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The lost freshwater goby fish fauna (Teleostei, Gobiidae) from the early Miocene of Klinci (Serbia)

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Abstract

Freshwater gobies played an important role in the Miocene paleolakes of central and southeastern Europe. Much data have been gathered from isolated otoliths, but articulated skeletons are relatively rare. Here, we review a rich assemblage of articulated gobies with abundant otoliths in situ from the late early Miocene lake deposits of Klinci in the Valjevo freshwater lake of the Valjevo-Mionica Basin of Serbia. The fauna was originally described by Anđelković in 1978, who noted many different fishes, including one goby (*Gobius multipinnatus* H. v. Meyer 1848), and was subsequently revised by Gaudant (1998), who collapsed all previously recognized species into a single gobiid species that he described as new, namely *Gobius serbiensis* Gaudant 1998. Our review resulted in the recognition of three highly adaptive extinct freshwater gobiid genera with four species being divided among them: *Klincigobius andjelkovicæ* n.gen. and n.sp., *Klincigobius serbiensis* (Gaudant 1998), *Rhamphogobius varidens* n.gen. and n.sp., and *Toxopyge campylus* n.gen. and n.sp. Otoliths were found in situ in all four species, which allowed for the allocation of multiple previously described otolith-based species to these extinct gobiid genera. With the help of correlations among isolated otoliths, it is now possible to outline putative paleobioprovinces of fishes in the early Miocene freshwater lakes of central and southeastern Europe. The gobiid freshwater fauna from the early to early middle Miocene of Europe was found to not be related to any of the extant European freshwater or brackish water gobies. Instead, they likely represented an earlier cycle of freshwater adaptation in a warm, subtropical environment that vanished after the Miocene Climate Optimum at c. 14 Ma, when it gave way to a new phase of freshwater goby adaptation that led to the present day Ponto-Caspian goby stock.

Keywords Gobiidae · *Klincigobius* · *Rhamphogobius* · *Toxopyge* · Otoliths in situ · Serbian Lake System

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Introduction

The early and middle Miocene was a time with numerous ephemeral freshwater lakes across the Dinarid Mountains in Bosnia-Herzegovina, Croatia, and Serbia (Neubauer et al. 2015a, b; Mandić et al. 2019).

Klinči, which is located in the Valjevo Lake of the Valjevo-Mionica Basin of Serbia, is known for its superbly preserved fish fauna, with many articulated skeletons with otoliths having been found in situ. Anđelković (1978) was the first to describe this fauna and identified nine different fish species representing various families and orders (*Aspius elongatus*, *Aspius* cf. *elongatus*, *Gobius multipinnatus*, *Leuciscus macrurus*, *Lepidocottus brevis*, *Smerdis* cf. *macruurus*, *Smerdis formosus*, *Smerdis elongatus* and *Perca uraschista*). Anđelković studied skeletons only and did not comment on otoliths in her study. In 1998, Gaudant reviewed the Klinči collection and recognized only a single species of the family Gobiidae, into which he collapsed the various taxa reported by Anđelković in 1978 and described it as *Gobius serbiensis*. He also figured a drawing of an otolith found in situ in one of the skeletons.

Here, we conduct a new review of the Klinči fish fauna and discover multiple otoliths in situ in many of the skeletons. We come to the same conclusion as Gaudant in recognizing all fishes as representing gobies, but we also find a considerably larger diversity reflected in the presence of three distinct genera, all of which are extinct, with four species, one of which is now referred to as *Klincigobius* n.gen. *serbiensis* (Gaudant 1998).

Materials and methods

The articulated skeletons, many of which have otoliths in situ, were recovered from a water well on a private property in the village of Klinči (Western Serbia). In total, 21 skeletons were recovered, 19 of which have otoliths in situ; in addition, six isolated otoliths were found scattered in the sediment. The fish specimens are preserved in a thin-bedded gray marlstone. Most of the articulated skeletons are very well preserved.

The skeletons with otoliths were carefully prepared and mechanically cleaned. Otoliths are principally preserved with the inner side down and, therefore, obscured, which requires extraction to study their inner face. We concluded that the extraction of otoliths is recommended not only to better describe their morphological characters but also to lessen the risk of damage to or potential future loss of otoliths. In the course of extracting otoliths, it is important to handle them carefully to avoid possible damage. The dorsal pterygiophore formula follows Birdsong et al.

(1988). The morphological terminology of otoliths was established by Koken (1891) and modified by Weiler (1942), and by Schwarzhan (2014) for gobioid otoliths.

Regional geology and locality

As one of major geotectonic units, the Dinarides represent the southern branch of the Alpine-Carpathian-Dinaride system, which resulted from the collision of Europe and Asia that followed the closure of the Vardar Ocean during the late Jurassic and Cretaceous (Dimitrijević 1997; Karamata 2006; Schmid et al. 2008) (Fig. 1a). Intra-oceanic subduction resulted in the emplacement of the ophiolites and associated mélanges over the Adriatic passive continental margin (Western Vardar Ophiolites). The following Cretaceous–Eocene orogenic shortening was characterized by the development of a number of thrust sheets subdivided into internal and external thrust belts (i.e., the Internal and External Dinarides—Schmid et al. 2008; Simić et al. 2017 and references therein). The Internal Dinarides consist of composite units, including Palaeozoic metamorphic basement covered by Mesozoic carbonates carrying ophiolites in the upper structural position (e.g., Jadar–Kopaonik composite block [Schmid et al. 2008]). The Internal Dinarides were affected by a slow rate of extension during the upper Oligocene—lower Miocene (Erak et al. 2017; Sant et al. 2018b), which accelerated to reach peak tectonic activity at ca. 15–14 Ma (Stojadinović et al. 2017; Andrić et al. 2017; Sant et al. 2018a). This extension was associated with the opening of the Pannonian Basin (Bálazs et al. 2016) and led to the reactivation of former sutures, thrusts, and nappe contacts as low-angle normal faults, which exhumed parts of the tectonic units that had been deeply buried by previous tectonic events (Matenco and Radivojević 2012; Toljić et al. 2013; Erak et al. 2017; Simić et al. 2017). The final stage of shortening and extension in the Dinarides provided accommodation space for the formation of numerous freshwater lakes (e.g. the Serbian Lake System [SLS] in the internal Dinarides, see Krstić et al. 2003, 2012; Harzhauser and Mandić 2008). This extensional tectonic phase coincided with the Middle Miocene Climatic Optimum (Mandić et al. 2012; Neubauer et al. 2015a,b). These predominantly intramountain lakes were separated from the Paratethys Sea and inhabited by an endemic fauna (Harzhauser and Mandić 2008, Krstić et al. 2012; Neubauer et al. 2015a; Sant et al. 2018a). During the Miocene, these lakes were subjected to several phases of expansion and reduction governed by a combination of climate variability and geodynamic processes (Simić et al. 2017). Glacio-eustatic sea level changes additionally controlled the depositional architecture of the basins (Anđelković et al. 1991; Mandić et al. 2012; Sant et al. 2018b). In the Internal Dinarides, intense magmatic

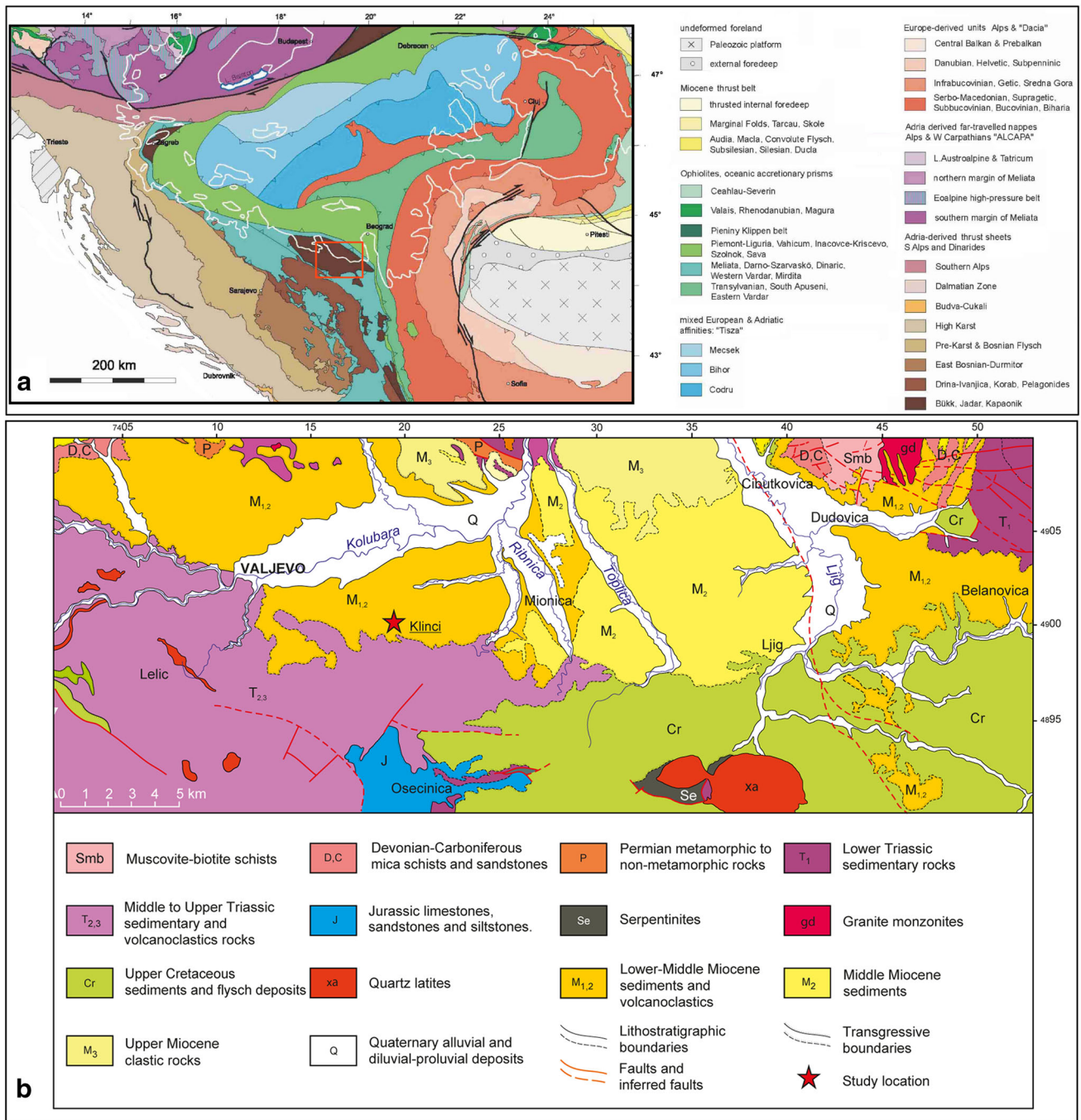


Fig. 1 Location plate and stratigraphy. **a** Tectonic map of the Alps–Carpathians–Dinarides orogenic system (Schmid et al. 2008). The red rectangle indicates the location of the Valjevo–Mionica Basin (VMB), as shown in 1b. White contour indicates Badenian transgression. The

distribution of the overlying Miocene basins is not shown. **b** Simplified geological map of the VMB (modified after Filipović et al. 1971 and Mojsilović et al. 1975) with position of studied site (Klinci) marked

activity influenced the lake chemistry and thus played a significant role in affecting the basin fill (Cvetković et al. 2004, 2013; Bradic-Milinovic et al. 2018). In the Dinarides of Serbia, a combination of all of these factors resulted in the formation of at least three lacustrine depositional cycles in a period ranging from the Oligocene to the middle Pliocene (Dolić 1998; Krstić et al. 2003, 2012; Obradović

and Vasić 2007; Simić et al. 2017). The endemic nature of the fauna and absence of other independent age controls make establishing chronostratigraphic and regional correlations among the individual lake phases difficult (Rundic 2013; Simić et al. 2017). Accordingly, it is still debated whether all of these basins were formed simultaneously as a part of one huge lake or as separate and isolated entities

(i.e., system of lakes) that may have been connected at certain points in time (Krstić et al. 2012; Sant et al. 2018a; Rundić et al. 2018).

The Valjevo-Mionica Basin (VMB) is situated in western Serbia. It covers an area of 350 km² and represents the western part of the so-called Valjevo-Mionica-Belanovica Graben (Fig. 1b). This graben was formed during the Ottnangian–Karpatian and later became inverted (Marović et al. 2007). Based on geophysical data, the Neogene series (lacustrine to marine-brackish and brackish sediments) may reach thicknesses of up to 1000 meters at the center of the basin (e.g., Obradović and Vasić 2007; Kilpatrick 2010) (Fig. 2). The overall surrounding area of the basin is characterized by the complex geological setting of the Jadar Block terrain (Dimitrijević 1997; Karata 2006). In the northern neighboring area, Paleozoic units are represented with Devonian, Carboniferous, and Permian metamorphic to non-metamorphic rocks, whereas the Lower Triassic sedimentary unit is mostly exposed in tectonic contact with these older units (Filipović et al. 1971; Mojsilović et al. 1975). The southern bordering area of the basin is composed of Upper Triassic sedimentary

rocks, which prevail in the south-eastern part, and Upper Cretaceous sedimentary or flysch deposits, which dominate the south-western part of this area (Fig. 1b). The eastern part of the VMB between the Toplica and Ljig Rivers (Mionica area) is characterized by marine-brackish and lacustrine deposits of Sarmatian and Pannonian age (middle and late Miocene), which disconformably overlay the older early Miocene deposits of the SLS. The western part of the VMB in the 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 (Figs. 1b, 2).

During more than a century of investigations of the VMB, varied and sometime contradictory views have been published concerning the age of the basin infill (Rundić 2017 and references therein). Sedimentological and paleontological data have been used as the main criteria for age determination. Fossil assemblages of freshwater gastropods, bivalves, ostracods, fishes, and floral remains exhibit an endemic character and are insufficient for biostratigraphic purposes (Rundić 2013). Up to now, no independent age control by means of radiometric and magnetostratigraphic data has been performed (Rundić 2017).

The following brief historical review of the most important studies in this field reflects the diversity of the debate over the development of the VMB. The first study of the VMB's ichthyofauna by Gorjanović-Kramberger (1884), in which he described *Leuciscus macrurus* Agassiz and suggested an early Miocene Aquitanian (i.e., Egerian-Egenburgian) age for the so-called “Šušeočka White Rock” in village Šušeočka, near the village of Beloševac (which is located near Klinči). A few years later, Žujović (1889) arrived at a similar conclusion based on fish remains identified as *Gobius (Cottus) brevis*. More than 70 years later, during field campaigns for the Basic Geological Map, 1:100,000 (sheets Valjevo and G. Milanovac), authors classified these sediments as a middle to upper Miocene sedimentary succession (Filipović et al. 1971; Mojsilović et al. 1975; Stevanović 1953, 1957, 1977). At approximately the same time, Anđelković (1970, 1978) published a study on a fossil fish assemblage from thin-layered marls of a well drilled in the village of Klinči, which she considered as being of middle Miocene age. Conversely, other researchers suggested a lower Miocene (Petković and Novković 1975), lower Miocene–Egerian-Egenburgian (Dolić 1983, 1984), or Egenburgian-Ottangian age (Anđelković et al. 1991) based on lithofacies comparison, fossil assemblages of freshwater mollusks, ostracods, and fish and floral remains. Anđelković and Anđelković (1985)

Stratigraphy		Thickness (m)	Lithology	Lithostratigraphy & rocks	Environment
M I O C E N E	Late Pannonian	0		Bogovada Fm. (sand, gravel, silt, clay)	Lacustrine, terrigenous
		200		Vračević Fm. (marl, silt)	Marine-brackish, brackish
	Middle Sarmatian	400		Mađarlija Fm. (sand, gravel, marl, silt, tuff interbeds)	
		Early unspecified	600		Tabanović Fm. (marl, silt, tuff)
	800			Valjevo Fm. (marl, silt, clay, tuff, sand)	
1000			Mionica Fm. (laminated marl, silt, tuff, sandstone, pyrobituminous marl, conglomerate, and breccia)		
Upper Cretaceous		600		Limestone, sandstone, conglomerate	Marine (Neotethys Ocean)

Fig. 2 Generalized stratigraphic section of the VMB compiled from Jovanović et al. (1994), Obradović and Vasić (2007), Šajnović et al. (2008), and Lazarević et al. (2013). Formation thicknesses not to scale. Klinči marl level with fish fossils indicated by grey bar

presented an overview of earlier studies and offered a revised view of the stratigraphy of the Klinci marls. On the basis of an analysis of the stratigraphic range of fossil fishes that they had identified, they concluded that the Bela Stena (White Rock) series corresponds to the Egenburgian-Ottungian age. However, their identifications have subsequently been reviewed by Gaudant (1998) and this study, both of which reached conclusions that differ entirely from Anđelković's original interpretation. We do not consider the fish remains from Klinci to provide sufficient correlation potential to justify a stratigraphic interpretation in their own right.

