015; Schwarzhans et al., 2017a-e; Fig. 7). The limited data currently available seem to favor a more gradual transition, which suggests that relict faunas may have survived for a certain period of time in restricted areas; such a phenomenon may be captured here by the samples taken in the Vračević area. Such an interpretation would be consistent with the more gradual transformation observed with regard to freshwater and terrestrial mollusks (Neubauer at al., 2016, 2020). NEUBAUER et al. (2020) considered the mollusk fauna of the late middle Miocene of the SLS as a "stepping stone from the earlier DLS freshwater fauna to the Lake Pannon fauna." Such an evolution is not seen in the fish fauna and particularly not in the goby associations. The late early and early middle Miocene freshwater goby association evident from Klinci carried on into the Vračević lake system with minor changes and some putative endemic evolutions but did not give rise in any way to the Ponto-Caspian fish fauna or that of the Sarmatian Sea or Lake Pannon. Instead, it vanished completely from the European freshwater systems, probably not much later than the end of the MMCT. The fish fauna of Lake Pannon and Ponto-Caspian fish fauna originated from the marine to transitional marine Sarmatian s.s. fish fauna, as is well documented in Bratishko et al. (2015), Schwarz-HANS et al. (2017a-e). This interpretation is also consistent with the recent analysis of the transitional Sarmatian s.s. fish fauna from the Apuseni region by REICHENBACHER et al. (2018).

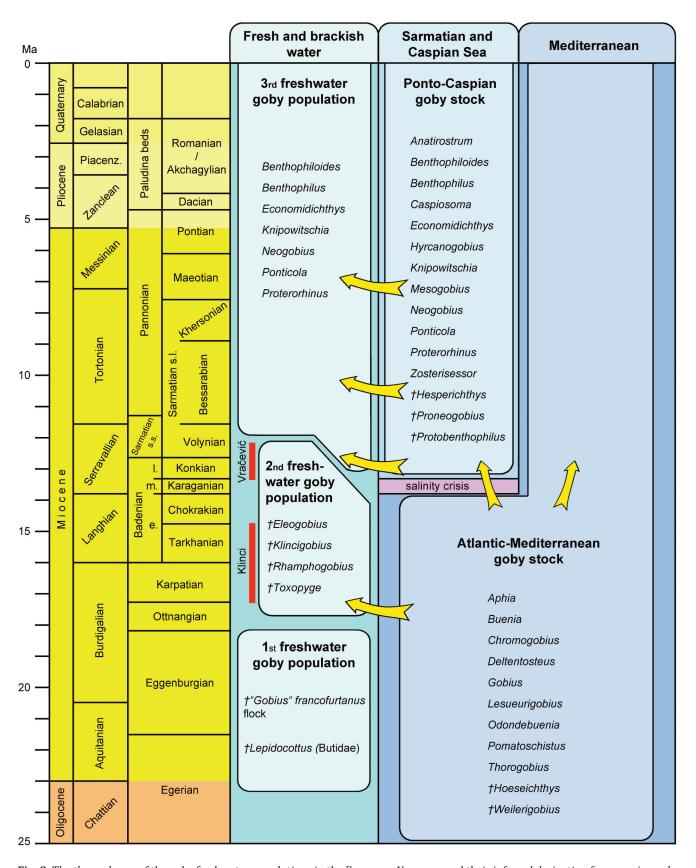
### **Conclusions and Outlook**

The rich otolith-based fish fauna from Vračević represents an additional piece in the puzzle of the history of the European freshwater fish fauna. The asso-

ciation is dominated by gobies, and the composition is extremely similar to the slightly older one previously described from Klinci (Bradić-Milinović et al., 2019), which was based on articulated skeletons with otoliths in situ. The emerging picture is that of a rich late early to middle Miocene freshwater goby fauna in southeastern and central Europe that likely derived from a contemporary Mediterranean/Paratethyan goby stock (Fig. 7). It does not seem to be related to either an earlier late Oligocene to early Miocene freshwater goby association known from central Europe (REICHENBACHER, 2000; GIERL et al., 2013) or to the late Miocene freshwater goby stock that has been observed in Lake Pannon (Schwarzhans, 2010 and literature cited therein) and Ukraine (BRATISHKO et al., 2017). In addition, it appears to have evolved at a time when the Paratethyan Sea had already been separated from the world ocean (Fig. 8) and may have given rise to the modern Ponto-Caspian goby stock. The freshwater goby fauna of Vračević and Klinci shows no overlap with the coeval marine to brackish water goby associations of the adjacent Central Paratethys (Schwarzhans et al., 2017c, 2020; Reichenbacher et al., 2018). The same is true for the cyprinodontid species found in Vračević as compared to the species from the coeval brackish sediments of the Apuseni region (RE-ICHENBACHER et al., 2018).

