



# Diversity of gobioid fishes in the late middle Miocene of northern Moldova, Eastern Paratethys—Part II: description of †*Moldavigobius helenae* gen. et sp. nov.

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## Abstract

The middle Miocene (upper Serravallian, lower Volhynian) deposits at Karpov Yar near Naslavcea, northern Moldova, are among the few settings in which fossil fish are preserved with otoliths in situ. Here, we describe the new gobiid †*Moldavigobius helenae* gen. et sp. nov. from this locality. The taxon is characterized by small size (up to 34.2 mm SL), a compact body (body depth 17–21% SL), a fan-shaped caudal fin, large ctenoid scales (< 30 scales in the longitudinal row) and nearly square otoliths (sagittae) with a slender, shoe sole-shaped sulcus. It has 27 vertebrae, six spines in the first dorsal fin, one spine and 11 soft rays in both the second dorsal and the anal fin, 15–17 pectoral-fin rays, and 17 (9/8) segmented caudal-fin rays. The meristic characters of †*Moldavigobius* gen. nov., together with its sagitta shape, suggest a relationship with *Lesueurigobius* Whitley, 1950, but its fan-shaped caudal fin and the unique sulcus contour of the otoliths preclude its attribution to that genus. In addition, we re-assign an otolith-based species previously described as *Knipowitschia suavis* Schwarzhans, 2014 as a second member of †*Moldavigobius* gen. nov. Accordingly, †*Moldavigobius* gen. nov. was represented by at least two species in the Serravallian of the Eastern Paratethys (†*M. helenae* gen. et sp. nov., †*M. suavis* nov. comb.). Moreover, †*M. suavis* is also known from the Serravallian ichthyofauna of the SE Mediterranean. †*Moldavigobius* gen. nov. thus demonstrates the key role of fossil skeletal material with otoliths in elucidating the ancient diversity of the Gobioidi.

**Keywords** Gobiidae · Fish fossils with otoliths in situ · New genus · Eastern Paratethys · Northern Moldova · Serravallian

## Introduction

Like many other types of Cenozoic sediments, the marine sediments of the middle Miocene from the Central and Eastern Paratethys region have yielded numerous specimens of fossil fish otoliths, while fish skeletons are comparatively

rare in these deposits. This is also the case for the fossil remains of gobioid fishes ('gobies'); indeed, it is mainly their otolith-based record that reveals that gobies were an abundant component of the marine middle Miocene ichthyofauna in the Central and Eastern Paratethys (Bratishko et al. 2015; Reichenbacher et al. 2019; Schwarzhans et al. 2020b). Interestingly, there is little overlap between the solely otolith-based fossil goby species known from the Central and Eastern Paratethys and those that are attested by skeletal material with otoliths in situ (see Carnevale et al. 2006; Schwarzhans et al. 2017; Reichenbacher and Bannikov 2022). This may in part be attributable to ecological and taphonomic factors, but the relative rarity of fossil skeletons may also play a role. Consequently, the discovery of goby skeletons that have retained their otoliths can shed new light on the overall composition of the middle Miocene goby fauna. In some cases, such fossils may also help to clarify the taxonomic status of fossil goby species that have been recognized on the basis of otolith data alone (see Reichenbacher and Bannikov 2022).

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The locality Karpov Yar, near the township of Naslavcea, northern Moldova, is one of the very few localities that have yielded well preserved fossil goby skeletons with otoliths in situ, thus providing complementary sources of information for taxonomic classification. However, until recently, the goby fossils recovered from Karpov Yar have been left unidentified or in open nomenclature (Ionko 1954; Bannikov 2009, 2010, 2017, 2018). The present study is the second contribution based on our ongoing research on the goby fossils from Karpov Yar. In the first one (Reichenbacher and Bannikov 2022), we described four new extinct genera of the family Gobiidae, represented by six species. All of these displayed skeletal characters and scales reminiscent of the extant gobiid genus *Lesueurigobius* Whitley, 1950. However, their otoliths were incompatible with such a classification, and we interpreted these fossils as a stem lineage of the European *Aphia* clade within the Gobiidae. In this study, we present another new gobiid genus and species from Karpov Yar—†*Moldavigobius helenae* gen. et sp. nov.—which may be a relative of *Lesueurigobius*. In addition, we show that isolated fossil otoliths previously described as *Knipowitschia suavis* Schwarzhans, 2014 from the Serravallian of the SE Mediterranean and Eastern Paratethys represent another species of †*Moldavigobius* gen. nov.