Two studies of macroflora taken from the western and central part of the VMB suggest an early Miocene age (Lazarevic et al. 2013). Currently, six different formations have been recognized within a time interval ranging from lower to upper Miocene: (1) Mionica Fm. (lacustrine, pyrobituminous); (2) Valjevo Fm. (lacustrine, marly), which contains the fish fossils from Klinci; (3) Tabanović Fm. (lacustrine, clastic); (4) Mađarlija Fm. (marine-brackish, carbonate-clastic); (5) Vračevići Fm. (brackish, marly); and (6) Bogovađa Fm. (terrigenous) (Jovanović et al. 1994; Obradović and Vasić 2007; Lazarevic et al. 2013; Rundic 2017). There is no transition between the lacustrine and marine sediments; instead, the middle Miocene Sarmatian marine-brackish sediments transgressively and disconformably overlay the early Miocene lacustrine deposits (Jovanović and Dolić 1994; Dolić 1995; Lazarevic et al. 2013).

Systematic paleontology

Order Gobiiformes Günther 1880

Family Gobiidae Cuvier 1816

Genus *Klincigobius* Bradić-Milinović, Ahnelt, Schwarzzhans n.gen.

Type species *Gobius serbiensis* Gaudant (1998)

Etymology Named after the type location Klinci, Valjevo-Mionica Basin, Serbia, in combination with the genus name *Gobius*.

Diagnosis A genus of the family Gobiidae, subfamily Gobiinae, with the following combination of characters: 27–28 vertebrae, of which 12 are abdominal; five branchiostegal rays; first dorsal fin with six spines, second dorsal fin with one spine and eight to 11 fin rays; anal fin with one spine and eight to nine rays. Last first dorsal fin pterygiophore inserts between neural spines six and seven; free interneural space between neural spines seven and eight; first pterygiophore of second dorsal fin inserts between neural spines nine and 10; dorsal fin pterygiophore formula 3-221101; anal fin originates distinctly posterior of

origin of second dorsal fin, with its spine opposing third ray of second dorsal fin; two pterygiophores of anal fin preceding first haemal spine; base of anal fin reaches to vertical through seventh caudal vertebra and terminates posterior to termination of second dorsal fin. One epural. Scales ctenoid. Head long but narrow, dorsally depressed, lower jaw distinctly longer than upper jaw, head length mean 34.0%, head depth mean 22.9% of standard length (SL). Mouth cleft long. Pectoral fin length 9.4–11.7% of SL. Dentary long and slender, ending in a shallow coronoid process with numerous canine-like teeth anteriorly that are bent inwards. Premaxilla with posterior process. Maxilla long, narrow, and terminating anteriorly in antero-lateral process. Otolith slightly longer than high (OL:OH = 1.1–1.35), parallelogram-shaped. Sulcus with low ostial lobe. Subcaudal iugum distinct, below anterior part of cauda, slightly projecting onto sulcus.

Discussion *Klincigobius* is a fossil genus of the Gobiinae and is considered to be a representative of the *Gobius* group of Birdsong et al. (1988) and related to *Gobius*, with which it shares the dorsal fin pterygiophore formula (3-221101), the number of total vertebrae (27–28), the presence of one epural, and the presence of a posterior process on the premaxilla. It differs from *Gobius* and other members of the *Gobius* group in having 12 abdominal vertebrae (vs 11). From *Gobius*, which appears to be the most closely related genus, it differs further in the low number of rays in the second dorsal and anal fins (I + 8–11 vs I + 11–16 and I + 8–9 vs I + 10–14, respectively) and the long and slender dentary. Twelve abdominal vertebrae in combination with 15 to 16 caudal vertebrae are found in few genera of the *Gobiosoma* group from America of Birdsong et al. (1988), but these have different dorsal fin pterygiophore formulas. The Ponto-Caspian gobies, for example those of the genera *Neogobius* and *Ponticola*, have 12 abdominal vertebrae but 21 or more caudal vertebrae. The otoliths of *Klincigobius* also resemble those of *Gobius* but are remarkable for their subcaudal iugum, which extends somewhat over the deepened sulcus.

Also similar are the fishes of the extinct genus *Eleogobius* Gierl and Reichenbacher 2015. *Klincigobius* shares with *Eleogobius* the low number of rays in the second dorsal fin (I + 8–11 vs I + 9–11) and the anal fin (I + 8–9 vs I + 7–11) and the number of vertebrae (27–28) and abdominal vertebrae (12). The pterygiophore formula has neither been reported in Gierl and Reichenbacher (2015) nor in preceding publications dealing with articulated skeletons of fishes now placed in *Eleogobius* (Reichenbacher et al. 2007; Brzobohaty and Gaudant 2009), but a photograph of a very well-preserved specimen figured in Brzobohaty and Gaudant (their Fig. 2) clearly shows the same formula (3-221101). *Eleogobius*, however, was

established by Gierl and Reichenbacher as a fossil gobiiform with a mosaic set of characters. The authors referred to the presence of six branchiostegal rays in *Eleogobius*, which are not found in the Gobiidae, while another diagnostic character, namely the T-shape of the anterior tip of the palatine, is shared with the Gobiidae. Basal gobioids including Butidae and Eleotridae have two short, slender branchiostegal rays inserted at the rear of the narrow anterior part of the ceratohyal and four long blade-like branchiostegal rays inserted along the broad rear section of the ceratohyal (Gosline 1955). In the Gobiidae, there is only one short, slender branchiostegal ray inserted at the rear of the narrow anterior part of the ceratohyal resulting in a total of five branchiostegals, which is regarded as a synapomorphy of the family (Akihito 1969). Figure 2b in Gierl and Reichenbacher (2015), which depicts *Eleogobius gaudanti*, shows two short, slender anterior branchiostegals, but one of these is located much further anterior than usual, almost at the tip of the ceratohyal. Figure 2d in the same study depicting *Eleogobius brevis* shows a similar position of the putative first branchiostegal ray, which is, however, also considerably longer than the second ray. This difference in length is also an unusual character. The same appears to be the case in Fig. 3a of *Eleogobius brevis* in Reichenbacher et al. (2007), then known as *Gobius brevis*. In our view, these differences raise concerns regarding whether the anterior-most putative branchiostegal ray in *Eleogobius* is homologous to the status observed in basal Gobioidae. In any case, the branchiostegal ray pattern in *Eleogobius* represents a viable distinguishing characteristic to *Klincigobius*. In addition, otoliths of *Eleogobius* differ from those of *Klincigobius* in the absence of a subcaudal iugum. In conclusion, we here consider *Eleogobius* as a gobiid, possibly related to but distinct from *Klincigobius*. *Eleogobius* has been described from late early Miocene to early middle Miocene strata of the Vienna Basin (Brzobohaty and Gaudant 2009), the Bavarian Molasse Basin (Reichenbacher et al. 2007; Gierl and Reichenbacher 2015), western Switzerland (Reichenbacher and Weidmann 1992; Reichenbacher 1993), and northern Croatia (Mandic et al. 2019). Recently, *Eleogobius prochazkai* Reichenbacher, Filipescu and Miclea 2018 has been described from the Sarmatian of Romania as a replacement for the commonly recorded ‘*Gobius multipinnatus* (H. v. Meyer 1848)’ otolith specimens, which became necessary after a review of fishes with otoliths in situ previously assigned to that species (Gierl and Reichenbacher 2015). However, the long preventral and postdorsal projections, as well as the lack of a subcaudal iugum, would in our view be more consistent with otoliths of the Ponto-Caspian genus *Ponticola*.

The early Miocene freshwater to brackish water environment of the Mainz Basin contains yet another group of

possibly related freshwater gobies, “*Gobius*” *francofurtanus* Koken 1891, which is known from isolated otoliths and articulated skeletons partly with otoliths in situ, and the otolith-based species “*Gobius*” *rostratus* Weiler 1963, “*Gobius*” *altus* Weiler 1963, and “*Gobius*” *moenanius* Weiler 1963. All these species appear to be closely inter-related, and we henceforth refer to them as the “*Gobius*” *francofurtanus* group for convenience. Skeletons of “*Gobius*” *francofurtanus* have been briefly described by Weiler (1961) and Eikamp and König (1981), but these do not allow for a detailed comparison. The otoliths of the species of this group, however, differ from those of *Klincigobius* in the absence of a subcaudal iugum, although, in “*Gobius*” *rostratus*, a very small subcaudal iugum is occasionally discernable (Malz 1978; Reichenbacher 2000). A further species, “*Gobius*” *schadi* Weiler 1963, represents a completely different otolith morphology resembling eleotrid (butine) otoliths and is here referred to as *Butis?* *schadi*.

Species Two species from the early Miocene of the Valjevo freshwater lake in Serbia: *Klincigobius andjelkovicae* n.sp. and *K. serbiensis* (Gaudant 1998). No isolated otolith-based species are placed in *Klincigobius*.

Klincigobius serbiensis (Gaudant 1998)

(Figs. 3, 4, 5; Table 1)

Lepidocottus brevis (Agassiz 1839).—Anđelković 1978: Fig. 1, Fig. 2.

Aspius elongatus H. v. Meyer 1852.—Anđelković 1978: Fig. 1, Fig. 3.

Aspius cf. *elongatus* H. v. Meyer 1852.—Anđelković 1978: Fig. 1, Fig. 4.

Smerdis formosus H. v. Meyer 1852.—Anđelković 1978: Fig. 2, Figs. 1a, 2.

Gobius serbiensis Gaudant 1998.—Gaudant: p. 108 (pars), no Figure (non Fig. 2 = *Klincigobius andjelkovicae*).

Material Eight articulated skeletons, thereof seven with otoliths in situ: RGFAJ 65, 73, 74, 84 (holotype), 87, 103, 104, 115.

Diagnosis The extremely brief and general diagnosis by Gaudant (1998), which covered all four now-recognized gobiid species of Klinci, necessitates a new diagnosis: a *Klincigobius* (see genus diagnosis) species with 12 abdominal and 15–16 caudal vertebrae, with the neural spine of PU2 short and only slightly expanded; second dorsal fin short with one spine and eight to nine fin rays; postmaxillary process of praemaxilla developed as short shallow crest; dentary long and slender with two rows containing many large canine-like teeth with tips curved inwards; the anterior end of the palatine T-shaped with the edge between both processi slightly concave. Otoliths

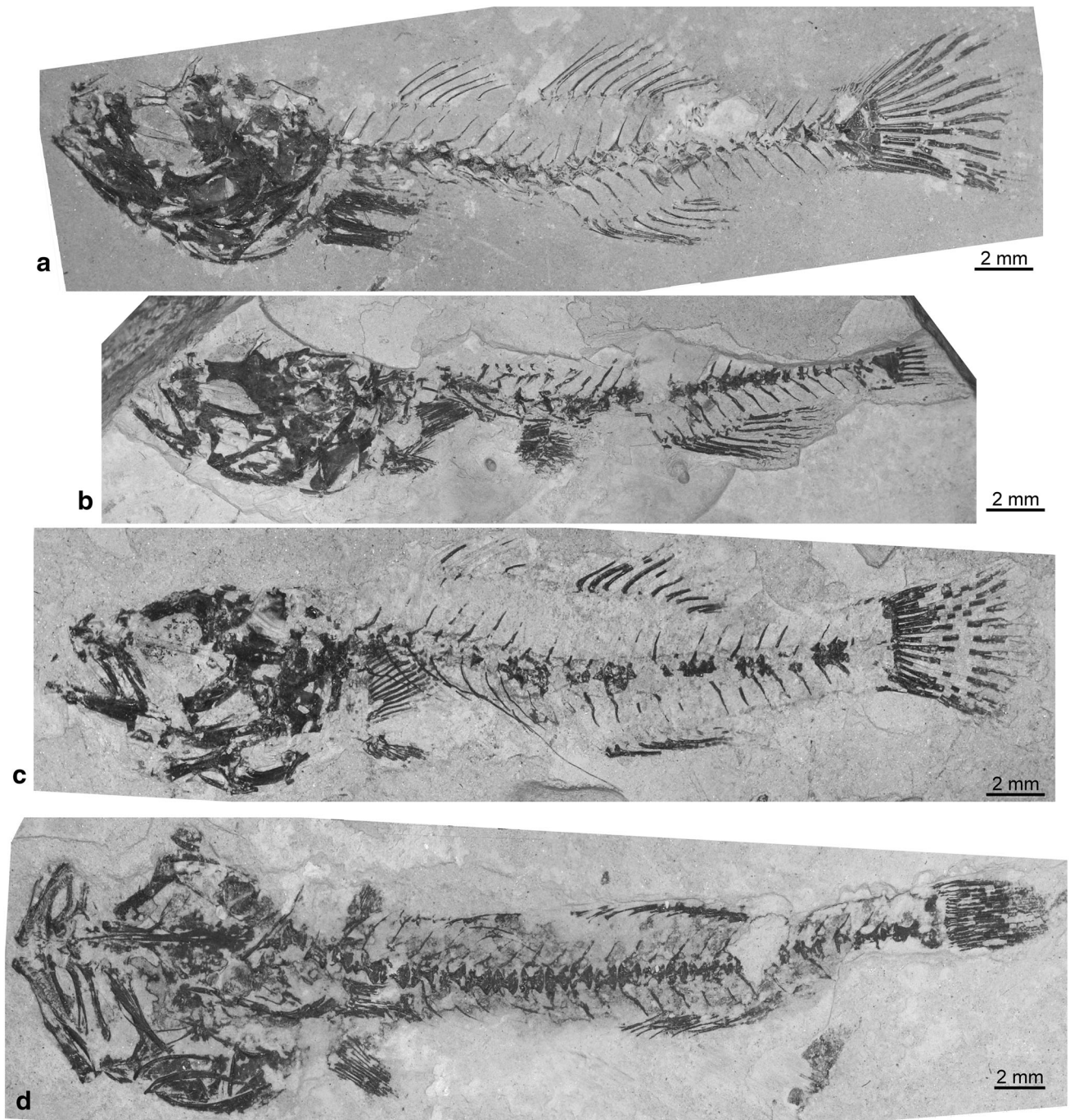


Fig. 3 *Klincigobius serbiensis* (Gaudant 1998). Articulated skeletons. **a** RGFAJ 84 (holotype). **b** RGFAJ 104. **c** RGFAJ 73. **d** RGFAJ 65

subrectangular (OL:OH = 1.1–1.2) with a short, broadly rounded preventral and a moderate postdorsal projection. Sulcus inclined at 11°–14°.

Description Counts and measurements are reported in Table 1.

Neurocranium. The skull is laterally compressed in one of the three specimens and dorso-ventrally compressed in the other two specimens. Most bones are damaged and/or

fragmented and their shapes are thus only partially recognizable. In particular, the occipital section of the skull is completely crushed in all specimens. The frontals, which form a large part of the cranial roof, are rather complete, with a narrow interorbital region that then widens posteriorly; the interorbital section and the edge of the frontals, which form the posterior rim of the orbit, show a distinct groove-like depression for the supraorbital canal of the

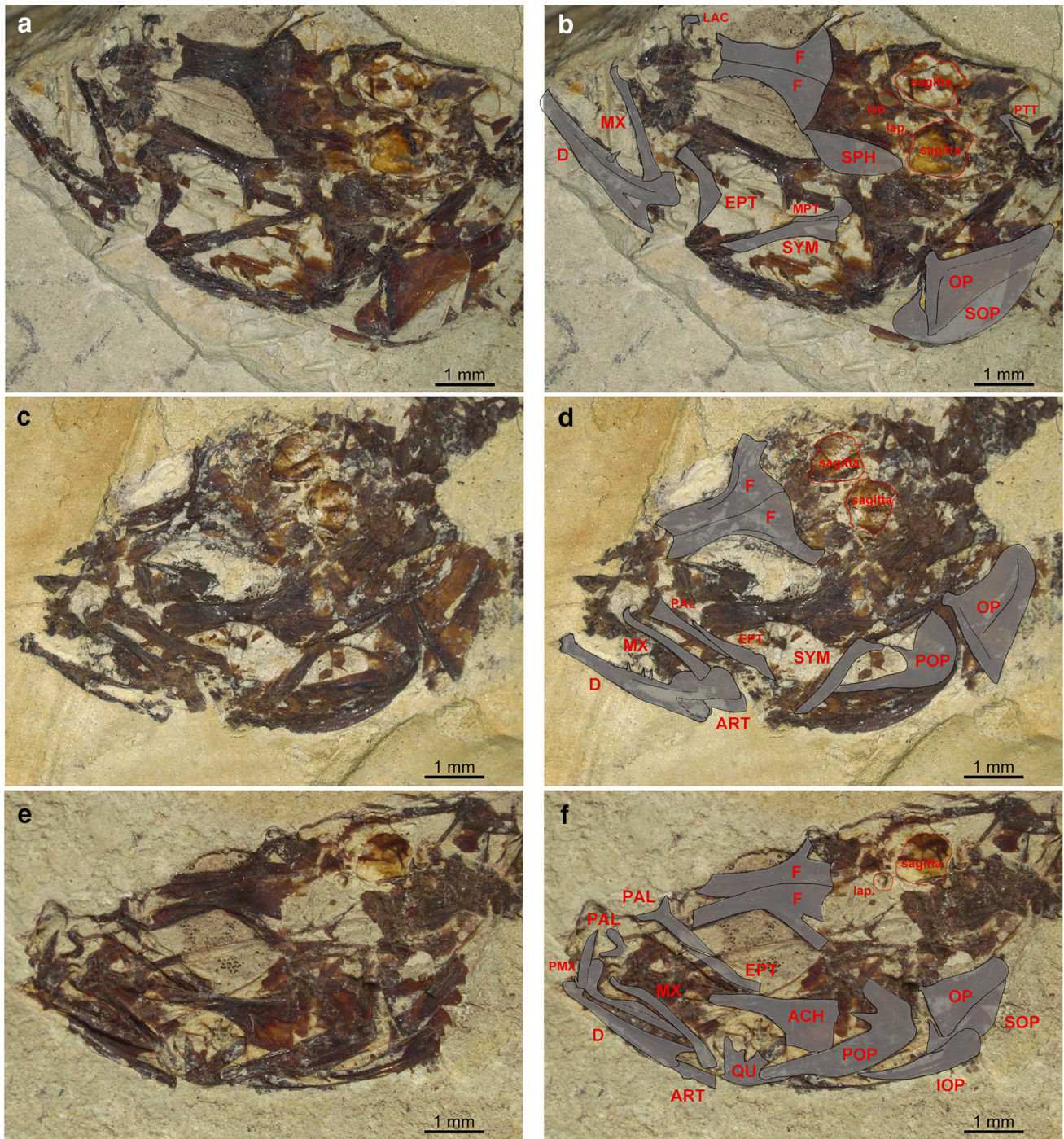


Fig. 4 *Klincigobius serbiensis* (Gaudant 1998). Close-up photographs of heads; left side detailed photographs, right side with overlay of selected interpretation of skull bones. **a, b**, RGFAJ 104. **c, d**, RGFAJ 103. **e, f** RGFAJ 74

head lateral-line system (Fig. 4a, b, e–f). An oval sphenotic is present posterior of the frontal.