The otolith association from Vračević described here also exemplifies the new insights that can be expected when studying fossil European freshwater fish faunas from various locations and time intervals. We are aware that many more such faunas can be explored for freshwater fish otolith associations, particularly in southeastern Europe. The exact timing and sequence of faunal turnovers and shifts in the currently recognized three subsequent freshwater goby populations will certainly be subject to refinement once further comparable lake sediments have been studied. In addition, we hope that further studies of biotic and abiotic traits in the sediments of Vračević and Klinci will make it possible to better constrain the exact stratigraphic age of the fish fauna that it contains.

We plan to further expand our investigation in the area of the VMB (e.g., the small streams around Gornji Mušić) in order to arrive at a more complete picture of the evolution of the Vračević Lake and its



**Fig. 8.** The three phases of the goby freshwater populations in the European Neogene, and their inferred derivation from marine goby assemblages. The position of the two goby assemblages studied from the Serbian Lake System (SLS), Klinci, and Vračević are highlighted. Arrows indicate assumed migration routes and provenances.

fauna during the Miocene and a better understanding of its chronostratigraphic position.

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### References

- Böhme, M., Winklhafer, M. & Ilg, A. 2011. Miocene precipitation in Europe: Temporal trends and spatial gradients, *Palaogeography, Palaeoclimatology, Palaeoecology*, 304: 212–218.
- Bradić-Milinović, K., Rundić, Lj. & Bojić, Z. 2018. A contribution for stratigraphy of the Miocene of Vračević (Valjevo-Mionica Basin). *Proceedings of XVII Congress of the Geologists of Serbia*, 1: 110–114.
- Bradić-Milinović, K., Ahnelt, H., Rundić, Lj. & Schwarzhans, W. 2019. The lost freshwater goby fish fauna (Teleostei, Gobiidae) from the early Miocene of Klinci (Serbia). *Swiss Journal of Paleontology*, 138: 285–315.
- Bratishko, A., Schwarzhans, W., Reichenbacher, B., Vernihorova, Y. & Ćorić, S. 2015. Fish otoliths from the Konkian (Miocene, early Servallian) of Mangy shalk (Kazakhstan) testimony of an early endemic evolution in the Eastern Paratethys. *Palaontologische Zeitschrift*, 89: 839–889.
- Bratishko, A., Kovalchuk, O. & Schwarzhans, W. 2017. Bessarabian (Tortonian, late Miocene) fish otoliths from a transitional freshwater-brackish environment of

- Mykhailivka, southern Ukraine. *Palaeontologia Electronica*, 20.3.44A: 1–13.
- Bruch, A., Utescher, T., Mosburgger, V. & NECLIME members, 2011. Precipitation patterns in the Miocene of Central Europe and the development of continentality. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 304: 202–211.
- DE LEEUW, A., MANDIC, O., VRANJKOVIC, A., PAVELIC, D., HARZ-HAUSER, M., KRIJGSMAN, W. & KUIPER, K. F. 2010. Chronology and integrated stratigraphy of the Miocene Sinj Basin (Dinaride Lake System, Croatia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292 (1–2): 155–167.
- De Leeuw, A., Krijgsman, W., Kuiper, K. & Hrvatović, H. 2011. A chronostratigraphy for the Dinaride Lake System deposits of the Livno-Tomislavgrad Basin: the rise and fall of a long-lived lacustrine environment. *Stratigraphy*, 8: 29–43.
- Dolić, D. 1995. Valjevo basin. In: Mihajlović, Đ. & Dolić, D. (Eds.): *Lacustrine and brackish Neogene of western part of Yugoslavia*. IGCP Project 329, Belgrade.
- Filipović, I., Marković, B., Pavlović, Z., Rodin, V. & Marković, O. 1978. Osnovna geološka karta SFRJ 1:100.000. Tumač za list Gornji Milanovac L 34-125. 137 [Basic Geologic Map of Former Yugoslavia 1:100 000. Explanatory booklet for the Sheet Gornji Milanovac in Serbian]. Savezni geološki zavod, Beograd.
- GAGLIARDI, F., MARIDET, O. & BECKER, D. 2021. The record of Deinotheriidae from the Miocene of the Swiss Jura Mountains (Jura Canton, Switzerland). *bioRxiv*, the preprint server for Biology: 1–28.
- Gaudant, J. 1998. L'ichthyofaune des eaux continentals miocenes de Serbie (Yugoslavie): une revision. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 207: 107–123.
- GIERL, C., REICHENBACHER, B., GAUDANT, J., ERPENBECK, D. & PHARISAT, A. 2013. An extraordinary gobioid fish fossil from southern France. *PLoS ONE*, 8: e64117.
- Gradstein, M., F., Ogg, G., J. & Hilgen, J., F. 2012. On the Geologic Time Scale. *Newsletters on stratigraphy*, 45 (2): 171–188.
- Gunther, A. 1861. Second list of Siamese Reptiles. *Proceedings of the Zoological Society of London*, 4: 187–189.
- Harzhauser, M. & Mandic, O. 2008. Neogene lake systems of Central and South-Eastern Europe: faunal diversity, gradients and interrelations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 260: 417–434.