## Geological setting

The sediments exposed in the Karpov Yar ravine in northern Moldova are lower Volhynian in age (Sarmatian sensu lato, c. 12 Ma; Reichenbacher and Bannikov 2022: fig. 1). The palaeogeographic location of Karpov Yar is situated in the western sector of the Eastern Paratethys, which was at that time a semi-closed inland sea with limited connections to the Central Paratethys and the Mediterranean Sea (Reichenbacher and Bannikov 2022: fig. 2). The fish-bearing sediments at Karpov Yar consist of diatomites and marls with some thin layers bearing mass occurrences of fossil fishes. For details of the geological profile at Karpov Yar, the fossil molluscs and previously described fish fauna from this locality, see Reichenbacher and Bannikov (2022).

## Materials and methods

### Fossil material

Articulated skeletons of six fossil specimens are included in this study. They are deposited in the Borissiak Palaeontological Institute of the Russian Academy of Sciences in Moscow, under the inventory numbers PIN 5274/49, PIN 5274/69, PIN 5274/73 [holotype], PIN 1306/68a, PIN 1306/68b, PIN 1306/68c. With the exception of PIN

1306/68b, all skeletons were preserved with otoliths in situ. Slabs revealing both the part (head to the right) and counterpart (head to the left) of the fossil skeleton were recovered for PIN 5274/73 and PIN 5274/49. The otoliths are kept in the Bavarian State Collection for Palaeontology and Geology (SNSB–BSPG) in Munich, Germany, under the inventory number SNSB–BSPG 2021 XI.

### Methods

The fossil skeletons and otoliths were examined and photographed under a Leica M165 FC stereomicroscope equipped with a digital camera (Leica DC 200). Otoliths preserved in situ in the paratypes PIN 1306/68c (both sagittae) and PIN 1306/68a (right sagitta, left lapillus), and in the referred specimen PIN 5274/69 (right sagitta), were carefully extracted and stored separately; the right sagitta of each paratype and the lapillus were used for SEM imaging (HITACHI SU 5000 Schottky FE–SEM, Department of Earth and Environmental Sciences, LMU Munich). For the established terminologies of the gobiid sagitta and lapillus, see Reichenbacher and Bannikov (2022: fig. 4).

The morphometric parameters of the skeletons and otoliths correspond to those used in previous publications on extant goby species (e.g., Miller 2004; Liu et al. 2009; Iglésias et al. 2021) and in Reichenbacher and Bannikov (2022). All measurements were recorded to the nearest 0.1 mm using ImageJ (Schneider et al. 2012) and were normalized based on the standard length (SL) of the measured fish. Meristic characters comprised counts of abdominal and caudal vertebrae (including the terminal centrum), counts of fin rays (every discernible ray was counted), and, where possible, determination of the pterygiophore formula of the first dorsal fin (according to Birdsong et al. 1988) and the number of scales in the longitudinal row. Topographical terms refer to the natural anatomical location of the structure concerned, even when this is rotated or displaced in the fossil.

### Calculation of the standard lengths of incomplete fish fossils

The paratypes PIN 1306/68a and PIN 1306/68b and the referred specimen PIN 5274/49 are incomplete, so their standard lengths could not be measured directly. In these cases, we used the length of the in-situ sagitta to calculate the corresponding SL for each specimen, based on the assumption that the standardized sagitta length should be the same (i.e., 4.65% SL) as that obtained from the (complete) holotype (PIN 5274/73) and the (complete) referred specimen (PIN 5274/69). This approach appears reasonable, because the ratio between the length of the sagitta and the SL is relatively stable within a gobiid species when specimens of the same size class are considered (Więcaszek et al. 2020), as is the case here.

The only specimen that had no otoliths is the paratype PIN 1306/68b, which is an almost complete specimen but lacks the terminal centrum, hypural plates and caudal fin. We calculated the SL of PIN 1306/68b by assuming that it has the same size proportions as those measured in the holotype with respect to (i) the penultimate vertebra, terminal centrum and hypural plate, and (ii) head length and standard length. Both estimates resulted in a SL of 24.2 mm for PIN 1306/68b.