Jaws The premaxilla is long and narrow with three processes: two at its anterior end separated by a deep notch, with a long and narrow ascending process, and a wider but shorter maxillary process; a third, postmaxillary process is

developed as a shallow crest, which reaches its highest point at about the middle of the premaxilla before gradually decreasing to the pointed end of the premaxilla (Fig. 4e–f). The premaxillary teeth are arranged in two rows of conical teeth, with a few large and canine-like teeth at the anterior end (Fig. 5a, b). The outer row has slightly longer conical teeth than the second row so that the teeth

sometimes look as if of alternating length. The premaxilla is of similar length as the dentary. The maxilla is long, narrow, and slightly convex, and it slightly widened posteriorly; anteriorly, it ends in an upturned hook-like feature (Fig. 4a–f). The entire lower jaw, especially the dentary, is long and slender. The dentary increases in height posteriorly and terminates in a short coronoid process; its posterior edge is notched. The dentition of the dentary differs from that of the premaxilla in showing many large canine-like teeth along its entire length, with their tips curved inwards (Figs. 4a–d, 5a, b) but also contains two rows of conical teeth similar to the premaxilla. The anguloarticular inserts with its dorsal arm medially in the posterior notch of the dentary. The ventral edge of the lower jaw forms a smooth line due to the weakness of its ventral ramus (Figs. 4e–f, 5a, b). The retroarticular is not discernible.

Opercular series The opercle is large and approximately triangular in shape (Fig. 4e–f). The long, blade-like interopercle is shifted backwards, partly covering the hook-like subopercle (Fig. 4e–f). The preopercle is crescent-shaped; its very wide dorsal part carries a distinct symplectic process, which, together with the narrow ventral part of the preopercle, forms the postero-ventral margin of the well-developed foramen suspensorium (suspensorial interspace) (Fig. 4c, d).

Suspensorium The quadrate is formed by an anterior laminar body and shows ventrally a narrow process extending postero-dorsally (Fig. 4e–f). The metapterygoid is short and narrow (Fig. 4a, b), lying immediately anterior to the dorsal part of the symplectic. The symplectic is long and rod-like and expands at its dorsal end. This expansion shows posteriorly a preopercular process, which, in combination with the posterior edge of the symplectic, forms the anterior-dorsal margin of the well-developed foramen suspensorium (Fig. 4c, d). The ectopterygoid is elongated, with an expanded posterior part (Fig. 4a, b). The anterior end of the palatine carries two processes, which results in a T-shaped appearance: antero-laterally the maxillary process, medio-dorsally the ethmoid process; the edge between both processi is slightly concave (Fig. 4e–f). The narrow anterior part of the ectopterygoid is tightly attached to the narrow posterior part of the palatine; both bones are of about equal size (Fig. 4c, d).

Hyoid bar and gill arches Only the massive, and axe-shaped anterior ceratohyal is well-preserved (Fig. 4e–f).

Axial skeleton The vertebral column consists of 27–28 vertebrae including urostyle, of which 12 are abdominal and 15–16 caudal vertebrae (Fig. 3a, b). The neural and haemal spines are narrow, elongated, pointed, and of similar length, except those of the second preural vertebra (PU2), which are modified; the neural spine of PU2 is

slightly expanded and short; the haemal spine is elongated and distinctly expanded (Fig. 5d). The neural and haemal spines insert anterior on the vertebral centrum, except those of PU2–5, which insert posterior (Fig. 3a–d). Eight pleural ribs are developed, extending laterally from abdominal vertebra 3–10; no rib is discernible on the last abdominal vertebra (Fig. 3d). The parapophyses of vertebrae 10–11 are ventrally directed (Fig. 3c). Epineural ribs are also present (Fig. 3c, d).

Caudal skeleton The caudal skeleton consists of an elongated parhypural; two hypural plates, the first formed by the fused hypurals 1 + 2, the second by the fused hypurals 3 + 4; the first hypural plate inserts on the ventral side of the urostyle; the second plate is fused to its posterior end; the hypural 5 is small and narrow; the single epural is large (Fig. 5d). Sixteen caudal fin rays are inserted between the epural and the haemal spine of PU2, of which 14 principal rays extend from the parhypural to the hypural 5. Gradually decreasing procurrent spines extend anterior from the fin rays, nine dorsal and seven ventral (Fig. 5d).

Median fins The first dorsal fin has six spines, each carried by one pterygiophore. The first two pterygiophores insert in interneural space three (IS3), the third and the fourth in IS4, the fifth in IS5, and the sixth in IS6. There is one free interneural space (IS7) between the first and the second dorsal fin. The first pterygiophore of the second dorsal fin inserts in IS8 (Fig. 3a, c). Thus, the dorsal pterygiophore formula is 3-221101. The second dorsal fin has one spine and nine fin rays (I + 9); each pterygiophore supports one fin element, except the last, which carries two rays. The second dorsal fin is distinctly higher than the first dorsal fin. The gap between both dorsal fins is moderately wide. The anal fin has one spine and eight fin rays (I + 8); the first pterygiophore supports the spine and the first fin ray; the following pterygiophores support one fin ray each, except the last, which carries two rays. The anal fin originates distinctly posterior of the origin of the second dorsal fin; its spine opposes the third ray of the second dorsal fin (Fig. 3a, c, d). Two pterygiophores of the anal fin precede the first haemal spine (Fig. 3c). The base of the anal fin reaches to the sixth caudal vertebra (Fig. 3b).

Paired fins and girdles None of the elements of the pectoral and pelvic girdles are clearly discernible. The pectoral fins have 15 rays. The exact number of the pelvic fin rays is not discernible (Fig. 3a–d).

Scales Only a few scales are preserved in specimens RGF AJ 74 and 84; these scales are located near the base of the second dorsal fin. They are ctenoid, about 0.8 mm in diameter, and carry a single row of 10–12 densely placed cteni along the distal rim. The scales are arranged in six rows from second dorsal fin spine to third fin ray (Fig. 5l).

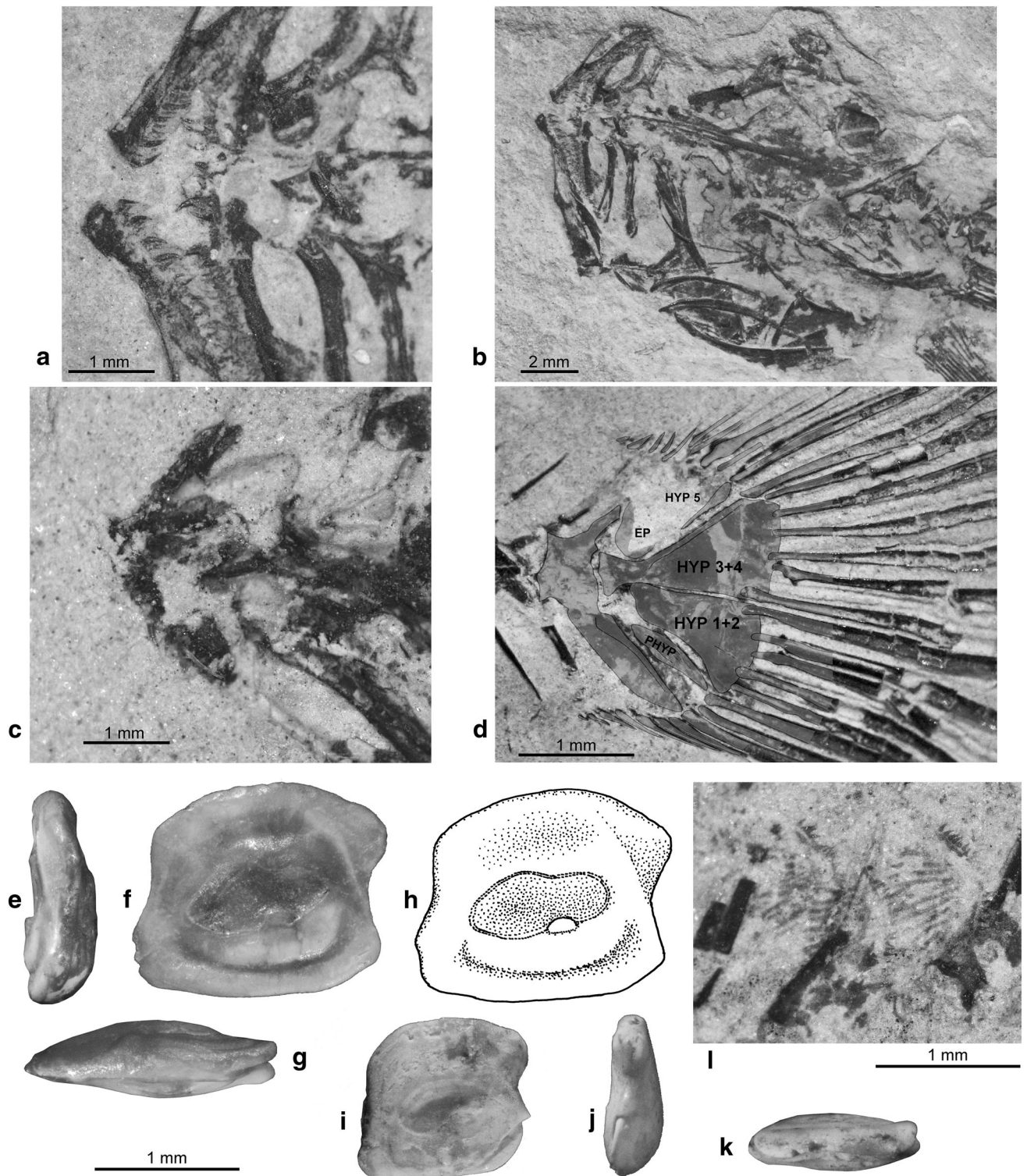


Fig. 5 *Klincigobius serbiensis* (Gaudant 1998). Detail photographs and drawings. **a, b** Dentition of jaw (dentary and premaxilla) of RGFAJ 65; **a** close-up of **b**. **c**, Dentary of RGFAJ 73. **d** Caudal skeleton of RGFAJ 84 (holotype) with interpretative overlay. **e**–

h Otolith of RGFAJ 104; **e** view from posterior, **5f** inner face, **5g** view from dorsal, **h** interpretative drawing of inner face. **i**–**k** Otolith of RGFAJ 65; **5i** inner face, **5j** view from posterior, **k** view from dorsal. **l** Close-up view of ctenoid scales of RGFAJ 74

Otolith (sagitta) The otoliths are subrectangular in shape with a gently curved and smooth dorsal rim and a flat,

horizontal, smooth ventral rim. The largest specimen, of 1.8 mm in length (Fig. 5e–h), stems from specimen

Table 1 Meristics and morphometrics of *Klincigobius serbiensis* and *K. andjelkovicæ*

	<i>Klincigobius serbiensis</i>		<i>Klincigobius andjelkovicæ</i>
	HT-RGFAJ84	7 PT's	HT-RGFAJ67
SL (mm)	29	28.8–45.3	48.5
Otolith in situ	Yes		Yes
<i>Meristics</i>			
Precaudal vertebrae	12	12	
Total vertebrae	27	27–28	(3) + 16
D1	VI	V–VI	VI
D2	I + 8	I + 8–9	I + 11
A	I + 9	I + 8–9	I + 9
Pectoral		13–15	
D1 last ray between NS	NS6–NS7	NS6–NS7	
Empty neural spines	NS7–NS8	NS7–NS8	
D2 first Pt between NS	NS8–NS9	NS8–NS9	
Caudal principle	16		
Dorsal Pt formula	(3)221101	(3)221101	
Anal Pt1 to opposite to	D2/3	D2/3	
Postmaxillary process on PMX	Present	Present	Present
EP	1	1	
AP	2	2	2
SOP anterior-ventral shape	Hook-like	Hook-like	
Scale type	Ctenoid	Ctenoid	
<i>Morphometrics (% of SL)</i>			
Head length	33.4	31.5–37.4	32.6
Head height	21.7	18.5–22.9	19.4
Max. body height	20.0	17.9–22.9	19.4
Orbit diameter	9.3	9.3–11.2	
D1 length	14.2	14.2–15.3	
A length	23.4	17.6–23.4	19.8
PL-pectoral length	11.7	9.4–11.7	
predorsal to D1	40	40–42.6	
Predorsal to D2	59.6	59.6–61.1	
Pereanal	64.8	58.7–64.8	66.2
Base of D1	10.3	9.4–10.3	
Base of D2	20.3	15.3–20.3	
Base of A	14.5	14.5–17.0	15.1
Distance of D1 to D2	7.9	8.6–7.9	

RGFAJ 104 with an SL of 45.3 mm. OL:OH = 1.1–1.2; OH:OT = 2.7–2.8. The dorsal rim shows a high, rounded predorsal angle and a moderate postdorsal projection, which is only slightly bent outwards. The ventral rim shows a broadly rounded, short preventral projection that is not bent outwards and a similarly strongly projecting and sharper postventral angle. The anterior rim is nearly vertical with no or a shallow concavity at the level of the ostium. The posterior rim is about as high as the anterior rim with a distinct, wide, and regularly curved concavity at about the level of the cauda.

The inner face is slightly convex. The sulcus is short, moderately wide, somewhat deepened, and inclined at 11° to 14°. OL:SuL = 1.8–1.9. The ostial lobe is low and gently rounded. A distinct feature is the small, oval sub-caudal iugum situated below the anterior part of the cauda, which slightly projects over the deepened sulcus like a promontory. The dorsal field shows a moderately large and moderately deep depression with gradual transitions. The area leading to the postdorsal projection is set off on the inner face by a distinct, diagonal edge. The ventral field shows a distinct, deep, and broad ventral furrow running at considerable distance to the ventral rim of the otolith from

the anterior tip of the ostium to the posterior tip of the cauda and does not cross the edge setting off the postdorsal projection. The outer face is approximately as convex as the inner face, thickest ventrally, and smooth.

Discussion See discussion of *Klincigobius andjelkovicae*.

Klincigobius andjelkovicae Bradić-Milinović, Ahnelt, Schwarzahns n.sp.

(Fig. 6)

Gobius multipinnatus H. v. Meyer 1848.—Anđelković 1978: Figs. 1 and 5.

Gobius serbiensis Gaudant 1998.—Gaudant: p. 108 (pars), only Fig. 2 (otolith).

Holotype RGFAJ 67, an articulated skeleton measuring 48.5 mm SL with otoliths in situ, Klinči, Serbia, early Miocene.

Paratypes Two incompletely preserved articulated skeletons with otoliths in situ, RGFAJ 85, 93, and an isolated otolith, RGFAJ 113.

Etymology Named after the late Jelene Anđelković, a pioneer of Serbian paleoichthyology and the first to describe the fishes from Klinči.

Diagnosis A *Klincigobius* (see genus diagnosis) species with 16 caudal vertebrae, with the neural spine of PU2 short but distinctly expanded; a long second dorsal fin with one spine and 11 fin rays; a shallow postmaxillary process of the premaxilla; a long and slender dentary that ends in a shallow coronoid process; teeth on the anterior end of the dentary large, conical, and arranged in three to four rows; the anterior end of the palatine T-shaped and the maxillary process distinctly larger than the ethmoidal process. Otoliths moderately elongate (OL:OH = 1.25–1.35) with distinctly developed preventral and postdorsal projections. Sulcus inclined at 16°–20°.

Description Counts and measurements are presented in Table 1.

Neurocranium The skull of one specimen is laterally compressed, while that of the other specimen is dorsally compressed. Most bones are fragmented or entirely absent (Fig. 6a–c). The vomer is preserved as an imprint. It is T-shaped with a wide, thin head and a long and narrow median process pointing posteriorly; it carries three to four rows of small roundish imprints along the wings, which indicate granular teeth (Fig. 6b).