- Holbourn, A., Kuhnt, W., Kochhann, K., Andersen, N. & Meier, S. 2015. Global perturbation of the carbon cycle at the onset of the Miocene Climatic Optimum. *Geology*, 42 (2): 123–126.
- Ivanov, D., Utescher, T., Mosburgger, V., Syabryaj, S., Djordjević-Milutinović, D. & Molchanoff, S. 2011. Miocene vegetation and climate dynamics in Eastern and Central Paratethys (Southeastern Europe). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 304: 262–275.
- Jovanović, M. & Đurić, D. 2005. Fosilna herpetofauna sela Vračević kod manastira Bogovađa (Centralna Srbija). [Fossil herpetofauna of the village of Vračević near the monastery of Bogovađa (Central Serbia) in Serbian]. Proceedings of the 14th Congress of Geologists of Serbia and Montenegro. 78–80.
- Jovanović, G. & Đurić, D. 2016. Mollusks and ectothermic vertebrates from the Middle Miocene (Sarmatian) Lake Vračević (Serbia). In: Mandić O. et al. (Eds.). Lake Basin Evolution. RCMNS Interim Colloquium & Croatian Geological Society Limnogeology Workshop, 20-24 May 2016, Zagreb, 28–30.
- Jovanović, M., Đurić, D. & Marković, Z. 2002. Tertiary reptiles of the central part of the Balkan peninsula, 67–75. *Proceedings of the 11th Ordinary General Meeting of Societas Europea Herpatologica* (SEH), Zalec, Slovenia, July 13–17, 2001. Biota 3 (1–2).
- Jovanović, O. & Dolić, D. 1994. New discovery of Sarmatian in the vicinity of Tabanović (Valjevo-Mionica basin). *Vesnik*, 46 (A, B): 183–192.
- Jovanović, O., Grgurević, D. & Zupančić, N. 1994. The Neogene sediments in Valjevo-Mionica basin. *Vesnik*, 46: 207–222.
- Kovalenko, V. 2004. Lymnaeidae iz mestonahodždeni Trijebine i Vračević (Lymnaeidae from localities Trijebine and Vračević), Serbia. *Bulletin de l'Academie Serbe des Sciences et des Arts* 42, 327–339.
- Krstić, N., Savić, LJ, Jovanovć, G. & Bodor, E. 2003. Lower Miocene lakes of the Balkan Land. *Acta Geologica Hungarica*, 46 (3): 291–299.
- Krstić, N., Knežević, S. & Pavić, S. 2007. Fauna of Large Middle Miocene Lake of Serbia. *Joannea Geologie und Paläonologie* 9: 51–54.
- Krstić, N., Savić, Lj. & Jovanović, G. 2012. The Neogene Lakes on the Balkan Land. *Geološki anali Balkanskoga poluostrva*, 73: 37–60.
- Laskarev, V. 1948. About the findings of Deinotherium in Serbia. *Bulletin Natur. Hist. Mus.* (In Serbian), 1 (A), 1–20.