**Abbreviations used in the text.**  $\alpha$ , inclination angle of sulcus; D1, first dorsal fin; D2, second dorsal fin; SL, standard length. A dagger (†) precedes the name of an extinct genus or species.

**Institutional abbreviations.** IRSNB, Royal Institute of Natural Sciences Belgium; NMP, National Museum Prague, Prague, Czech Republic; PIN, Borissiak Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia; ZM-CBSU, Zoological Museum Collection of the Biology Department at Shiraz University, Iran; ZSM, Bavarian State Collection of Zoology, Munich, Germany.

## Systematic palaeontology

Infraclass **Teleostei** Müller, 1845 sensu Arratia (1999)  
Order **Gobiiformes** Günther, 1880 sensu Betancur-R et al. (2017)

Suborder **Gobioidei** Jordan and Evermann, 1896 sensu Thacker et al. (2015)

Family **Gobiidae** Cuvier, 1816 sensu Nelson et al. (2016).

Genus †*Moldavigobius* gen. nov.

*Type species.* †*Moldavigobius helenae* gen. et sp. nov. (Figs. 1, 2, 3f–h).

*Other species.* †*Moldavigobius suavis* (Schwarzahns, 2014) comb. nov. (Fig. 3a–e), which is an otolith-based species previously assigned to the extant oxudercid genus *Knipowitschia* Iljin, 1927 (see below).

*Etymology.* The name refers to where the taxon was first discovered (Moldavia) and to its general similarity to members of the Gobiidae. Gender masculine.

*LSID ZooBank.* This new genus is registered under urn:lsid:zoobank.org:pub:4C1FF532-2350-45A8-BF4D-C40A5A8F8810.

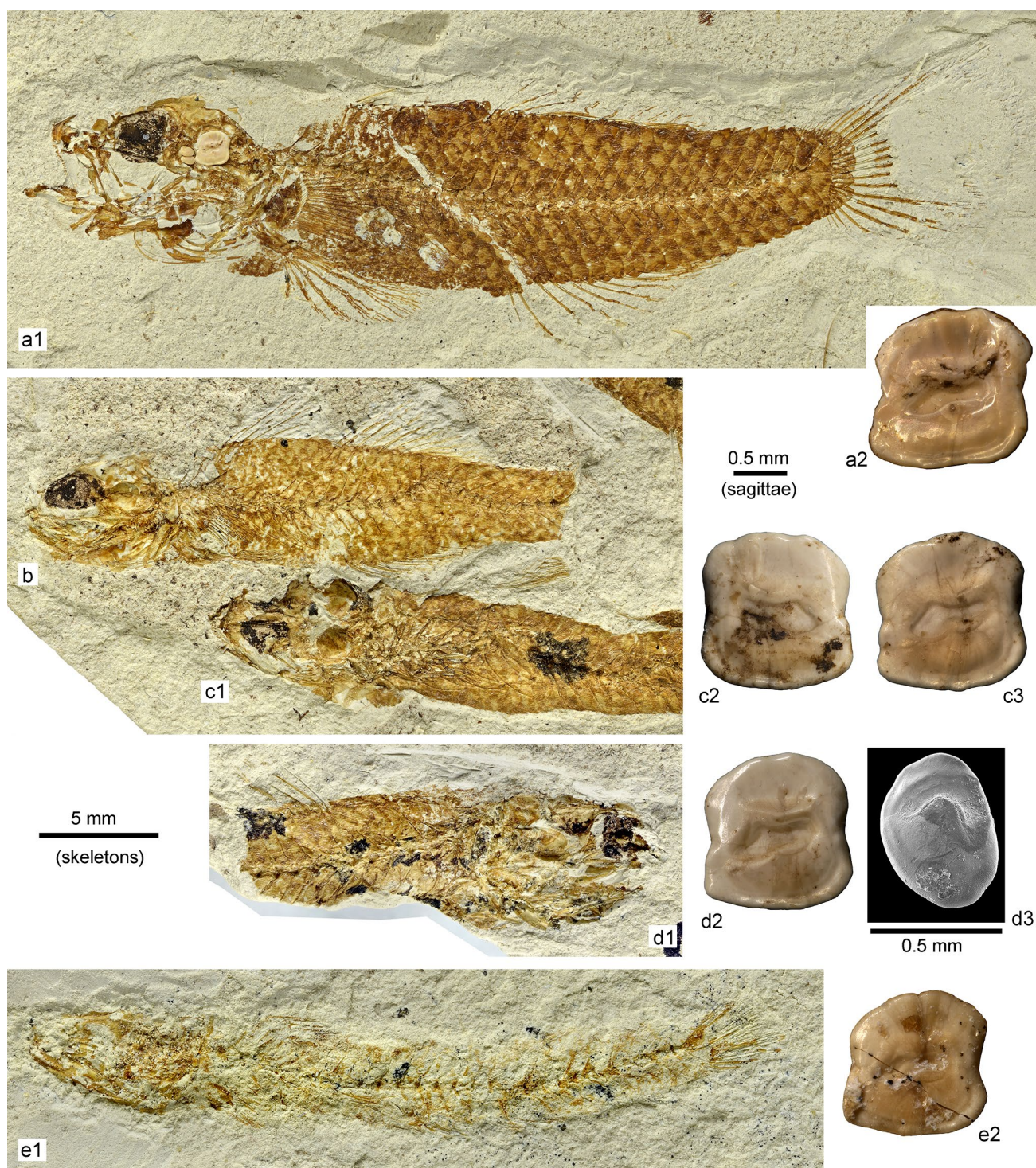
*Stratigraphic range.* Middle Miocene (upper Serravallian, lower Sarmatian, lower Volhynian).