Jaws The premaxilla is long and narrow with three processes: two anteriorly, a long and narrow ascending process and a wider but shorter maxillary process; these processes are separated by a deep notch; the postmaxillary process

forms a shallow crest that reaches its highest point at about the middle of the premaxillary. A part of the posterior section of the premaxillary crest is not preserved across the dentary; teeth of the premaxilla are not preserved (Fig. 6c, d). The left maxilla is long and narrow, terminating anteriorly in a knob-like antero-lateral process. The posterior end of the left maxilla and the entire right maxilla are not preserved. The dentary is long and slender, ending in a shallow coronoid process. The teeth on the dentary are well exposed anteriorly and are arranged in three or four rows of large, canine-like teeth, which are bent inwards (Fig. 6c, d).

Opercular series Not preserved.

Suspensorium Only the anterior-most part of the left palatine is preserved; its anterior end is T-shaped and convex, with the maxillary process distinctly larger than the ethmoidal process (Fig. 6c).

Hyoid bar and gill arches Not preserved.

The entire postcranial skeleton is poorly preserved (Fig. 6a). The trunk seems to be elongate, but this is seemingly artificial, as all vertebrae are obviously detached from each other.

Axial skeleton The caudal part of the vertebral column consists of 16 caudal vertebrae (the 14th caudal vertebra is missing), including the urostyle (Fig. 6a). Only the three last abdominal vertebrae are detectable (Fig. 6a). The neural and haemal spines are narrow, elongated, pointed, and of similar length, except those of the second preural vertebra (PU2), which are modified. The neural spine of PU2 is short and distinctly expanded; the haemal spine is only partly preserved and seemingly elongated and expanded (Fig. 6a). The neural and haemal spines insert anterior on the vertebral centrum, except those of PU2–5, which insert posterior (Fig. 6a). Pleural and epineural ribs are developed (Fig. 6a).

Caudal skeleton Only the urostyle and parts of the first hypural (hypural 1 + 2) and second hypural (hypural 3 + 4) are preserved (Fig. 6a). The caudal fin is rounded, and 16 fin rays are detectable along its rims.

Median fins The first dorsal fin has six spines. The second dorsal fin is long, with one spine and 11 fin rays (I + 11) (Fig. 6a, Table 1). Most pterygiophores of the dorsal fin and most abdominal vertebrae are not preserved; hence, the pattern of the dorsal pterygiophores is not discernible. However, there appears to be only one interneural space between both dorsal fins. The gap between both dorsal fins is not distinct. The anal fin has one spine and nine fin rays (I + 9). It originates slightly posterior to the origin of the second dorsal fin with the spine opposite the first fin ray of

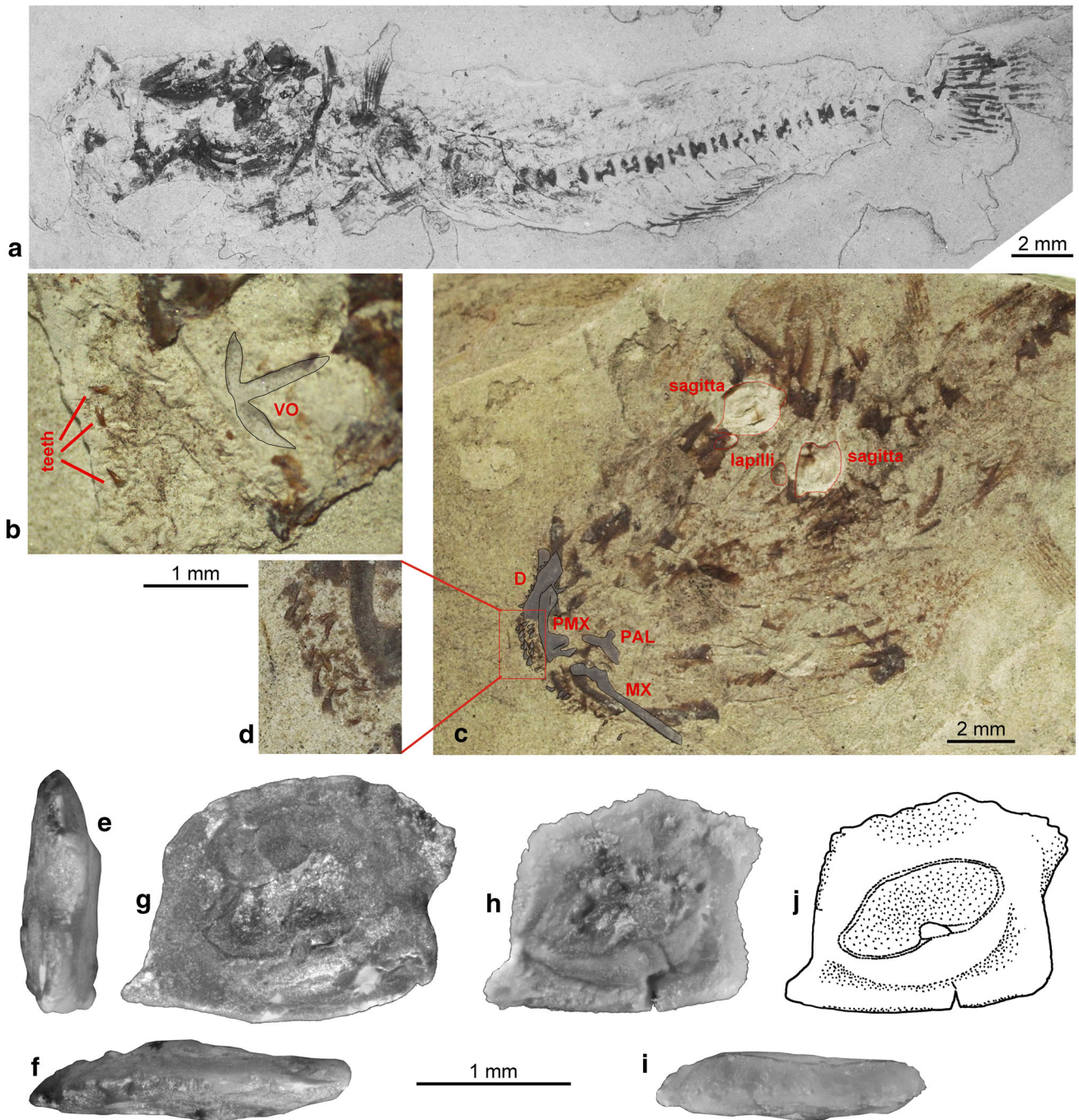


Fig. 6 *Klincigobius andjelkovicae* Bradić-Milinović, Ahnelt, Schwarzahns n.sp. **a** Articulated skeleton of RGFAJ 67, holotype. **b** Detail of head of RGFAJ 67 (holotype), partly disintegrated, some teeth and imprint of vomer highlighted. **c**, **d** Head of RGFAJ 85 with

interpretative overlay; **c** close-up of dentary of **d**. **e–g** Otolith of RGFAJ 85; **e** view from posterior, **f** view from dorsal, **g** inner face. **h–j** Otolith of RGFAJ 67 (holotype); **h** inner face, **i** view from dorsal, **j** interpretative drawing of inner face

the second dorsal fin (Fig. 6a). Two pterygiophores of the anal fin precede the first haemal spine (Fig. 6a).

Paired fins and girdles The dorsally bifurcated, long, and straight cleithrum and the elongate and narrow supraclithrum of the pectoral girdle are partly preserved. No elements of the pelvic girdles are clearly discernible. The

pectoral and pelvic fins are partly preserved, but fin rays cannot be counted (Fig. 6a).

Scales No scales are preserved.

Otolith (sagitta) The otoliths are parallelogram-shaped. The largest specimen is 2.2 mm long (Fig. 6e–g), and a 1.8-mm-long specimen (Fig. 6h–j) stems from the

holotype, RGFAJ 67, with an SL of 48.5 mm, which was also the otolith figured by Gaudant (1998). OL:OH = 1.25–1.35; OH:OT = 3.0–3.3. The dorsal rim is gently curved and irregularly undulating. It shows a high, rounded predorsal angle and a distinct postdorsal projection, which is longer than the postventral angle and only slightly bent outwards. The ventral rim is shallow, almost flat, horizontal, and smooth. It shows a pointed, distinct, and rather long preventral projection that is not bent outwards and a blunt, short, rounded postventral angle. The anterior rim is inclined at about 75° to 80° and shows no concavity. The posterior rim is about as high as the anterior rim, and similarly parallel inclined with a distinct, moderately wide concavity at about the level of the cauda.

The inner face is slightly convex. The sulcus is large, wide, somewhat deepened, and inclined at 16° to 20°. OL:SuL = 1.8–2.1. The ostial lobe is very low and gently rounded. A distinct feature is the small, oval subcaudal iugum situated below the anterior part of the cauda, which is slightly projecting over the deepened sulcus. The dorsal field shows an indistinct and poorly marked depression. The area leading to the postdorsal projection is not significantly set off on the inner face. The ventral field shows a distinct, deep, and broad ventral furrow that runs a considerable distance at a shallower angle to the ventral rim of the otolith from the anterior tip of the ostium to the posterior tip of the cauda. The outer face is almost flat and smooth.

Discussion *Klincigobius andjelkovicæ* differs from *K. serbiensis* in the larger number of rays of the second dorsal (I + 11 vs I + 8–9), three or four rows of canine teeth on the dentary (vs one or two), presence of a knob-like anterolateral process at the anterior tip of the maxilla (vs smooth), and a more slender otolith (OL:OH = 1.25–1.35 vs 1.1–1.2) characterized by rather prominent preventral and postdorsal projections and a more steeply inclined sulcus (16°–20° vs 11°–14°).

Genus *Rhamphogobius* Bradić-Milinović, Ahnelt, Schwarzahns n.gen.

Type species *Rhamphogobius varidens* Bradić-Milinović, Ahnelt, Schwarzahns n.sp.

Etymology From *rhamphos* (Greek = beak), due to the resemblance of the preserved lower jaw to a beak in combination with the genus name *Gobius*.

Diagnosis A genus of the family Gobiidae, subfamily Gobiinae, with the following combination of characters: 26 vertebrae, of which 11 are abdominal; five branchiostegal rays; first dorsal fin with five to six spines, second dorsal fin with one spine and nine rays; anal fin with one spine and eight or nine (?) rays. Last first dorsal

fin pterygiophore inserts between neural spines six and seven; two free interneural spaces between neural spines seven and eight and eight and nine; first pterygiophore of second dorsal fin inserts between neural spines nine and 10; dorsal fin pterygiophore formula 3-2211001. Anal fin originates slightly behind origin of second dorsal fin; its spine opposes second ray of second dorsal fin; two pterygiophores of anal fin precede first haemal spine; base of anal fin reaching to about vertical line through sixth caudal vertebra and terminates below termination of second dorsal fin base. Scales ctenoid. Head massive, large, with short terminal snout, head length mean 34.9% SL, head depth mean 26.8% SL; mouth cleft short. Pectoral fin length 18% of SL. Dentary narrow and anteriorly downward bent; teeth at its symphysis, with few canine-like teeth followed by numerous straight, slender, densely packed cylindrical teeth. Premaxilla with posterior process. Maxilla long, narrow, and straight. Otolith nearly quadratic in outline (OL:OH = 0.95). Sulcus with near continuously bent dorsal margin with only incipient ostial lobe. Subcaudal iugum distinct, below anterior part of cauda.

Discussion *Rhamphogobius* is readily recognized by the strange shape of the anterior tip of the dentary, which appears to be bent downward. This apparent bend may in fact be a result of compression (at least to some extent) of an unusually broad and wide but short snout, and a short mouth cleft. Despite some uncertainty with respect to the number of epurals and the unusual two empty neural spaces between the two dorsal fins, the pterygiophore formula of 3-2211001 in combination with 26 vertebrae, of which 11 are abdominal, characterize *Rhamphogobius* as a gobiine, probably of the *Gobius* group of Birdsong et al. (1988). The preservation of the caudal skeletons of the specimens is not adequate to determine whether the remnants discernable are that of a single epural, as would be expected in gobiines, or indeed that of two epurals, which would be more in line with gobionellines. However, the presence of a postmaxillary process on the premaxilla again favors a gobiine (McKay and Miller 1997). Due to the highly specialized snout and dentition, we are unable to delineate any more detailed interrelationships with extant gobies.

Rhamphogobius differs from extant Atlanto-Mediterranean gobies and the coeval fossil *Klincigobius* in the short snout, the shape of the dentary, and the specialized dentition of the dentary with few symphyseal canine teeth and many columnar, slender, and narrow placed lateral teeth. In addition, its otoliths are much more compressed (OL:OH = 0.95 vs 1.1–1.35) and without significant preventral or postdorsal processes, but they share with *Klincigobius* a distinct, albeit not extending, subcaudal iugum.

The otolith-based species *Rhamphogobius helvetiae* (Salis 1967) from the Karpatian and early Badenian of western Switzerland (Jost et al. 2006, 2015) and the early Badenian of northern Croatia (Mandic et al. 2019), *Rhamphogobius doppleri* (Reichenbacher 1993) from the Ottnangian and Karpatian of southern Germany and western Switzerland (Jost et al. 2006) and the early Badenian of northern Croatia (Mandic et al. 2019), and *Rhamphogobius gregori* (Reichenbacher 1993) from the Ottnangian of southern Germany and Karpatian of western Switzerland (Jost et al. 2006, 2015) share the compressed otolith shape and the presence of a mild subcaudal iugum. *Rhamphogobius helvetiae* differs from *R. varidens* in its more strongly undulating dorsal rim and the more consistent concavity at the anterior rim above the level of the ostium. These species also show a more orthogonal postventral angle (vs rounded). *Rhamphogobius doppleri* shows a more strongly developed postdorsal process and a rather small and narrow, sometimes indistinct, subcaudal iugum. *Rhamphogobius gregori* is more similar to *R. varidens* but differs in the shallower dorsal rim, which is also expressed in the higher OL:OH ratio (1.0–1.1 vs 0.95), the wider and larger sulcus, and the narrow or absent subcaudal iugum (vs distinct) (see Jost et al. 2006, 2015 for figures of *R. gregori*).

Species A single species based on articulated skeletons with otoliths in situ from the early Miocene of the Valjevo freshwater lake in Serbia, *Rhamphogobius varidens* n.sp. Three otolith-based species, *Gobius doppleri* Reichenbacher 1993 from the Ottnangian and Karpatian of southern Germany and western Switzerland, *Gobius gregori* Reichenbacher 1993 from the Ottnangian of southern Germany and Karpatian of western Switzerland, and *Gobius helvetiae* Salis 1967 from the Karpatian of western Switzerland, are here also referred to as *Rhamphogobius*, *Gobius doppleri*, and *Gobius helvetiae*, have recently also been described from the Karpatian to early Badenian of the Požega paleolake in northern Croatia (Mandic et al. 2019).

Rhamphogobius varidens Bradić-Milinović, Ahnelt, Schwarzahans n.sp.

(Figs. 7, 8, 9).

Smerdis elongatus H. v. Meyer 1852.–Anđelković 1978: Figs. 2 and 3.

Holotype RGFAJ 70, an articulated skeleton measuring 23.4 mm SL with otoliths in situ, Klinici, Serbia, early Miocene.

Paratypes One articulated skeletons with otoliths in situ, RGFAJ 9, and three isolated otoliths RGFAJ 53, 81, 120.

Etymology From *varius* (Latin = diverse) and *dens* (Latin = tooth), referring to the different types of teeth observed in this species.

Diagnosis See diagnosis of genus.

Description Counts and measurements are reported in Table 2.

Neurocranium The skull is dorso-laterally compressed in both figured specimens. Most bones are incompletely preserved or fragmented, and their shapes are only partly

Table 2 Meristics and morphometrics of *Rhamphogobius varidens*

	<i>Rhamphogobius varidens</i>	
	HT-RGFAJ70	PT-RGFAJ9
SL (mm)	23.4	26.0
Otolith in situ	Yes	Yes
<i>Meristics</i>		
Precaudal vertebrae	11	11
Total vertebrae	26	26
D1	V	VI
D2	I + 9	I + 9
A		I + 8or9
Pectoral		15
D1 last ray between NS	NS6–NS7	NS6–NS7
Empty neural spines	NS7–NS8	NS7–NS8
D2 first Pt between NS	NS8–NS9	NS8–NS9
Caudal principle	17	17
Dorsal Pt formula	(3)2211001	
Anal Pt1 to opposite to	D2/2	D2/2
Postmaxillary process on PMX	Present	Present
EP		1 large or 2 small
AP	2	2
SOP anterior-ventral shape	Not preserved	Not preserved
Scale type	Ctenoid	Ctenoid
<i>Morphometrics (% of SL)</i>		
Head length	31.2	38.5
Head height	28.6	25.0
Max. body height	17.9	24.2
Orbit diameter		11.5
D1 length		16.9
A length	20.5	21.2
PL-pectoral length		18.8
predorsal to D1	40.6	44.2
Predorsal to D2	56.4	66.2
Pereanal	62.4	63.1
Base of D1		11.5
Base of D2	17.9	16.2
Base of A	14.5	18.5

recognizable. The occipital region is completely crushed. The frontals, which form the largest part of the cranial roof, are partly preserved; they are narrow at the interorbital and widen posterior to the orbit (Fig. 8a, b). A small nasal is occasionally preserved anterior to it (Fig. 8a, b). The parasphenoid, which forms the largest part of the cranial base, is long and narrow; it widens posteriorly and narrows again towards its termination (Fig. 8a, b). The large, T-shaped vomer is preserved in one specimen (Fig. 8a, b). The basioccipital bone is discernable as well and marks the point where the first vertebra contacts the skull (Fig. 8a, b).