- Lazarević, Z., Milivojević, J., Bogićević, K. & Nenadić, D. 2013. Early Miocene flora from the Valjevo-Mionica Basin (Western Serbia). *Neues Jahrbuch für Geologie und Palaeontologie Abhandlungen*, 267 (3): 297–307.
- MANDIC O., DE LEEUW A., VUKOVIĆ B., KRIJGSMAN W., HARZHAUSER M. & KUIPER, K.F. 2010. Palaeoenvironmental evolution of Lake Gacko (Bosnia and Herzegovina): impact of the middle Miocene climatic optimum on the Dinaride Lake System. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 299: 475–492.
- MANDIC, O., DE LEEUW, A., BULIĆ, J., KUIPER, K. F., KRIJGSMAN, W. & JURIŠIĆ-POLŠAK, Z. 2012. Paleogeographic evolution of the Southern Pannonian Basin: 40Ar/39Ar age constraints on the Miocene continental series of Northern Croatia. *International Journal of Earth Sciences (Geologische Rundschau)*, 101: 1033–1046.
- Mandic, O., Hajek-Tadesse, V., Bakrač, K., Reichenbacher, B., Grizelj, A. & Miknić, M. 2019. Multiproxy reconstruction of the middle Miocene Požega palaeolake in the southern Pannonian Basin (NE Croatia) prior to the Badenian transgression of the Central Paratethys Sea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 516: 203–219.
- Marić, D., Srećković-Batoćanin, D., Vasić, N., Radisavljević, M. & Đekić, T. 2019. History of the Belanovica (Serbia) Neogene lake basin inferred from petrological and geochemical data. *Geologia Croatica*, 72 (1): 5–18.
- Marković, Z. 2003. The Miocene small mammals of Serbia, a review. In: Reumer, J.W.F. & Wessels, W. (Eds): Distribution and migration of Tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn. *Deinsea* 10: 393–398.
- Marković, Z. & Milivojevic, M. 2010. The Neogene Small Mammals from Serbia Collection Methods and Results. *Bulletin of the Natural History Museum*, 3: 105–114.
- MARKOVIĆ, Z. & PAVIĆ, S. 2005. MN7/8 locality of fossil mammals in Vračevići (central Serbia). 14<sup>th</sup> Congress of geologist of Serbia and Montenegro with international participation, 77.
- MAROVIĆ, M., TOLJIĆ, M., RUNDIĆ, Lj. & MILIVOJEVIĆ, J. 2007. *Neoalpine Tectonics of Serbia*. Serbian Geological Society, 87 pp.
- Matenco, L. & Radivojević, D. 2012. On the formation and evolution of the Pannonian Basin: Constraints derived from the structure of the junction area between the Carpathians and Dinarides. *Tectonics*, 31(6): TC6007.
- NEUBAUER, T. A., MANDIC, O. & HARZHAUSER, M. 2011. Middle

- Miocene freshwater mollusks from Lake Sinj (Dinaride Lake System, SE Croatia; Langhian). *Archiv fur Molluskenkunde*, 140: 201–237.
- Neubauer, T. A., Mandic, O. & Harzhauser, M. 2013. The middle Miocene freshwater mollusk fauna of Lake Gacko (SE Bosnia and Herzegovina): taxonomic revision and paleoenvironmental analysis. *Fossil Record*, 16: 77–96.
- Neubauer, T. A., Harzhauser, M., Georgopoulou, E., Kroh, A. & Mandic, O. 2015a. Tectonics, climate, and the rise and demise of continental aquatic species richness hotspots. *PNAS*, 112 (37): 11478–11483.
- Neubauer, T. A., Harzhauser, M., Kroh, A., Georgopoulou, E. & Mandic, O. 2015b. A gastropod-based biogeographic scheme for the European Neogene freshwater systems. *Earth-Science Reviews*, 143: 98–116.
- Neubauer, T., Harzhauser, M., Mandic, O. & Jovanović, G. 2016. The late middle Miocene non-marine mollusk fauna of Vračević (Serbia): filling a gap in Miocene land snail biogeography. *Bulletin of Geosciences*, 91 (4): 731–778.
- Neubauer, T. A., Mandic, O. Jovanović, G. & Harzhauser, M. 2020. The Serbian Lake System: a stepping stone for freshwater molluscs in the middle Miocene. *Papers in Paleontology*, 1–37.
- Obradović, J. & Vasić, N 2007. *Neogene lacustrine basins of Serbia*. Serbian academy sciences et arts, Monographs 662, Department of Mathematics, Physics and Geo Sciences, 3, 310 pp, Beograd (in Serbian, English summary).
- Prysjazhnjuk, V., Kovalenko, V. & Krstić, N. 2000. On the terrestrial and fresh-water mollusks from Neogene of western Serbia. In: Кагамата, S. & Janković, S. (Eds.), Geology and metalogeny of the Dinarides and the Vardar Zone: 219–224. Academy of Science and Arts of Republic of Srpska, Banja Luka Serbian Sarajevo.
- Prisyazhnyuk, V.A. & Rudyuk, V.V. 2005. Bulimidae I Planorbidae (Mollusca, Pulmonata) iz mestonakhozhdeniya Vrachevich (Serbiya). In: Gozhik, P.F. (Ed.). Biostratyhrafichni kryterii rozchlenuvannya ta korelyatsii vidkladiv fanerozoyu Ukrainy [prevod in koji jezik ]. Natsionalna Akademiya Nauk Ukrainy, Instytut geologichykh nauk, Paleontologischne tovarystvo, 224–232.
- REICHENBACHER, B. 1993. Mikrofaunen, Palaogeographie und Biostratigraphie der miozanen Brack und Sußwassermolasse in der westlichen Paratethys unter besonderer Berucksichtigung der Fisch-Otolithen. Senckenbergiana lethaea, 73 (2), 277–374.