*Diagnosis.* †*Moldavigobius* gen. nov. is a small gobioid fish; SL between 24.2 and 34.2 mm. Head moderately large (23.4–26.9% SL); body probably laterally compressed (as all specimens are preserved in lateral view); body depth 17.2–21.0% SL at origin of D1; anal fin inserted one vertebra behind D2; caudal peduncle relatively short (16.1–17.2% SL); caudal fin approximately as long as head (24.3% SL); length of abdominal part of vertebral column 63.9–66.4% of that of caudal part. Number of vertebrae 27 (10 + 17); D1 with six spines, last spine slightly further from preceding one (interspine distance is 3.8–4.4% SL); D1 pterygiophore formula not completely clear owing to some distortion of the neural spines, but it is probably 3-22110; D2 with relatively long spine (8.2–10.3% SL) and 11 segmented rays; anal fin with moderately long spine (4.1–6.2% SL) and 11 segmented rays. Pectoral fin with 15 to 17 rays; pelvic fin with relatively short spine (c. 3.8% SL) and five rays, rays terminating distant from anal-fin origin. Caudal fin fan-shaped, with 17 segmented rays (nine rays in the upper lobe) and a relatively large number of procurrent rays (9 dorsally, 8 ventrally). Relatively large ctenoid scales on body, number of scales in longitudinal row < 30.

Otoliths–Sagittae almost square, no marked postero-dorsal projection (Fig. 3a–h). Sulcus moderately inclined ( $\alpha < 10^\circ$ –19.8°); shoe sole-shaped, with slender cauda and well developed dorsal ostial lobe; crista inferior with long, pronounced subcaudal iugum. Lapillus only known from type species, ovate with deep sulculus (Fig. 1d3).

*Differential diagnosis.* †*Moldavigobius* gen. nov. can be distinguished from the previously described ‘*Lesueurigobius* look-alikes’ from Karpov Yar (i.e., †*Katyagobius* Reichenbacher and Bannikov, 2022, †*Pseudolesueurigobius* Reichenbacher and Bannikov, 2022, †*Sarmatigobius* Reichenbacher and Bannikov, 2021, †*Yarigobius* Reichenbacher and Bannikov, 2022) by its fan-shaped caudal fin (vs. longish–lanceolate), fewer rays in D2 (11 vs. 14–16) and in anal fin (11 vs. 13–15), and a relatively longer abdominal portion of the vertebral column (64–66% of the length of the caudal part of the vertebral column, vs. 49–54%) (see Reichenbacher and Bannikov 2022: table 1). Furthermore, †*Moldavigobius* gen. nov. displays meristic counts, osteological traits and otolith characters that clearly set it apart from previously described Miocene marine and brackish fossil goby genera from the western Mediterranean and Paratethyan regions, i.e., †*Eleogobius* Gierl and Reichenbacher, 2015; †*Hesperichthys* Schwarzahns, Ahnelt, Carnevale and Japundžić, 2017; †*Lepidocottus* Sauvage, 1875; †*Proneogobius* Schwarzahns, Ahnelt, Carnevale and Japundžić, 2017; and †*Protobenthophilus* Schwarzahns, Ahnelt, Carnevale and Japundžić, 2017. In addition, the almost square shape of the otolith as well as the slender cauda and well-developed dorsal ostial lobe allow †*Moldavigobius* gen. nov. to