Jaws. The premaxilla is elongate with three processes, the two anterior processes are separated by a deep notch, and consist of a narrow ascending process, and a somewhat shorter but wider maxillary process; posteriorly, the post-maxillary process is low and short; it is highest at its last third and thereafter decreases rapidly in height. Small, slender, and narrowly placed cylindrical teeth run along the entire length of the premaxilla. They are shorter than the outer row of teeth on the dentary (Fig. 8c, d). The maxilla is long, narrow, and straight, only inconspicuously widening at its posterior end and with a hook-like bend anteriorly (Fig. 8a–d). The dentary is narrow and distinctly downturned anteriorly, which, however, may at least partly be due to distortion as a result of compaction. The posterior part of the dentary is massive, with a distinct, rounded coronoid process; its posterior edge is notched, receiving medially the massive dorsal ramus of the anguloarticular; the ventral ramus is also well-developed but short, and thus leaves a distinct indentation in the ventral edge of the lower jaw (Fig. 8c, d). The dentary bears numerous teeth; anteriorly, close to the symphysis, the teeth are curved, relatively large and conical; grading laterally into a row of slender, straight, and narrowly packed cylindrical teeth along the premaxilla (Fig. 8e, f). There appears to be one additional inward lateral row with granular teeth. The retroarticular is not discernable. Overall, the mouth cleft is short, and the distorted anterior tip of the dentaries in both specimens indicates that the fish may originally have had a broad snout.

Opercular series Only the crescent-shaped preopercle is preserved. Its dorsal part is relatively narrow and carries a distinct symplectic process; its narrow anterior part is in close contact with the posterior process of the quadrate (Fig. 8c, d).

Suspensorium The quadrate is a large laminar body with a narrow, pointed process extending postero-dorsally (Fig. 8a, c, d). The long, rod-like symplectic expands dorsally, carrying a preopercular process at the posterior end of the widened dorsal part (Fig. 8a, c, d). The ectopterygoid is short and massive, with a distinctly

expanded posterior end (Fig. 8c, d). The palatine is short and massive; its anterior end carries two processes, an anterior maxillary process and a posterior ethmoid process, resulting in a T-shaped appearance; the anterior edge of the palatine is deeply concave (crescent-shaped) (Fig. 8c, d). The ectopterygoid and the palatine are of about equal length (Fig. 8c, d).

Hyoid bar and gill arches The hyoid bar is large and massive, with five branchiostegal rays attached ventrally: The first rib-like ray inserts on the narrow anterior part of the anterior ceratohyal, followed by four blade-like and gradually widening branchiostegals; rays 2–3 insert on the wide posterior part of the anterior ceratohyal; the fifth branchiostegal attaches at the posterior ceratohyal. The suture between both ceratohyals is not clearly discernible (Fig. 8c, d).

Axial skeleton The vertebral column consists of 26 vertebrae including urostyle, of which 11 are abdominal and 15 caudal (Fig. 7a, b). The neural and haemal spines are narrow, elongated, pointed, and of similar length, except those of the second and third preural vertebrae (PU2–PU3), which are modified. The haemal spine of PU3 is expanded to about twice the width of the preceding haemal spine; the neural spine of PU2 is expanded and distinctly shortened; the haemal spine of PU2 is elongated and distinctly expanded (Figs. 7a, 9a, b). Besides the modified PU2 and PU3, PU4 is also incorporated into the caudal skeleton, as the neural and the haemal spines of these three vertebrae extend in a somewhat steeper angle posteriad than the preceding. The neural and haemal spines insert anteriorly on the vertebral center, except those of PU2–5, which insert posteriorly on the center (Figs. 7a, 8, 9a, b). Eight pleural ribs are developed, extending laterally from abdominal vertebra 3–10; no rib is discernable on the 11th abdominal vertebra (Fig. 7a). The parapophyses of vertebrae 10 (Fig. 7b) and 11 (Fig. 7a) are ventrally directed. Epineural ribs are also present (Fig. 7a, b).

Caudal skeleton The caudal skeleton consists of an elongate parhypural; two hypural plates, the first formed by the fused hypurals 1 + 2, the second by the fused hypurals 3 + 4 (Fig. 9a, b); the first hypural plate is detached from the ventral side of the urostyle and shifted somewhat posteriad during fossilization; the second plate is fused to the posterior end of the urostyle; the hypural 5 is small and narrow; two narrow epural elements are potentially identified, but they could also represent remnants of a single large epural (Fig. 9a, b). Seventeen caudal fin rays insert between the epural and the haemal spine of PU2, 14 of which are principal rays from the parhypural to the hypural 5. Only a few procurrent spines are preserved, two of which are dorsal and four ventral (Fig. 9a, b).

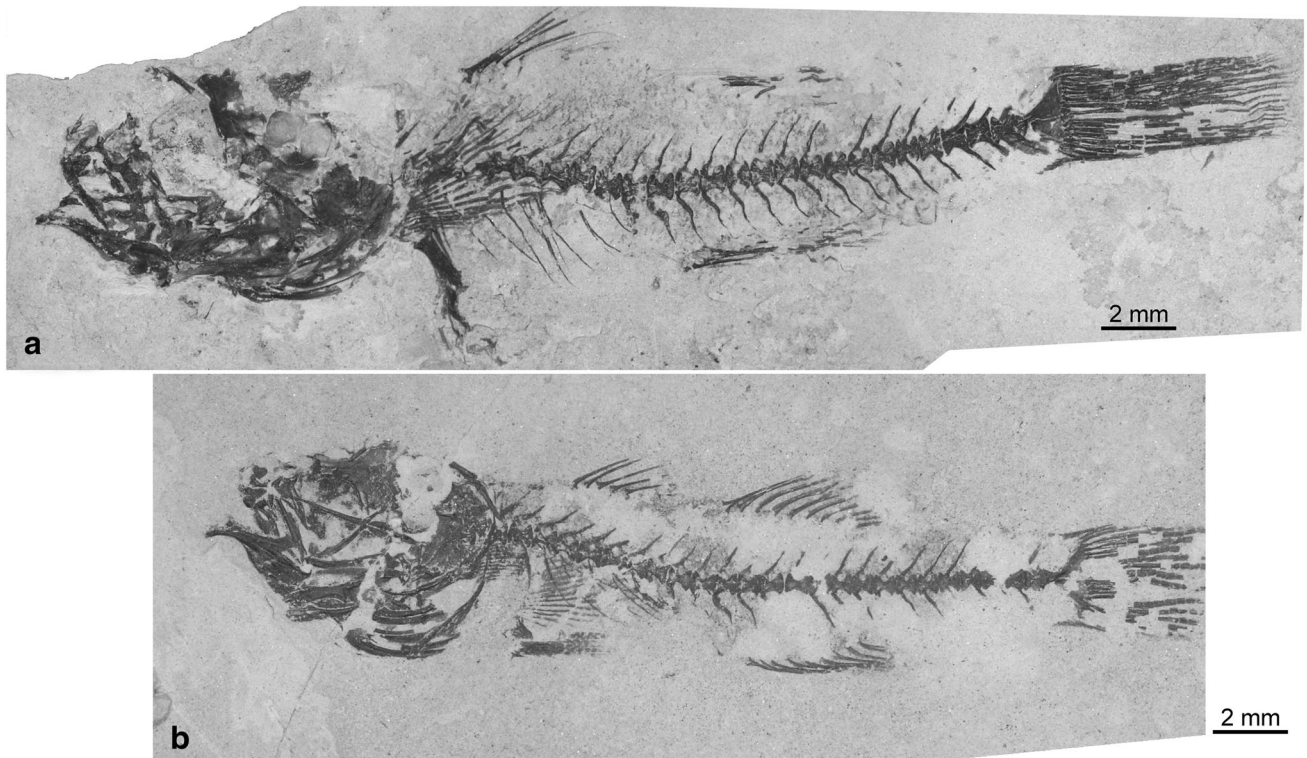


Fig. 7 *Rhamphogobius varidens* Bradić-Milinović, Ahnelt, Schwarzhans n.sp. Articulated skeletons. **a** RGFAJ 9, paratype. **b** RGFAJ 70, holotype

Median fins The first dorsal has six spines. Their pterygiophores are not discernible, but the position of the dorsal spines suggests the following: a dorsal pterygiophore pattern 3-2211001, the first two pterygiophores insert in interneural space three (IS3), the third and the fourth in IS4, the fifth in IS5, and the sixth in IS6, followed by two free interneural spaces (IS7 and IS8) between the first and the second dorsal fins. The first spine of the second dorsal fin inserts in IS9 (Fig. 7b). The second dorsal fin is higher than the first. The gap between both dorsal fins is distinct and wide. The second dorsal fin has one spine and nine fin rays (I + 9) (Fig. 7b). The anal fin has one spine and eight fin rays (I + 8). The anal fin originates slightly posterior of the origin of the second dorsal fin, with the anal spine opposite to the second fin ray of the second dorsal fin (Fig. 7b). Two pterygiophores of the anal fin seem to precede the first haemal spine. The anal fin base reaches to about a vertical line through the 10th caudal vertebra and terminates below the termination of the second dorsal fin base (Fig. 7b).

Paired fins and girdles Three elements are discernible: the long, dorsally bifurcated cleithrum; the narrow, elongated supracleithrum; and the posttemporal with both arms (Fig. 8a, b). The laminar body of the posttemporal is narrow and carries a groove for the posttemporal canal of the lateral line system; its dorsal arm is broad and long and its

ventral arm narrow and in contact with the intercalary (Fig. 8a, b). The pectoral fins have 15 rays (Fig. 8a, b). The pelvic girdle and exact number of pelvic fin rays are not discernible.

Scales Scales are preserved over large parts of the trunk of specimen RGFAJ 9. A series of scales with 10–12 cteni can be identified on the posterior rim ventral to the origin of the second dorsal fin. They are ctenoid and small. They are particularly small anteriorly, below the first dorsal and in the gap between both dorsals, at about 0.5 mm in diameter (Fig. 9c). Scales are slightly larger, at about 0.65 mm in diameter, along the rear part of the trunk below the second dorsal (Fig. 9d) and above the anal fin (Fig. 9e). The scales are arranged in six rows from second dorsal fin spine to third fin ray, all with cteni of the same size.

Otolith (sagitta) The otoliths are nearly quadratic in outline. Both extracted in situ specimens are 0.95 mm long (Fig. 9f–j). OL:OH = 0.95; OH:OT = 3.0. The dorsal rim is gently curved and somewhat irregularly undulating. Its predorsal and postdorsal angles are rounded, not notably projecting, and not bent outwards. The ventral rim is shallow, almost flat, horizontal, and smooth. It shows a rectangular preventral angle and a broadly rounded postventral angle. The anterior rim is straight and vertical, without concavity. The posterior rim is about as high as the

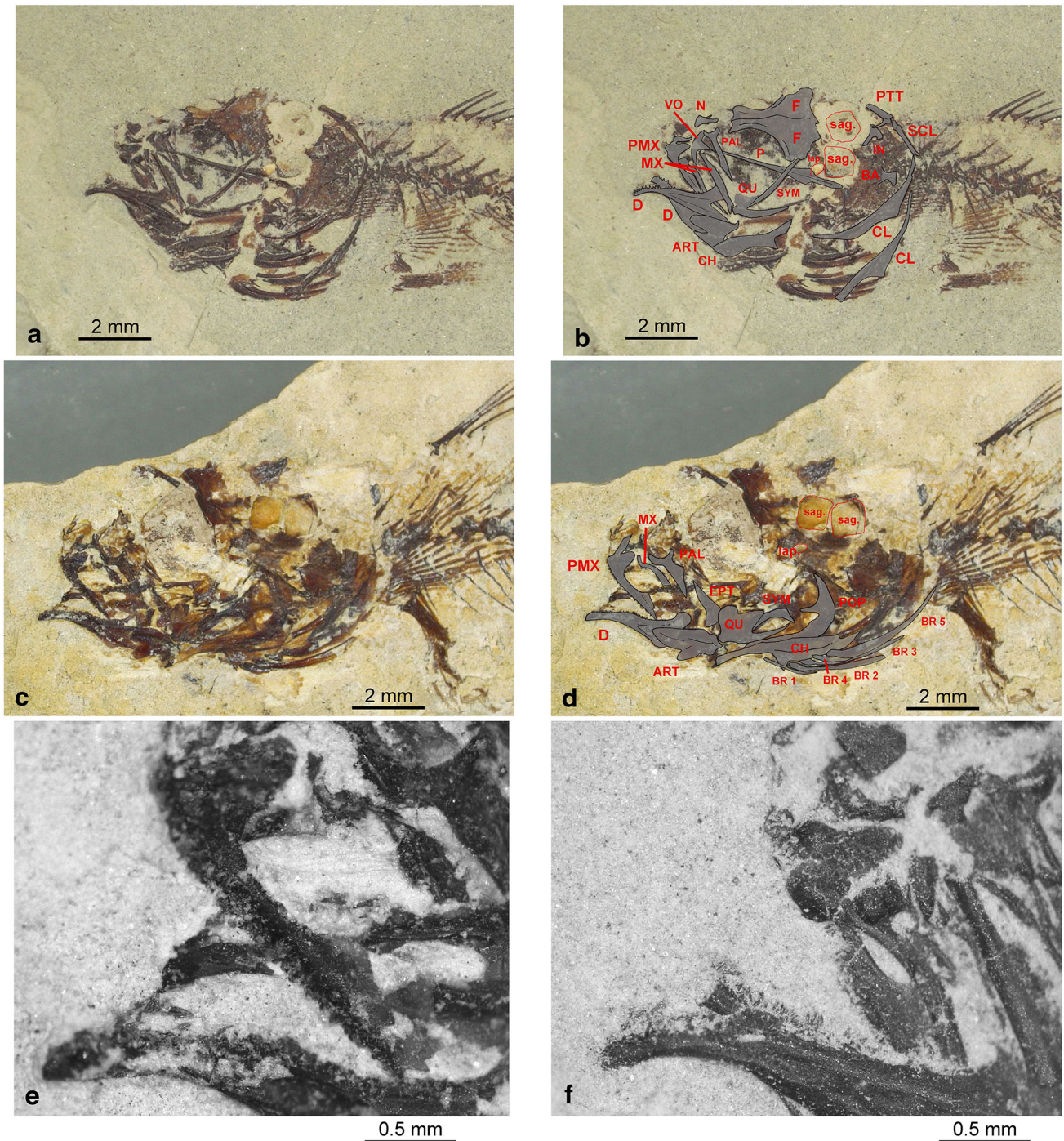


Fig. 8 *Rhamphogobius varidens* Bradić-Milinović, Ahnelt, Schwarzhan n.sp. Close-up photographs of heads and dentition. **a**, **b** RGFAJ 70 (holotype); **b** with interpretative overlay of photograph

anterior rim, vertical, and with a slight concavity at about the level of the cauda.