- REICHENBACHER, B. 2000. Das brackisch-lakustrine Oligozän und Unter-Miozän im Mainzer Becken und Hanauer Becken: Fischfaunen, Paläoökologie, Biostratigraphie, Paläogeographie. *Courier Forschungsinstitut Senckenberg*, 222: 1–143.
- REICHENBACHER, B., FILIPESCU, S. & MICLEA, A. 2018. A unique middle Miocene (Sarmatian) fish fauna from the coastal deposits in the eastern Pannonian Basin (Romania). *Palaeobiodiversity and Palaeoenvironments*, 99: 177–194.
- REICHENBACHER, B. & GAUDANT, J. 2003. On *Prolebias meyeri* (Agassiz) (Teleostei, Cyprinodontiformes) from the Oligo-Miocene of the Upper Rhinegraben area, with the establishment of a new genus and a new species. *Eclogae geologica Helvetiae*, 96: 509–520.
- Reichenbacher, B. & Kowalke, T. 2009. Neogene and present-day zoogeography of killifish (*Aphanius* and *Aphanolebias*) in the Mediteranean and Paratethys areas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 281: 43–56.
- REICHENBACHER, B. & WEILDMANN, M.1992. Fisch-Otolithen aus der oligo-/miozanen Molasse der West-Schweiz und der Haute-Savoie (Frankreich). Stuttgarter Beitrage zur Naturkunde Serie B (Geologie und Palaontologie), 184: 1–83.
- Rundić, Lj., 2017. The Valjevo-Mionica basin. In: Simić et al. (Eds.): *Evolution in Neogene Intramontane Basins in Serbia Field trip guide*. EGU series, Emile Argand Conference-13th Workshop on Alpine Geological Studies, Serbia-Zlatibor, September 2017, 20-28. Faculty of Mining and Geology, Belgrade
- Rundić, Lj, Vasić, N., Banješević, M., Prelević, Gajić, V., Kostić, B. & Stefanović, J. 2019: Facies analyses, biostratigraphy and radiometric dating of the Lower-Middle Miocene succession near Zaječar (Dacian basin, eastern Serbia). *Geološki anali Balkanskoga poluostrva*, 80 (2): 13–37.
- Sant, K., Mandic, O., Rundić, Lj., Kuiper, K. & Krijgsman, W. 2018a. Age and evolution of the Serbian Lake System: integrated results from Middle Miocene Lake Popovac. *Newsletter on Stratigraphy*, 51 (1): 117–143.
- Sant, K., Andrić, N., Mandic, O., Demir, V., Pavelic, D., Rundić, Lj., Hrvatović, H., Matenco, L. & Krijgsman, W. 2018b. Magneto-biostratigraphy and paleoenvironments of the Miocene freshwater sediments of the Sarajevo-Zenica Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 506: 48–69.