**Fig. 1 a–e** †*Moldavigobius helenae* gen. et sp. nov. from Karpov Yar, near Naslavcea, northern Moldova. **a1** holotype (counterpart), with right sagitta and both lapilli preserved in situ (PIN 5274/73b); **a2** close-up of sagitta. **b** Skeleton of paratype PIN 1306/68b (no otoliths in situ). **c1** Skeleton of paratype PIN 1306/68c (otoliths were extracted); **c2**, **c3** close-ups of left (**c2**) and right (**c3**) extracted sag-

ittae. **d1** Incomplete skeleton of paratype PIN 1306/68a (otoliths were extracted); **d2** close-up of extracted right sagitta; **d3** close-up of extracted left lapillus (SEM image). **e1** Skeleton of referred specimen PIN 5274/69 (otolith was extracted); **e2** close-up of extracted right sagitta



be differentiated from the two middle Miocene otolith-based goby genera for which no skeletal remains are known, i.e., †*Hoeseichthys* Schwarzhans, Brzobohatý and Radwańska, 2020, and †*Weilerigobius* Schwarzhans, 2017. Finally, its otolith morphology (nearly square shape, slender cauda, well developed dorsal ostial lobe) and some body-related characters (e.g., fan-shaped fin, moderately deep body) distinguish †*Moldavigobius* gen. nov. from the extant genus *Lesueurigobius* Whitley, 1950 and other extant gobiid genera with the same or similar meristic traits (see “Discussion” section).

**Remarks.** An otolith-based extinct species has been reported as *Knipowitschia suavis* Schwarzhans, 2014 from the upper Serravallian marine and brackish deposits in the Karaman Basin, SE Turkey. Later, in Bratishko et al. (2015), the same species was also reported from the lower Serravallian (Konkian) shallow marine deposits at Mangyshlak, western Kazakhstan (Eastern Paratethys). The otoliths of this species resemble those of †*Moldavigobius* gen. nov. in their nearly square shape, absence of a marked posterodorsal angle, and presence of a moderately inclined, relatively slender sulcus adjoined by a well-developed subcaudal iugum (Fig. 3a–e). They differ from otoliths of extant *Knipowitschia* species insofar as ostium and cauda lie on nearly the same inclination axis, whereas in *Knipowitschia* the inclination angle of the cauda is much shallower (sometimes almost horizontal) than that of the ostium (Fig. 3i; see also Schwarzhans et al. 2015: figs. 7.6–8 for otoliths of *K. longecauda* (Kessler, 1877), which is the type species of *Knipowitschia*). Moreover, the cauda is well developed in the fossil otoliths from the Karaman Basin and western Kazakhstan (Fig. 3a–e), and is not shortened or constricted like the otoliths of extant *Knipowitschia* species (Fig. 3i). Given the aforementioned similarities and differences, ‘*Knipowitschia*’ *suavis* can be assigned to †*Moldavigobius* gen. nov.

†*Moldavigobius helenae* gen. et sp. nov.

Figures 1, 2, 3f–h; Tables 1, 2

**Type material.** Holotype: PIN 5274/73; 34.2 mm SL; part (incomplete) and well-preserved counterpart with right sagitta and both lapilli preserved in situ (Fig. 1a). Three paratypes on a single slab: PIN 1306/68b is a well-preserved specimen but lacks the caudal skeleton and caudal fin (Fig. 1b), a mould of the sagitta is recognizable in its head; PIN 1306/68c is a posteriorly incomplete skeleton preserved in dorsolateral view, from which both sagittae were extracted (Fig. 1c); PIN 1306/68a is an incomplete skeleton from which a right sagitta and a left lapillus were extracted (Fig. 1d). This specimen is not included in Table 1 owing to its partial preservation.

**Other material.** The specimens PIN 5274/69 and PIN 5274/49 are tentatively assigned to †*M. helenae* gen. et sp. nov. on the basis of their otolith morphology. Specimen PIN 5274/69 is a complete, but poorly preserved skeleton with a right sagitta preserved in situ, which was extracted (Fig. 1e). PIN 5274/49 (part and counterpart) is a juvenile, largely incomplete specimen with both sagittae in situ. Its head is poorly preserved, while the abdominal vertebral column (comprising 10 vertebrae) and the first two caudal vertebrae can be discerned; this specimen is not included in Table 1 because of its poor preservation.