The inner face is almost flat. The sulcus is moderately large, moderately wide, somewhat deepened, and inclined at 14° to 20°. OL:SuL = 1.85–1.9. The dorsal margin of the sulcus forms an almost continuous arc with only an

shown in **a**, **c**, **d** RGFAJ 9 (paratype); **c** with interpretative overlay of photograph shown in **d**. **e** Close-up view of dentition of RGFAJ 9 (paratype). **f** Close-up view of dentition of RGFAJ 70 (holotype)

incipiently developed shallow ostial lobe. A small-to-medium-sized oval subcaudal iugum is situated below the anterior and middle part of the cauda. The dorsal field shows a wide but poorly marked depression. The ventral field shows a distinct, deep, relatively narrow, half-moon-shaped ventral furrow running at considerable distance

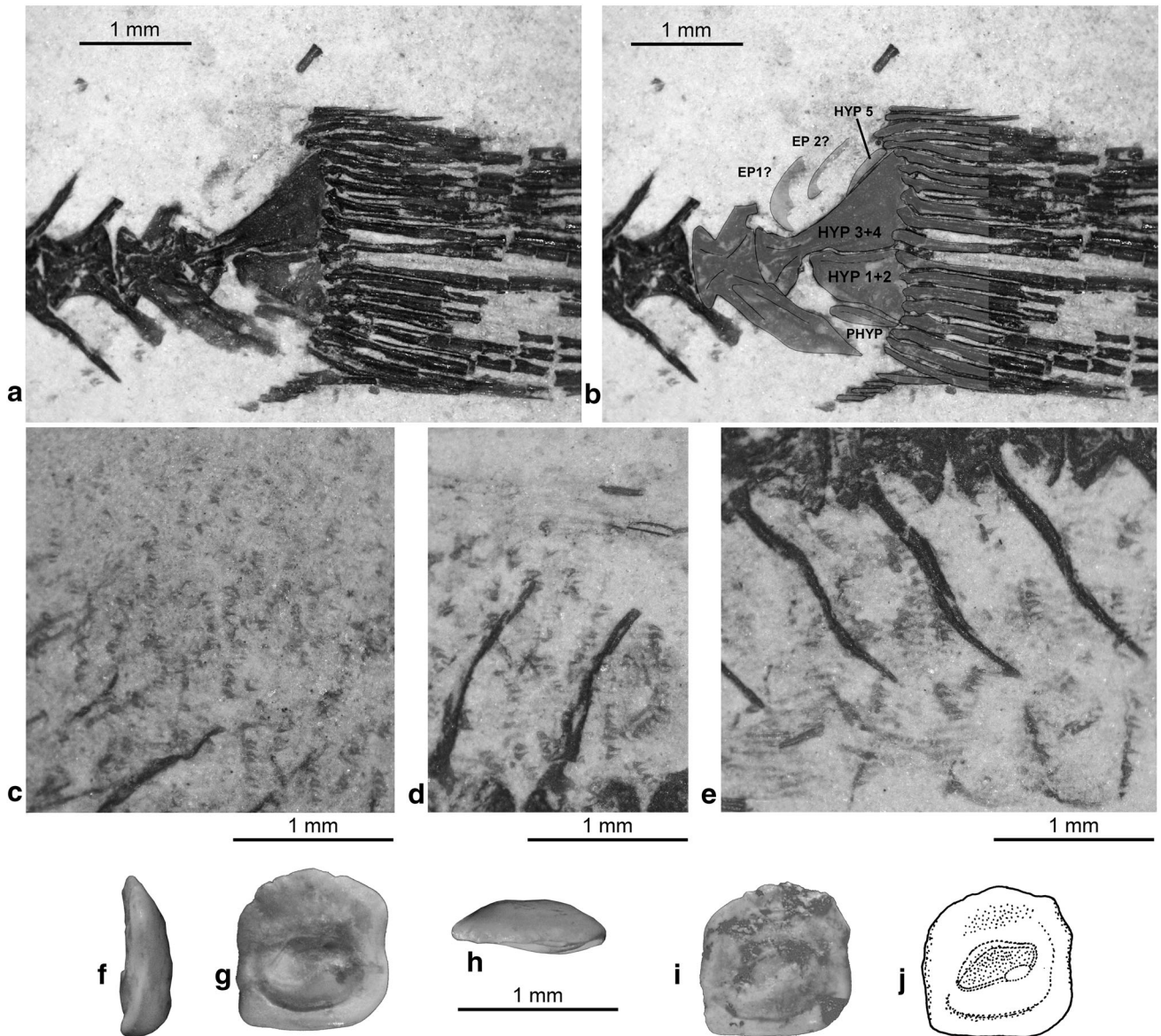


Fig. 9 *Rhamphogobius varidens* Bradić-Milinović, Ahnelt, Schwarzahns n.sp. Detail photographs and drawings. **a, b** Caudal skeleton of RGFAJ 9 (paratype); **b** with interpretative overlay of photograph shown in **a**. **c–e** Detail photographs of scales of RGFAJ 9 (paratype); **c** dorsally on trunk in front of first dorsal fin, **d** dorsally on

trunk behind first dorsal fin, **e** ventrally on tail. **f–h** Otolith of RGFAJ 9 (paratype); **f** view from posterior, **g** inner face, **h** view from dorsal. **i–j** Otolith of RGFAJ 70 (holotype), inner face; **j** interpretative drawing of **i**

from the ventral rim of the otolith, starting from the anterior tip of the ostium and continuing as a faint line behind the posterior tip of the cauda to meet the posterior area of the dorsal depression. The outer face is distinctly convex and smooth.

Genus *Toxopyge* Bradić-Milinović, Ahnelt, Schwarzahns n.gen.

Type species *Toxopyge campylus* Bradić-Milinović, Ahnelt, Schwarzahns n.sp.

Etymology From *toxon* (Greek = bow) and *pyge* (Greek = cheek), referring to the strongly bent and highly diagnostic shape of the maxilla. Gender masculine.

Diagnosis A genus of the family Gobiidae (subfamily indet.) with the following combination of characters: 26 vertebrae, of which 10 are abdominal; five branchiostegal rays; neural spines of vertebrae 1–4 distinctly depressed, those of 5–7 slightly. First dorsal fin with six spines, second dorsal fin with one spine and nine rays; anal fin with one spine and eight rays. Last first dorsal fin pterygiophore inserts between neural spines six and seven; two free

interneural spaces between neural spines 8–9 and 9–10; first pterygiophore of second dorsal fin inserts between neural spines nine and 10; dorsal fin pterygiophore formula 3-2211001. Anal fin originates slightly posterior to origin of second dorsal fin, with anal spine opposite first or second ray of second dorsal fin. One pterygiophore precedes first haemal spine. Anal fin base reaches to about vertical through seventh caudal vertebra and lines up with termination of second dorsal fin base. Scales ctenoid. Head massive, large, with terminal snout, head length mean 33.0% of SL, head depth 26.4% of SL; pectoral fin length mean 12.1% of SL. Dentary of lower jaw narrow and elongate, and its dorsal edge carries three to four rows of large canine teeth. Premaxilla without postmaxillary process. Maxilla convex, regularly bent but anteriorly distinctly hook-shaped. Otolith outline trapezoidal, without postdorsal process. OL:OH = 1.05–1.25. Inner face almost flat. Sulcus short, its dorsal margin regularly bent without ostial lobe. No subcaudal iugum.

Discussion *Toxopyge* is readily recognized by a unique combination of plesiomorphic and advanced characters. The 10 abdominal vertebrae is the first to mention. The number of precaudal and caudal vertebra in most basal gobiionellines, gobiines, and oxudercines is 10 +16 (total 26) (Larson 2001) as in *Toxopyge* and is considered to indicate a plesiomorphic character status (Gill 1994; Simonovic et al. 1996; McKay and Miller 1997). Then, the depressed neural spines on the anterior vertebrae must be considered a derived character and are very unusual in the Gobioidae. Another unusual character not observed in any other gobies known to us is the shape of the maxilla, which has a strong, hook-like bend at its anterior tip. Further putative apomorphic characters or unusual characters are the lack of the postmaxillary process on the premaxilla, the presence of two free interneural spaces between the pterygiophores of the first and the second dorsal fin, and the presence of only one anal pterygiophore preceding the first hemal spine. The otoliths are also highly diagnostic, showing a trapezoidal outline without postdorsal projection, a sulcus with a regularly bent dorsal margin without ostial lobe, and, finally, the absence of a subcaudal iugum. These are all considered plesiomorphic otolith character states commonly found in eleotrids but not gobiids.

There are no extant or fossil gobioid fishes with which we could comfortably compare *Toxopyge*. The lack of the postmaxillary process and the two free interneural spaces resemble the pattern found in European sand gobies, and both are considered as apomorphic characters of that group (McKay and Miller 1997). However, the dorsal pterygiophore formula of *Toxopyge*, the presence of only one anal pterygiophore preceding the first hemal spine, and the low number of abdominal vertebrae (10)

contradict a relationship with European sand gobies. In addition, the otolith pattern is not consistent with that found in extant sand gobies, or fishes of the *Gobius* group. We, therefore, regard *Toxopyge* as representing an extinct lineage of unresolved relationships within the family Gobiidae. However, there is an otolith-based species from the Karpatian of northeast Switzerland that bears some semblance: *Gobius longus* Salis 1967 (see Reichenbacher 1993 for figures), which is here also referred to as *Toxopyge*. The absence of a postdorsal projection and of a subcaudal iugum, as well as the broad ventral furrow, are shared between both species. However, the otoliths of *T. longus* show a much more regular outline than *T. campylus*, with very little sculpture and a relatively low dorsal rim. *Toxopyge longus* also differs in the commonly observed deep ingression of the ventral sulcus margin at the ostial-caudal joint, which is not observed in *T. campylus*.

Species A single species from the early Miocene of the Valjevo freshwater lake in Serbia: *Toxopyge campylus* n.sp. The otolith-based species *Gobius longus* Salis 1967 from the Karpatian of northeast Switzerland is here also referred to *Toxopyge*.

Toxopyge campylus Bradić-Milinović, Ahnelt, Schwarzhan n.sp.

(Figs. 10, 11, 12).

Holotype RGFAJ 57, an articulated skeleton measuring 31.1 mm SL with otoliths in situ, Klinči, Serbia, early Miocene.

Paratypes Six articulated skeletons, three of which with otoliths in situ, RGFAJ 18, 49, 68, 75, 101, 135, and two isolated otoliths, RGFAJ 76, 97.

Etymology From *campylos* (Greek = curved), referring to the curved maxilla.

Diagnosis See diagnosis of genus.

Description Table 3 presents counts and measurements.

Neurocranium The skull is dorso-laterally compressed in both figured specimens. Most bones are incomplete and fragmented, and their shapes are barely identifiable. The frontals are mostly complete, with a narrow interorbital region, and then widen distinctly posteriorly, forming a large part of the cranial roof; the interorbital section and the edge of the frontals form the posterior rim of the orbit and show a distinct groove-like depression for the supraorbital canal of the head lateral-line system (Fig. 11a–d). The parasphenoid is long and narrow and wider posteriorly; its posterior end not discernable (Fig. 11c, d).

Table 3 Meristics and morphometrics of *Toxopyge campylus*

	<i>Toxopyge campylus</i>	
	HT-RGFAJ57	6 PT's
SL (mm)	31.1	33.5–45.9
Otolith in situ	Yes	5
<i>Meristics</i>		
Precaudal vertebrae	10	10
Total vertebrae	26	26
D1	VI	VI
D2	I + 9	I + 9
A	I + 8	I + 8 (7)
Pectoral	17	
D1 last ray between NS	NS6–NS7	NS6–NS7
Empty neural spines	NS7–NS8	NS7–NS8
D2 first Pt between NS	NS8–NS9	NS8–NS9
Caudal principle	15	15
Dorsal Pt formula	nm	(3)11211001 (in RGFAJ101)
Anal Pt1 to opposite to	D1/1 or 2	D1/1 or 2
Postmaxillary process on PMX	No	No
EPU		
AP	1	1
SOP anterior-ventral shape	Hook-like	Hook-like
Scale type		Ctenoid
<i>Morphometrics (% of SL)</i>		
Head length	33.4	30.9–34.6
Head height	24.7	26.0–28.5
Max. body height	23.2	17.6–22.0
Orbit diameter	9.6	
D1 length	20.2	13.9–19.7
A length	21.5	15.4–17.3
PL-pectoral length	12.2	9.6–14.4
predorsal to D1	41.1	41.5–42.9
Predorsal to D2	63.0	58.8–60.1
Pereanal	66.2	63.0–64.7
Base of D1	13.2	11.5–14.6
Base of D2	16.4	19.1–19.8
Base of A	14.1	16.1–17.2

Jaws The premaxilla is elongate and very narrow, with two distinct processes: a long and narrow ascending process and a shorter but wider maxillary process. Both processes are separated by a deep notch; a postmaxillary process is not developed; teeth are large and conical close to the symphysis but decrease in length posteriorly (Fig. 11e–f); the premaxilla is long but shorter than the dentary (Fig. 11a–d). The maxilla is long, convex, gradually widening posteriorly, and anteriorly shows an unusual

large, regularly bent, and distinct hook-shaped beginning (Fig. 11a–d). The dentary is narrow and elongate; it increases in height gradually towards posterior in a distinct coronoid process; its posterior end is notched; the dorsal edge of the dentary is wide, carrying three or four rows of large, canine-like teeth; posteriorly, the teeth are smaller, and the number of tooth rows decreases (one to two rows) (Fig. 11e–f). The anguloarticular inserts with its large dorsal arm medially in the notch of the dentary; its ventral arm is weakly developed and short, thus leaving a distinct indentation in the ventral edge of the lower jaw; posteriorly, a large socket is developed (Fig. 11a–f). The retroarticular is triangular and attached to the postero-ventral edge of the anguloarticular.

Opercular series The opercle is large and more or less triangular in shape. The subopercle shows a distinct anterior hook, and the long, blade-like interopercle is mostly covered by the hyoid (Fig. 11a–d). The preopercle is crescent-shaped and shows a distinct symplectic process at its wider dorsal part, which, in combination with the narrow ventral part, forms the postero-ventral border of the well-developed foramen suspensorium (suspensorial interspace) (Fig. 11a–d).

Suspensorium The quadrate consists anteriorly of a large laminar body and a long, narrow process; this slightly curved process extends postero-dorsally and is closely connected to the ventral arm of the preopercle (Fig. 11a–d). The symplectic is long, rod-like, and distinctly widened at its dorsal end. The posterior edge of the symplectic in combination with the preopercular process forms the anterior-dorsal border of the well-developed foramen suspensorium (Fig. 11a–d). The ectopterygoid is short, with an expanded posterior part; anteriorly, it is attached to the palatine (Fig. 11c, d). The anterior end of the palatine shows two processi: antero-laterally, the maxillary process and, medio-dorsally, the ethmoidal process, resulting in the anterior tip of the palatine having a T-shaped appearance. The margin between both processi is deeply concave (crescent-shaped) (Fig. 11c, d).

Hyoid bar and gill arches. The hyoid bar is large and massive. Five branchiostegal rays are ventrally connected to it: The first, rib-like ray inserts on the narrow anterior part, followed by three blade-like branchiostegals of the wide posterior part of the anterior ceratohyal; the fifth branchiostegal, the widest, attaches at the posterior ceratohyal (Fig. 11a–d). Note that the branchiostegals of one specimen are detached and shifted antero-dorsally (Fig. 11a, b). The basihyal can be seen posteriorly between the lower jaws. It is a fan-shaped bone with a knob-like posterior end (Fig. 11c, d).

Axial skeleton The vertebral column consists of 26 vertebrae including urostyle, of which 10 are abdominal and 16 caudal (Fig. 10a–c). The neural and haemal spines are narrow, elongated, pointed, and of similar length, except those of the second and third preural vertebrae (PU2 – PU3), which are modified. The neural spines of the first six to seven vertebrae are depressed (angle of about 45° – 60°), and the subsequent ones are erected (angle of about 80°) (Fig. 10a–c). The neural and the haemal spines of PU3 are distally extended; the neural spine of PU2 is short and distinctly extended; the haemal spine is long and broad (Figs. 10a, b, 12a, b). In addition, PU4 is also incorporated into the caudal skeleton as the neural, and the haemal spines of these three vertebrae extend at a steeper angle posteriorly than the preceding. The neural and haemal spines insert anterior on the vertebral center, except those of PU2–5, which insert posterior on the center (Fig. 10a, b). Eight

pleural ribs are developed, extending laterally from abdominal vertebra 3–10; no rib is discernable on the 11th abdominal vertebra (Fig. 10b–c). The parapophyses of vertebrae 9–11 are ventrally directed. Epineural ribs are also present (Figs. 10c, 11).

Caudal skeleton The caudal skeleton consists of an elongate and narrow parhypural; two hypural plates, the first formed by the fused hypurals 1 + 2, the second by the fused hypurals 3 + 4; the first plate is attached ventrally to the urostyle; the second plate is fused to its posterior end; a small, narrow hypural 5; a single, large epural (Fig. 12a, b). Fifteen caudal fin rays insert between the epural and the haemal spine of PU2 (Fig. 12a, b).