- Schwarzhans, W. 2010. *The otoliths from the Miocene of the North Sea Basin*. Backhuys Publishers, Leiden & Margraf Publishers, Weikersheim, 352 p.
- Schwarzhans, W., Carnevale, G., Bannikov, F., A., Japundžić, S. & Bradić, K. 2017a. Otoliths in sizu from Sarmatian (Middle Miocene) fishes of the Paratethys. Part I: *Atherina suchovi* Switchenska, 1973. *Swiss Journal of Paleontology*, 136: 7–17.
- Schwarzhans, W., Carnevale, G., Bannikov, F., A., Japundžić, S. & Bradić, K. 2017b. Otoliths in situ from Sarmatian fishes of the Paratethys. Part II: Gadidae and Lotidae. *Swiss Journal of Paleontology*, 136: 19–43.
- Schwarzhans, W., Ahnelt, H., Carnevale, G., Japundžić, S., Bradić, K. & Bratishko, A. 2017c. Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part III: tales from the cradle of the Ponto-Caspian gobies. *Swiss Journal of Paleontology*, 136: 45–92.
- Schwarzhans, W., Carnevale, G., Japundžić, S., & Bradić-Milinović, K. 2017d. Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part IV: Scorpenide, Labridae and Gobiesocidae. *Swiss Journal of Paleontology*, 136: 93–108.
- Schwarzhans, W., Carnevale, G., Japundžić, S. & Bradić-Milinović, K. 2017e. Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part V: Bothidae and Soleidae. *Swiss Journal of Paleontology*, 136: 109–127.
- Schwarzhans, W., Brzobohatý, R. & Radwańska, U. 2020. Goby otoliths from the Badenian (middle Miocene) of the Central Paratethys from the Czech Republic, Slovakia and Poland: A baseline for the evolution of the European Gobiidae (Gobiiformes; Teleostei). *Bolletino della Società Paleontologica Italiana*, 59: 125–173.
- Schmid, S. M., Bernoulli, D., Fugenschuh, B., Matenco, L., Schefer, S., Schuster, R., Tischler, M. & Ustaszewski, K. 2008. The Alpine-Carpathian-Dinaridic orogenic system: correlation and evolution of tectonic units. *Swiss Journal of Geoscience*, 101: 139–183.
- Shevnell, E., A., Kennett, P., J. & Lea, W., D. 2004. Middle Miocene Southern ocean cooling and Antarctic cryosphere expansion. *Science*, 305 (5691): 1766–1770.
- Simić, V., Životić, D., Andrić, N. & Rundić, Lj., 2017. Evolution of Neogene Intramontane Basins in Serbia-Field Trip Guide. EGU series, Emile Argand Conference-13th Workshop on Alpine Geological Studies, Serbia-Zlatibor, September 2017, 58pp. Faculty of Mining and Geology, Belgrade.

- Stevanović, P. 1953a. Stratigraphic relations in the northern part Mionica Basin. *Herald SAN* (Stratigrafski odnosi u severnom delu Mioničkog basena. *Glasnik SAN*), 5 (1): 64–65.
- Stevanović, P. 1953b. Sarmatian deposits between rivers Ljig and Ribnica (Mionica basin). *Herald SAN* (Sarmatske naslage između reka Ljiga i Ribnice (Mioniočki basen). *Glasnik SAN*), 5 (2): 269–277.
- Utescher, T., Djordjević-Milutinović, D., Bruch, A. & Mosbrugger, V. 2007. Paleoclimate and vegetation change in Serbia during the last 30 Ma. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253: 141–152.
- Valdesalici, S., Langeneck, J., Barbieri, M., Castelli, A. & Maltagliati, F. 2015. Distribution of natural populations of the killifish *Aphanius fasciatus* (Valencienns, 1821) (Teleostei: Cyprinodontidae) in Italy: past and current status, and future trends. *Italian Journal of Zoology*, 82 (2): 212–223.
- Vasilieva, E.D., Schwarzhans, W.W., Medvedev, D.A. & Vasiliev, V.P. 2016. Cryptic species of Ponto-Caspian bighead goby of the genus *Ponticola* (Gobiidae). *Journal of Ichthyology*, 56: 1–18.