**Type locality and age.** Karpov Yar, Naslavcea, northern Moldova; lower Sarmatian (Volhynian).

**Etymology.** The species epithet honours Dr. Helen K. Larson (Museum and Art Gallery of the Northern Territory, and Museum of Tropical Queensland, Australia) for her meticulous work on the morphology, osteology and systematics of many extant goby genera and species.

**LSID ZooBank.** This new species is registered under urn:lsid:zoobank.org:act:8DDECDE1-BC3F-42EE-85C0-30719CAECB02.

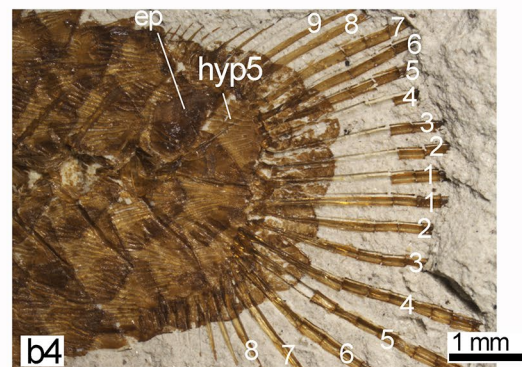
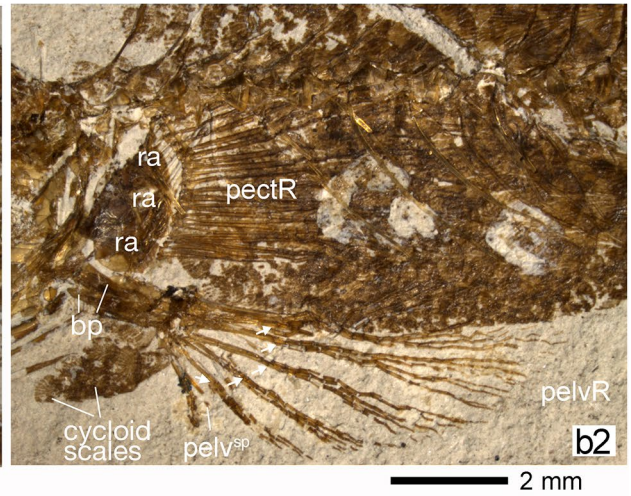
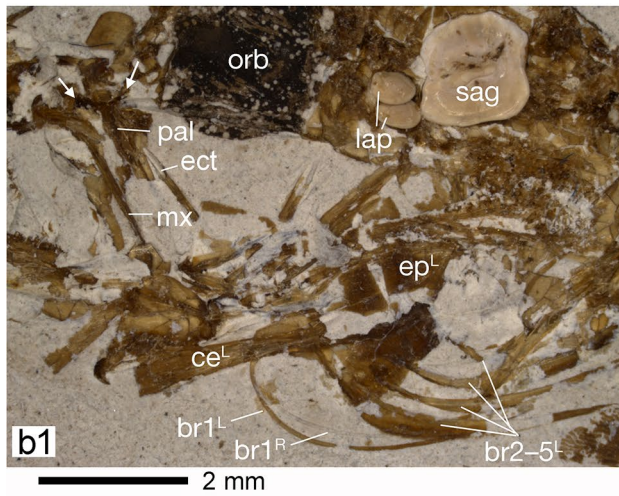
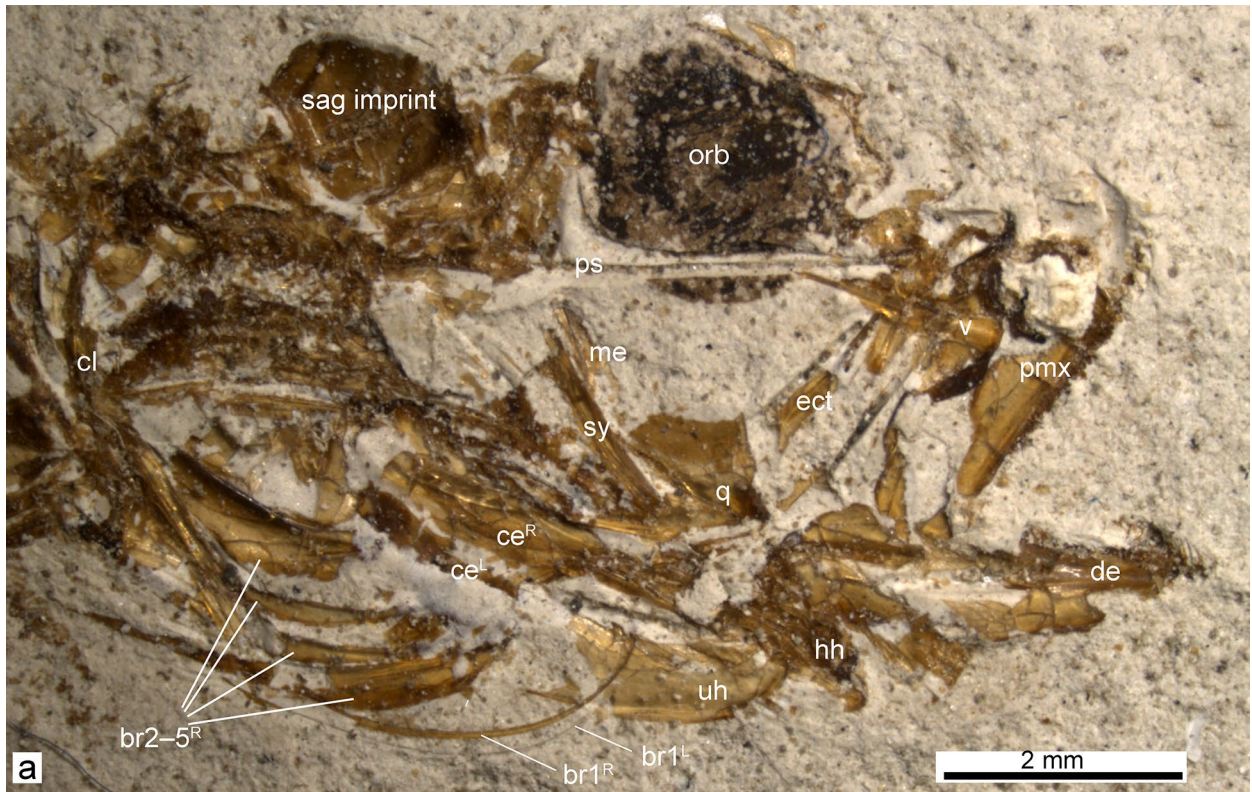
**Diagnosis.** Morphological and meristic characters as for the genus.