Median fins The first dorsal fin has five to six spines, each carrying one pterygiophore. The insertion scheme of the first pterygiophores is difficult to evaluate due to the

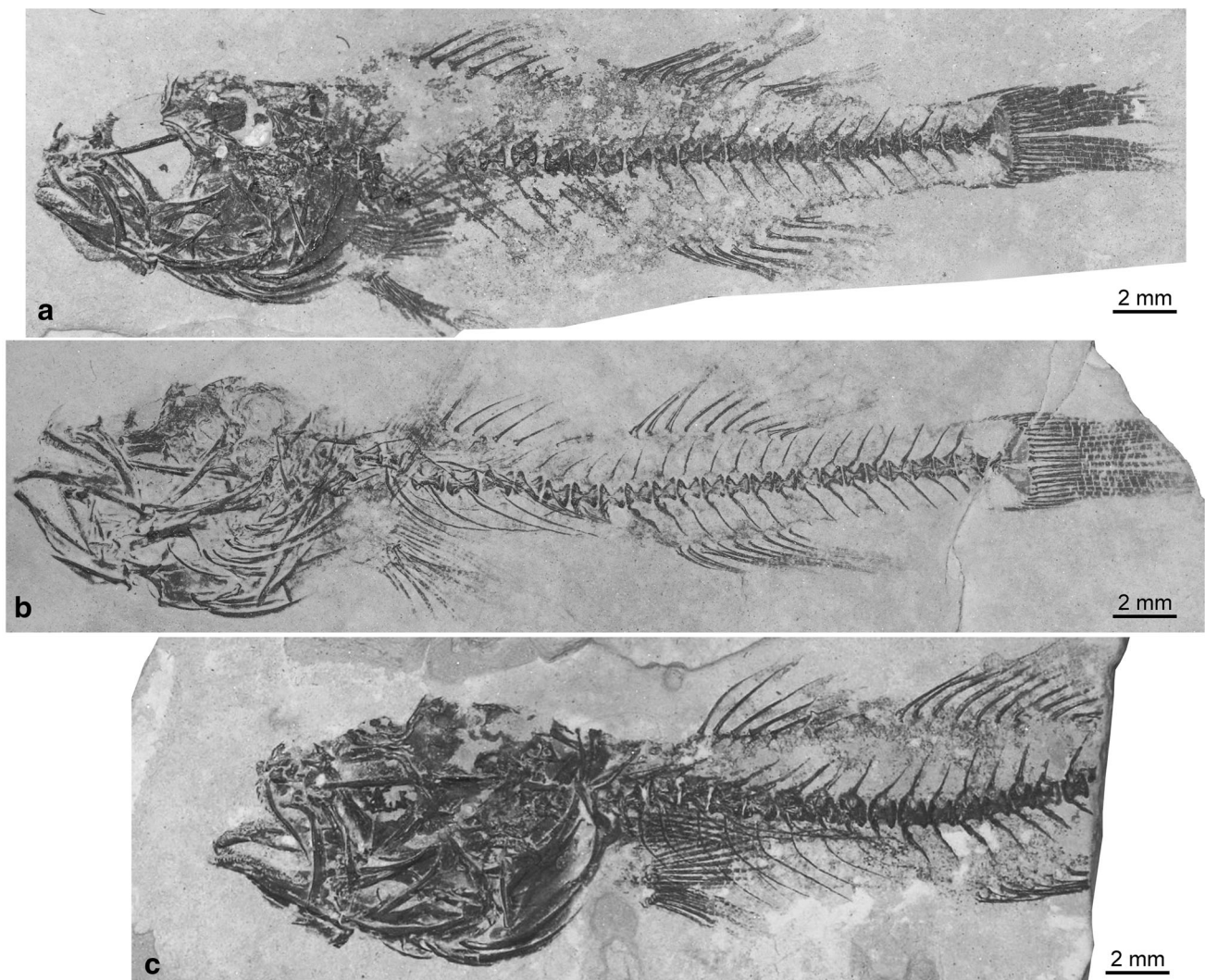


Fig. 10 *Toxopyge campylus* Bradić-Milinović, Ahnelt, Schwarzahns n.sp. Articulated skeletons. **a** RGFAJ 57 (holotype). **b** RGFAJ 18 (paratype). **c** RGFAJ 101 (paratype)

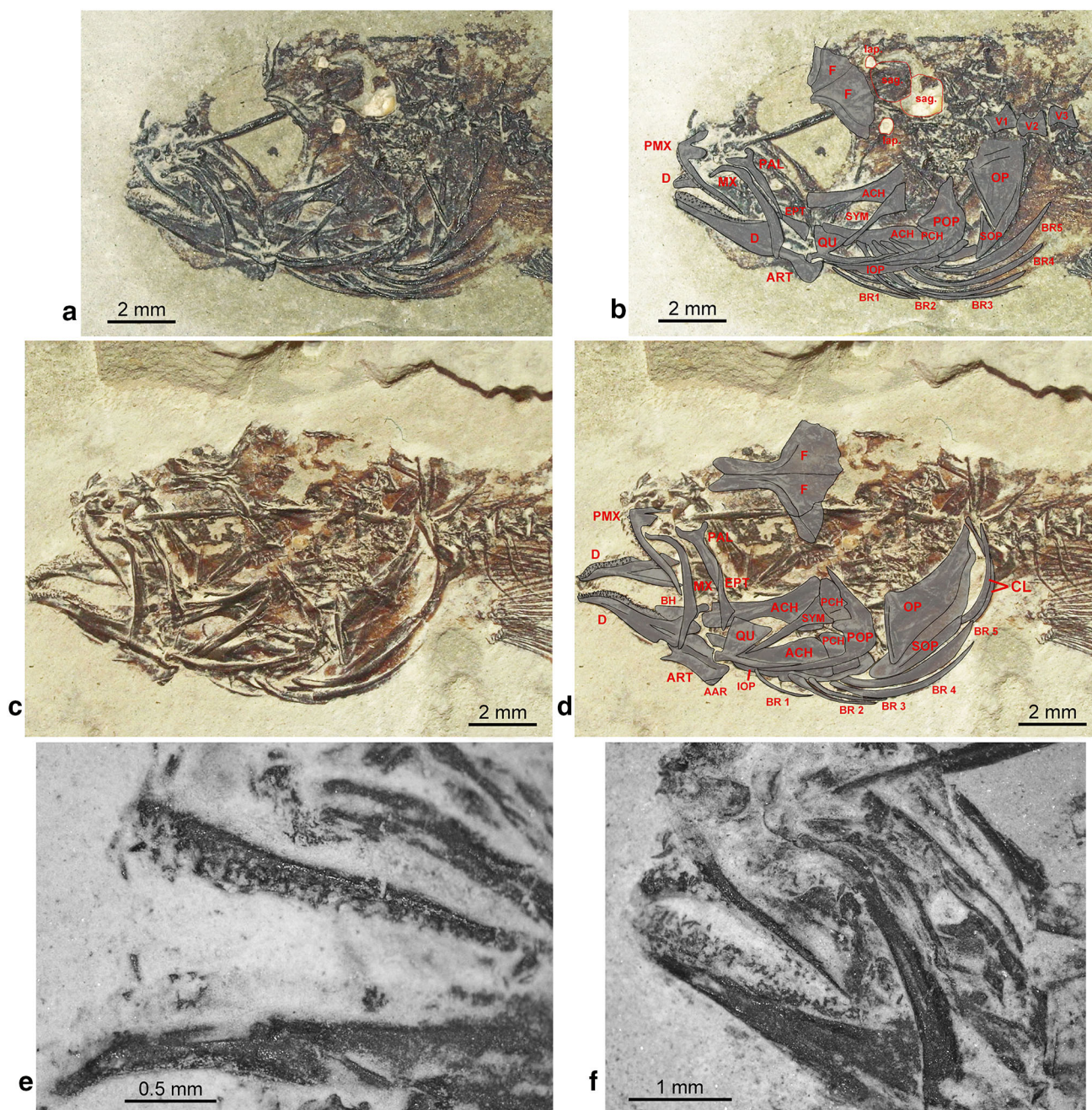


Fig. 11 *Toxopyge campylus* Bradić-Milinović, Ahnelt, Schwarzhanz n.sp. Close-up photographs of heads and dentition. **a**, **b** RGFAJ 57 (holotype); **b** with interpretative overlay of photograph shown in **a**. **c**,

d RGFAJ 101 (paratype); **d** with interpretative overlay of photograph shown in **c**. **e** Detail photograph of dentition in RGFAJ 18 (paratype). **f** Detail photograph of dentition in RGFAJ 57 (holotype)

depressed nature of the first neural spines and is best seen in RGFAJ 101 (Fig. 10c). The first two pterygiophores insert in interneural space three (IS3), the third and the fourth in IS4, the fifth in IS4, and the sixth in IS6. The dorsal pterygiophore formula is difficult to assess due to the nature of the depressed anterior neural spines and dislocation of pterygiophores; the pattern is best preserved in specimen RGFAJ 101 (Fig. 10c) and is interpreted as 3-2211001. Although the pterygiophores of the second

dorsal fin are not discernable, the first spine of the second dorsal fin is in a position such that its pterygiophore very likely inserts in IS9 (Fig. 10b, c). The second dorsal fin is distinctly higher than the first (Fig. 10a, b). The gap between both dorsal fins is moderately wide (Fig. 10a–c). The second dorsal fin has one spine and nine fin rays (I + 9) (Fig. 10a–c). The anal fin has one spine and eight fin rays (I + 8). The anal fin originates slightly posterior to the origin of the second dorsal fin, with the anal spine

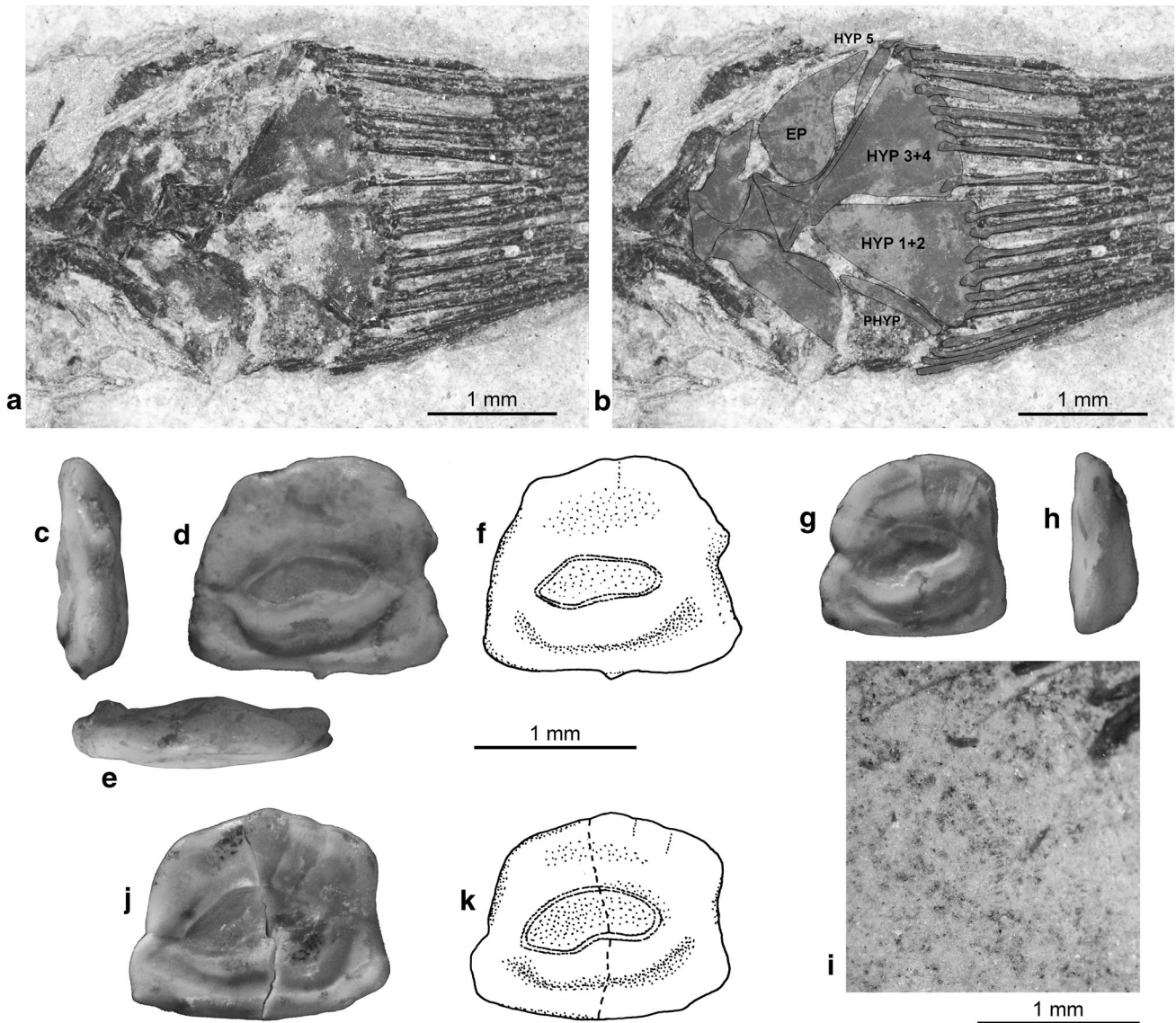


Fig. 12 *Toxopyge campylus* Bradić-Milinović, Ahnelt, Schwarzhans n.sp. Detail photographs and drawings. **a, b** Caudal skeleton of RGFAJ 49 (paratype). **c–f** Otolith of RGFAJ 49 (paratype); **c** view from posterior, **d** inner face, **e** view from dorsal, **f** interpretative

drawing of inner face. **g–h** Otolith of RGFAJ 57 (holotype); **g** inner face, **h** view from posterior. **i** Detail photograph of scales of RGFAJ 75 (paratype). **j–k** Otolith of RGFAJ 76 (isolated otolith); **k** interpretative drawing of inner face of **j**

opposite the first (Fig. 10b) or second (Fig. 10a, c) fin ray of the second dorsal fin. One pterygiophore precedes the first haemal spine. The anal fin base reaches to about a vertical through the seventh caudal vertebra and lines up with the termination of the second dorsal fin base (Fig. 10a, b).

Paired fins and girdles The pectoral and the pelvic girdle are not discernible. There appear to be 17 pectoral fin rays in specimen RGFAJ 57 (Fig. 10a). The pelvic fins each show one short spine and five rays (I + 5) (Fig. 10b).

Scales Only a few scales are preserved in specimens RGFAJ 49 and 75, near the base of the second dorsal fin.

They are ctenoid, rather large (at about 1.1 mm in diameter), and carry 18–20 cteni on the posterior rim ventral to the origin of the second dorsal fin (Fig. 12i). The scales are arranged in five rows from second dorsal fin spine to third fin ray, and all cteni are of the same size.

Otolith (sagitta) The otoliths show a trapezoidal outline. The largest specimen is 1.6 mm long (Fig. 12c–f) and stems from specimen RGFAJ 49, with an SL of 45.9 mm. OL:OH = 1.05–1.25, apparently increasing with size; OH:OT = 2.5–3.0. The dorsal rim is short, shallow, and highest at its middle, sometimes with an obtuse mediodorsal angle. Its predorsal and postdorsal angles are rounded; the postdorsal angle is reduced and not projecting.

The ventral rim is shallow, almost flat, horizontal, smooth, and distinctly longer than the dorsal rim. It shows slightly projecting pre- and postventral angles. The anterior rim is upward and backward inclined at about 75°–80° without concavity but sometimes with a narrow and shallow incision. The posterior rim is about as high as the anterior rim, upward and forward inclined at about 75°–85°, and with a very slight concavity at about the level of the cauda.

The inner face is almost flat. The sulcus is rather small, relatively narrow, somewhat deepened, and inclined at 8° to 15°. OL:SuL = 2.0. The dorsal margin of the sulcus forms an evenly curved continuous arc without ostial lobe. A subcaudal iugum is not developed. The dorsal field shows a wide but poorly marked depression. The ventral field shows a distinct, deep, half-moon-shaped ventral furrow that widens towards its terminations, which do not reach up to the anterior and posterior tips of the sulcus. It runs at considerable distance from the ventral rim of the otolith. The outer face is slightly convex and smooth.

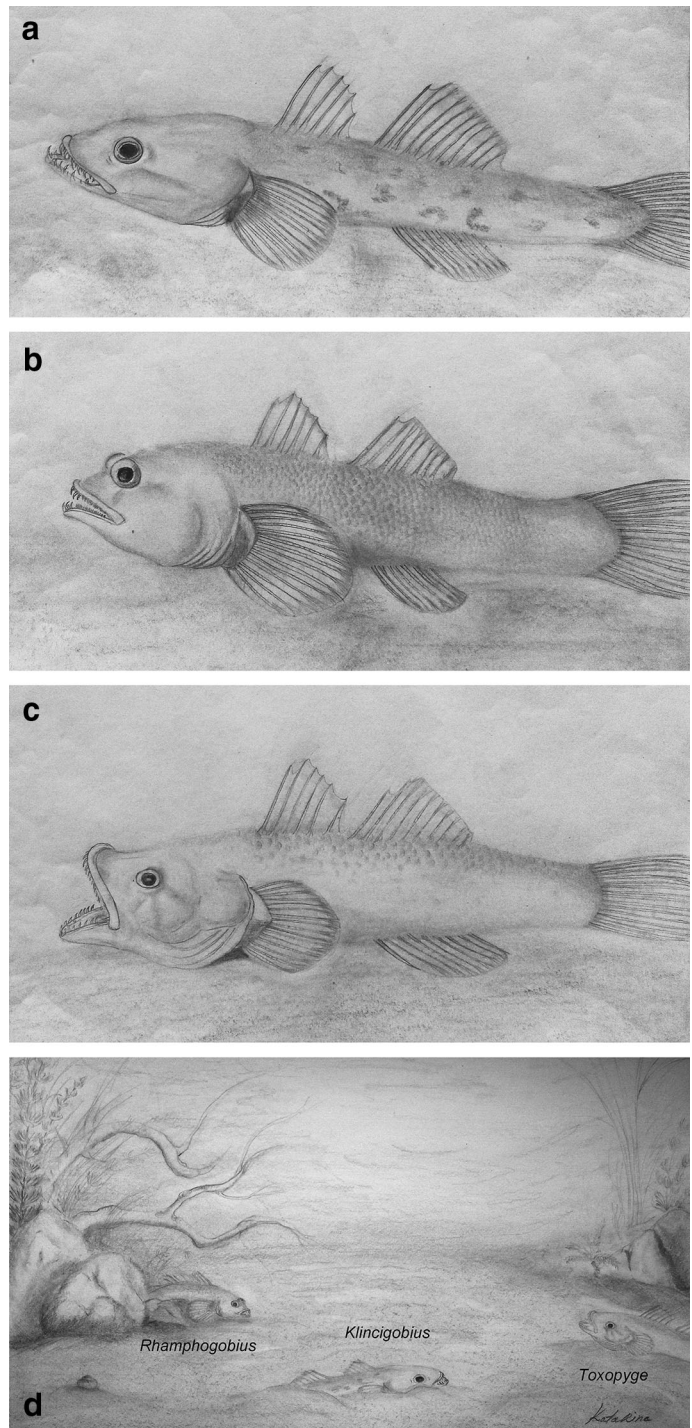
Faunal reconstruction of fishes in an early Miocene Serbian lake

The Valjevo-Mionica Basin (VMB) is a small basin within the larger Serbian Lake System (SLS), which formed during the late early and early middle Miocene prior to the Badenian transgression (Krstić et al. 2003, 2012; Sant et al. 2018a; Mandić et al. 2019). The VMB formed a narrow graben extension along the northwestern edge of the SLS that originated during the Ottnangian to Karpatian (Lazarević et al. 2013). The authors recognized three lacustrine formations prior to the Sarmatian transgressive marine-brackish sequence. These three lacustrine deposits are (in ascending order): the pyro-bituminous Mionica Formation, the marly Valjevo Formation, and the clastic Tabanovići Formation. The Mionica Formation is rich in plant fossils representing evergreen rain forests in a humid, subtropical environment (Lazarević et al. 2013). Gaudant (1998) identified isolated remnants of clupeids and cyprinids in the pyro-bituminous paper shales of the Mionica Formation. Both were probably fishes swimming closely below the surface of the paleolake, where “oxygen from the air had dissolved in the upper layer of the water column” (Lazarević et al. 2013). Furthermore, cyprinids are classical stenohaline freshwater fishes. The early stage, in which the lake was small and enclosed and had densely vegetated shores was characterized by weak horizontal circulation without major freshwater supply and an anaerobic environment in the deep lake (Jovanović et al. 1994). It appears that several small isolated lakes existed during the early phase of the formation of the SLS with similar anaerobic environments, which led to the deposition of kerogen-enriched oil shales (Šajnović et al. 2009).