#### Резиме

## Средњомиоценски отолити слатководних риба из језера Врачевић (Српски језерски систем)

Српски језерски систем (CJC) је термин који обухвата "мрежу" мањих или већих језерских басена који су егзистовали у старијем и средњем миоцену у Србији. Питање њихове изолованости или пак узајамне повезаности у том временском оквиру је врло актуелна тема. Појединачни басени су били тема бројних истраживања последњих неколико деценија (видети у нпр. Simić et al., 2017; SANT et al., 2018а и тамо цитиране референце). Одређене студије које су се фокусирале на западну Србију потврдиле су економски важне резерве сировина (нпр. Јадарски басен, јадарит), које су од изузетног националног значаја. Ваљевско-мионички басен (ВМБ) има мањи економски потенцијал (уљни шкриљци) али има одређену перспективу у том смислу. Међутим, о хроностратиграфском положају језерских седимената у овим басенима се и даље расправља и још увек није постигнута сагласност о тачном времену њиховог настанка (видети нпр. Jovanović & Đurić, 2016; Neubauer et al., 2015b, 2016, 2020; Bradić-Milinović et al., 2018, 2019). Проучаване локације у атару Врачевића познате су и по богатој фауни ситних сисара, која је коришћена за биостратиграфска зонирања. Утврђено је да те континентално-језерске наслаге одговарају зони МН 7/8 (Маккоvić & Pavić, 2005; Маккоvić & Мilivojević, 2010) тј. да припадају сармату s.str. Слично тврде и Neubauer et al. (2016) бавећи се анализом слатководних мекушаца из потока Грабовац.

По нашем мишљењу, овде проучавани седименти формације Врачевић имају шири временски оквир и укључују и старије пакете седимената (млађи баден). То је у складу са проценом да се сисарска зона МН 7/8 заправо протеже од горњег бадена до сармата s.str. (Gradstein et al., 2012). Сагледавајући целокупан литостратиграфски стуб миоцена у ВМБ са неколико циклуса језерске седиментације, формација Врачевић представља кључну литостратиграфску јединицу за решавање положаја различитих језерских седимената и њиховог односа према оближњим морско-бракичним наслагама. Циљ овог рада је да се то питање појасни и документује на основу анализе слатководних риба односно њихових отолита.

Из неколико малих, метарских изданака уз поток Грабовац (атар села Врачевић, ВМБ) прикупљен је занимљив и доста бројан фаунистички материјал. У ситнозрним кластитима континентално-језерске серије, пронађено је укупно 287 примерака отолита који идентификују девет врста слатководних риба палео-језера Врачевић (две припадају фамилији Cyprinodontidae и седам фамилији Gobiidae). Детерминисане су следеће врсте: Aphanius jeani, Aphanolebias bettinae n.sp., Klincigobius andjelkovicae, Klincigobus haraldahnelti n.sp., Klincigobius serbiensis, Klincigobius sp., Ponticola sp., Toxopyge campylus, Toxopyge vracevicensis n.sp. Нађена рибља фауна представља још један део "слагалице" која ће омогућити потпуније и реалније сагледавање еволуције слатководних риба у Европи. У асоцијацији доминирају представ-

ници гобида чији састав је врло сличан нешто старијој, претходно описаној фауни отолита из села Клинци (палео-језеро Ваљево) где су откривени добро очувани скелети риба са отолитима in situ (Bradić-Milinović et al., 2019). Састав фауне указује на одређену подударност између два палео-језера, али и на одређене елементе који могу указивати на временску (стратиграфску) разлику међу њима. Анализа рибљих отолита показује блиску везу са фауном из Клинаца, за коју се сматра да је ограничена на млађи доњи миоцен - старији средњи миоцен (Bradić-Milinović et al., 2019). С друге стране, та фауна не показује сличност ни са једном од релативно добро познатих сарматских s.str. асоцијација риба из централног Паратетиса и њиховим прелазима ка морско-бракичним водама. То је сигурно у великој мери последица палеоеколошких разлика, али, по нашем мишљењу, указује и на нешто старије време од сармата, можда горњи тј. млађи баден. С тог аспекта посматрано, може се претпоставити да богата фауна слатководних гобида у интервалу млађи доњи миоцен - старији средњи миоцен у централној и југоисточној Европи, води порекло од тадашњих медитеранских тј. паратетиских гобида (сл. 7). Чини се да та фауна није повезана са старијим, млађе олигоценским и старије миоценским заједницама слатководних гобида познатим из средње Европе (Reichenbacher, 2000, GIERL et al., 2013), као ни са савременијим слатководним гобидима који су познати из језера Панон (Schwarzhans, 2010 и тамо наведена литература) и Украјине (Вкатізнко et al., 2017). Слатководна фауна гобида Врачевића и Клинаца не показује преклапање са, временски сличним, морским и бракичним гобидама суседног Централног Паратетиса (Schwarzhans et al., 2017c, 2020; Reichenbacher et al., 2018). Исто важи и за ципринодонтидне врсте пронађене у Врачевићу у поређењу са оним из синхроних бракичних седимената Апусена (Reichenbacher et al., 2018).