The situation changed drastically with the onset of the marly Valjevo Formation and the cessation of the deposition of pyro-bituminous shales, which indicates better water circulation in a well-oxygenated lake, probably enhanced by some interconnectivity within the SLS. This environmental change would also have enhanced the population with more benthic lentic fishes such as the Gobiidae. The epipelagic Clupeidae and Cyprinidae of the preceding phase are no longer in evidence. The abundance of well-articulated gobiid skeletons found in the Klinči water well, however, indicates that the environmental situation of the Valjevo Lake may not have been consistently stable and that toxic phases may have occurred in which, for instance, interruptions of oxygen supply led to mass fish mortality events. One could further speculate that such oxygen-deficit phases only affected benthic fishes, that is, gobiids, which are, therefore, found in such large numbers, while epipelagic lake fishes are completely absent from the fossil record at Klinči.

The fishes of the three identified gobiid genera all show clear indications of highly specialized environmental adaptations (Fig. 13). *Klincigobius* is the largest of the three gobiid genera found in Klinči (Fig. 13a). It is characterized by a large mouth cleft, slender dentaries, and many long, fang-like conical teeth along the dentary and premaxilla. The head is rather broad, with a poorly bent ventral profile and a depressed dorsal profile. This is typical of an ambush hunter resting on the sea bottom or lurking (partly) submerged and preying on smaller fish (Fig. 13d). It was probably well camouflaged against the sea bed background. *Toxopyge* is the second largest goby found at Klinči (Fig. 13b). It differs from *Klincigobius* in having a more regularly shaped head. Its dentition shows large conical teeth anteriorly both on premaxilla and dentary and smaller teeth laterally. The most prominent feature is the strongly bent maxilla. This would probably enhance the widening of the mouth when opening, which, for instance, could have been beneficial for sucking in smaller invertebrates. *Rhamphogobius* is the smallest of all the Klinči gobies (Fig. 13c). It has a rather stout body shape and a broad head, with a short, broad snout and a short mouth cleft. The strange bent of the anterior tip of the dentary is probably largely a taphonomic effect. The other unusual feature of *Rhamphogobius* is the dentition, which mostly consists of short cylindrical teeth, often very narrowly packed, and just a few long conical teeth at the tip of the dentary. *Rhamphogobius* was probably a highly specialized fish that fed on small invertebrates. The short, broad snout probably helped to feed from unyielding surfaces, such as hard grounds or leaves. Its stout body shape would have been helpful in terms of maneuvering in narrow space or between vegetated environments close to shore (Fig. 13d).

Fig. 13 Life in the Valjevo Lake during the late early Miocene, Valjevo Formation. The individual reconstructions aim at visualizing the external meristic and morphometric characters, including the head shape and proportions, as well as dentition: **a** *Klincigobius* (slender body and head shape, the latter with depressed dorsal profile; snout inferior, long, and with curved canine teeth). **b** *Rhamphogobius* (short body with broad head, short snout, few canine teeth anteriorly and predominantly columnar teeth laterally, and beak-like tip of dentary). **c** *Toxopyge* (moderately slender body shape and head, curved maxilla facilitating wide mouth opening, many canine teeth). **d** Visualization of the lives of the three gobiid genera in their putative natural habitat: *Klincigobius* (ambush predator partly hidden in sand), *Rhamphogobius* (agile small fish hiding in freshwater vegetation and feeding on small crustaceans), and *Toxopyge* (suck-in predator in ambush position)



The lost early to early middle Miocene freshwater fish fauna of Europe

The early to early middle Miocene freshwater systems of central and southeastern Europe have yielded a rich fish fauna that is mostly documented by otoliths and occasionally underpinned by articulated fish skeletons, some containing otoliths in situ (Reichenbacher 1993;

Reichenbacher et al. 2007; Brzobohaty and Gaudant 2009; Gierl et al. 2013; Gierl and Reichenbacher 2015). What has emerged thus far is a fish fauna that bears little resemblance to that found in European freshwaters of today. It contained a variety of cyprinodontids, gobies, atherinids, and more exotic groups, such as channids (Reichenbacher 1993) and eleotrids (butines) (Gierl et al. 2013), of which contemporary freshwater representatives are only known from

Southeast Asia. None of the early to early middle Miocene freshwater fishes appear to be related to any of the extant freshwater fishes of the region. Instead, they were indicative of a then much warmer, subtropical climate and probably became extinct in Europe during the middle Miocene (compare with e.g., Bratishko et al. 2017 and Reichenbacher et al. 2018).

The fishes described here from Klinici, Serbia, further add to our knowledge of the lost early to early middle Miocene freshwater fish fauna of Europe. Two (*Rhamphogobius*, *Toxopyge*) of the three gobiid genera recognized are not related to extant European genera. The third, *Klincigobius*, may be related to present day marine gobines such as *Gobius*, but its lineage also does not seem to have persisted. The dominant modern European brackish and freshwater gobiid group, the Ponto-Caspian gobies, has first been observed in the late middle Miocene Konkian and Sarmatian (Schwarzahns et al. 2015, 2017 and Bratishko et al. 2017). The timing of the faunal turn-over during middle Miocene is consistent with that observed in freshwater gastropods (Neubauer et al. 2015a). Neubauer et al. explained the faunal turn-over after the Miocene climate optimum (MCO, c. 14 Ma) as a result of a combination of global cooling, decreasing regional precipitation, and increasing tectonic destruction of lake environments. The fossil freshwater gastropod database is much superior to that of freshwater fishes, and it would be logical to expect similar mechanisms at work for both faunal components.

The family Gobiidae is one of the largest of all teleosts. Their otoliths are highly characteristic but offer only a limited amount of morphological diversity for the identification of diagnostic characters at the genus level. This has hampered a more detailed analysis of isolated gobiid otolith finds in European freshwater sediments and has led to many of the nominal otolith-based species being recorded as species of *Gobius*. In reality, however, attribution to the genus “*Gobius*” must in many instances be understood as a mere representation of “a gobiid otolith.” Janssen (2012) introduced a method for such instances whereby the name-giving genus of the family associated with a “?” should be used to indicate an unknown genus of this family that could be extant or fossil (*Gobius?* species in this case). The find of many otoliths in situ in the fishes of Klinici, therefore, also represents a helpful discovery for the calibration of isolated otoliths. It has been shown that the two extinct gobiid genera *Rhamphogobius* and *Toxopyge* contain additional species to those observed in Klinici, which have hitherto been recorded as “*Gobius*” species, and that both genera were more widely distributed in the early to early middle Miocene of the European freshwater systems (Fig. 14). This repeatedly emphasizes how important otolith in situ calibrations truly are and how they contribute to improved understanding of past fish faunas.

Thus, a picture is now emerging of a diverse early to early middle Miocene gobiid freshwater fauna in central and southeastern Europe that vanished sometime after the MCO and is unrelated to the origin of the Ponto-Caspian gobiid association, which is found in contemporary seas, rivers, and lakes stretching from Italy through southeastern Europe to the Caspian Sea. The Gobiidae are not “primary freshwater fishes” in the sense of being stenohaline freshwater like, for instance, most Ostariophysii. Instead, many gobies are euryhaline fishes of brackish water environments that may migrate into freshwater environments and may then become adapted to them. Consequently, the extant Ponto-Caspian and Illyrian freshwater gobies are considered to have derived from migrated marine or brackish-marine stocks (Penzo et al. 1998). Schwarzahns et al. (2015, 2017) demonstrated that the origin of the Ponto-Caspian goby stock was intimately connected to the fractionation and brackish water development of the Sarmatian Sea in the Paratethys. The gobiid fishes in the freshwaters of the early to early middle Miocene, including the ones described here from the VMB in Serbia, stem from an earlier freshwater immigration, which at present cannot be dated. However, none of the early to early middle Miocene freshwater gobies have been found in coeval marine sediments, indicating that the colonization process of these fishes had reached maturity at the time. The same is true for any of the other early Miocene freshwater fishes, such as the Eleotridae, Atherinidae, or Channidae.

Neubauer et al. (2015) developed a gastropod-based biogeographic scheme for the European Neogene freshwater systems. They identified three European bioprovinces in the early Miocene and six in the middle Miocene. Fossil fish data are not nearly as dense and well-known as those of gastropods, but what is available thus far is consistent with these author’s scheme. In gobiids, we currently recognize at least three different faunal associations during this time interval (Fig. 14): (1) a Central European goby association in the early Miocene (Aquitania) in the Mainz, Hanau-Wetterau, and Upper Rhein basins, which is characterized by the “*Gobius*” *francofurtanus* group. This is a group of species which is partly known with articulated skeletons with otoliths in situ (Weiler 1961; Eikamp and König 1981) but requires review and probably represents a fossil lineage (see above). (2) The Upper Freshwater Molasse association of Switzerland, southern Germany, and the Czech Republic of Ottnangian to Karpatian age is particularly rich in gobies. It contains the genera *Eleogobius* (two species), *Rhamphogobius* (three species), and *Toxopyge* (one species), as well as two further gobiid species, which, at present, cannot be allocated to a genus (*Gobius?* *bolligeri* Reichenbacher 1993 and *Gobius?* *brzobohatyi* Reichenbacher 1993). Recently, the two *Eleogobius* species and two of the three

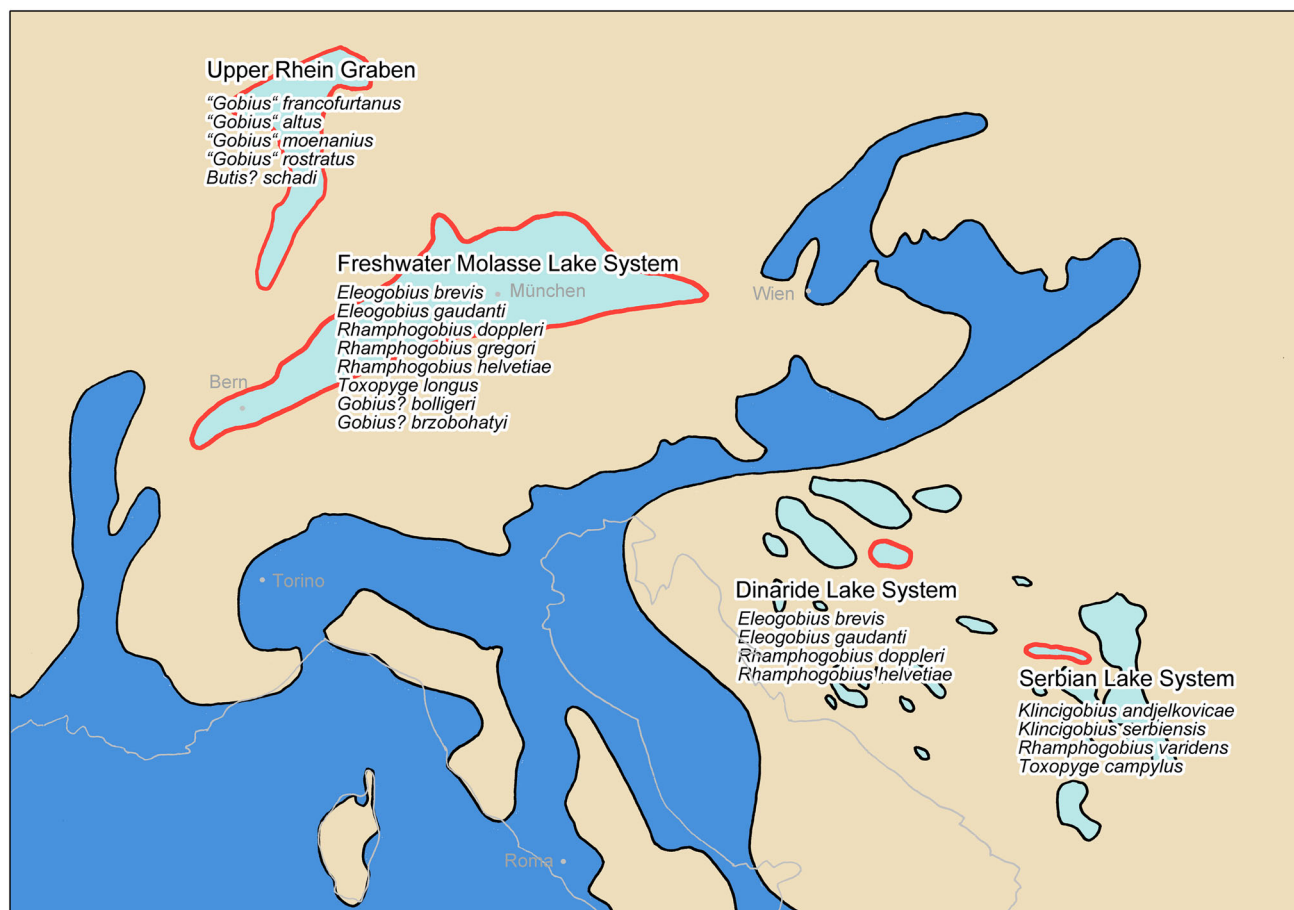


Fig. 14 The freshwater lake systems of central and southeastern Europe during the early and early late Miocene and the distribution of gobioid fishes. Paleogeographic reconstruction during early Badenian based on Mandić et al. (2019). Dark blue indicates marine

environments, light green–blue freshwater lake environments. Annotated faunal list reflects entire early Miocene to early middle Miocene time interval. Lakes or lake systems with gobioid freshwater fossils marked by red outlines

Rhamphogobius species have also been found in the late Karpatian—early Badenian Požega paleolake (Mandić et al. 2019). This association would span part of the early Miocene Central-West European bioprovince and of the middle Miocene Illyrian bioprovince of Neubauer et al. (2015). (3) The early Miocene gobioid association of Klinci in the VMB is part of the late Karpatian—early Badenian SLS described here. It contains the genera *Klincigobius* (two species) and *Rhamphogobius* and *Toxopyge* (one species each). *Klincigobius* is not known from outside this region, and *Rhamphogobius* and *Toxopyge* are represented by different species from those of the Požega Lake. The Klinci association would correspond to the Balkan bioprovince of Neubauer et al. (2015), who also noted that “this region is characterized by a high degree of endemic evolution” and that “the two close and coeval regions (meaning the Balkan and Dinarid/Illyrian regions) share very few taxa.” This observation is obviously consistent with our own concerning the fishes of the two regions.

Conclusion and outlook

The articulated skeletons of gobiid fishes from Klinci have opened a window to a lost highly adapted community of gobiid fishes in southeastern Europe during early and middle Miocene. The key findings are as follows:

1. Finds of multiple otoliths in situ allow for correlation of several otolith-based species that were described in the past.
2. The early to middle Miocene highly adaptive freshwater goby communities of central and southeastern Europe represent an early freshwater cycle in the history of the family that is unrelated to the present day Ponto-Caspian goby stock.
3. The extinction of this early adaptive freshwater goby community and the faunal turn-over likely occurred in the late middle Miocene, following the MCO at c. 14 Ma.

4. The goby community of Klinci represented a distinct paleobioprovince connected with the ancient Serbian Lake System.

Now, only a few fossil freshwater otolith-based goby species remain that cannot be conclusively allocated to genera known from articulated skeletons. One particular group, that is, the “*Gobius*” *francofurtanus* group from the early Miocene of the Rheingraben, still requires an integrated review of skeletal and otolith findings. The calibration of isolated otolith-based taxa with articulated skeletons via otoliths in situ now facilitates a better understanding of the spatial and stratigraphic distribution of freshwater gobies across the various lake deposits in the early and middle Miocene of Europe. We expect a biogeographic frame to emerge from such studies comparable to that established by the study of freshwater gastropods (Neubauer et al. 2015). We are confident that the adaptive power of gobies to the ever-changing environmental conditions in the geological history of Europe will provide many more insights into their evolution and may yield more yet unexpected results.

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