Од раније је познато да је средњи миоцен био период значајних климатских колебања (Shevnell et al., 2004; Holbourn et al., 2015). Према нашој претходној анализи фауне риба из Клинаца, закључили смо да она представља европску

слатководну асоцијацију гобида која је изумрла већ с почетком тзв. средњемиоценске климатске транзиције (СМКТ, 14.2-13.8 мил. год.). Такве климатске промене догодиле су се после дужег периода стабилне и оптималне климе у миоцену односно тзв. миоценског климатског оптимума (МКО, 17-14.7 мил.год.) (Holbourn et al., 2015; Bradić-Milinović et al., 2019). Резултати анализе рибље фауне из Врачевића, сугеришу да је фаунистичка промена међу слатководним рибама вероватно била постепенија у неким областима у којима су временски услови остали погодни за даљу егзистенцију те фауне, као што је на пример Српски језерски систем (СЈС). Компаративна анализа фауне отолита из Клинаца и Врачевића, показује да постоје три заједничке врсте (Klincigobius andjelkovicae, K. serbiensis and Toxopyge campylus). Четврта врста у Клинцима, Rhamphogobius varidens, и род Rhamphogobius више нису присутни у Врачевићу. Две нове врсте се јављају у Врачевићу унутар родова Klincigobius и Toxopyge, и то K. haraldahnelti и T. vračevićensis (плус потенцијално још једна врста означена као Klincigobius sp.) (сл. 7). Ова открића указују да старија неогена европска фауна слатководних гобида егзистује и у време СМКТ у систему српских језера. Алтернативна хипотеза била би да се фаунистички преокрет заиста догодио касније него у морском Паратетису тј. касније је покренут средњобаденском кризом салинитета (Вкатізнко et al. 2015, Schwarzhans et al. 2017a-e) (сл. 7). Чини се да тренутно доступни подаци фаворизују прву опцију тј. постепенији прелаз, који нуди потенцијал реликтним фаунама да преживе одређени временски период у ограниченим областима (а ово се можда догодило са фауном Врачевића). Такво тумачење било би у складу са постепеном трансформацијом примећеном код слатководних и копнених мекушаца (Neubauer et al., 2017, 2020). Ови аутори сматрају да је фауна мекушаца млађег средњег миоцена СЈС-а "одскочна даска тј. прелаз од старије слатководне фауне Динарског језерског система према фауни језера Панон" (NEUваиек et al., 2020). Ипак, такав развој се не види у фауни риба, а посебно не у фауни гобида.

Асоцијација слатководних гобида млађег доњег и старијег средњег миоцена, уочена код фауне Клинаца, наставила је егзистенцију и у језеру Врачевић са мањим променама и неким, претпостављено ендемским развојем. Она ни на који начин није имала утицаја на рибљу фауну сарматског мора и језера Панон или Понто-каспијску фауну риба. Уместо тога, потпуно је нестала из европских слатководних система, вероватно не много касније од краја СМКТ. Фауна језера Панон као и Понто-каспијска фауна, настала је од морских до прелазних сарматских s.str. бракичних форми риба, и то су добро документовали Вкатізнко et al. (2015) и Schwarzhans et al. (2017a-e). Сагласност у том смислу даје и анализа прелазне сарматске s.str. фауне риба из регије Апусена (RE-ICHENBACHER et al., 2018).

Фауна отолита из Врачевића такође илуструје нове приступе који се могу очекивати при даљем проучавању европских фосилних фауна слатководних риба са различитих локација и временских интервала. Свесни смо да подручје југоисточне Европе пружа много више потенцијала када говоримо о отолитима слатководних риба. Тајминг и редослед фаунистичких преокрета (квалитативних промена) и померања који су довела да тренутно знамо да постоје три сукцесивне популације слатководних гобида (сл. 8), сигурно ће бити још боље појашњени након што се проуче нови локалитети са сличним и упоредивим језерским седиментима (фаунама). Такође се надамо да ће даља проучавања биотичких и абиотичких својстава у седиментима ширег подручја Врачевића и Клинаца, омогућити боље ограничавање тачне стратиграфске старости рибље фауне. У том смислу, планирамо да проширимо даље истраживање на подручју ВМБ (нпр. мали потоци око Горњег Мушића) како бисмо дошли до потпуније слике еволуције језера Врачевић и његове фауне током старијег и средњег миоцена и бољег разумевања хроностратиграфског положаја тих седимената.

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