Sagittae almost square, length–height index  $0.97 \pm 0.05$  (Table 2), dorsal margin slightly lobed and weakly curved, no marked posterodorsal projection; sulcus shoe sole-shaped, moderately inclined ( $15.0^\circ$ – $18.9^\circ$ ), crista inferior with longish subcaudal iugum (Figs. 1a2, c2, c3, d2, e2, 3f–h). Lapillus ovate with well-developed sulculus (Fig. 1d3).

**Differential diagnosis.** The only other species of †*Moldavigobius* gen. nov. currently known is †*M. suavis* (Schwarzhans, 2014) comb. nov., of which only otoliths (sagittae) are known (see above and Fig. 3a–h). The otoliths of the two species differ in the curvature of the dorsal margin (faintly curved in †*M. helenae* gen. et sp. nov. vs. highly curved in †*M. suavis*), the configuration of the predorsal angle (sharp in †*M. helenae* gen. et sp. nov. vs. rounded), the position of the predorsal angle (same height as posterodorsal angle in †*M. helenae* gen. et sp. nov. vs. below posterodorsal angle), and the length of the subcaudal iugum (terminating before cauda end in †*M. helenae* gen. et sp. nov. vs. extending to cauda end and sometimes beyond). Further differential diagnosis as for the otoliths of the genus.

**General description.** Relatively small gobiid fish, with the largest (holotype) reaching 34.2 mm SL. Body moderately elongate and posteriorly slightly tapering, head of moderate







**Fig. 2** Details of the holotype of †*Moldavigobius helenae* gen. et sp. nov. **a** Head of holotype (part, PIN 5274/73a). Note premaxilla with prominent postmaxillary process, and hyoid bar with five branchiostegal rays. **b1–b4** Close-ups of holotype (counterpart, PIN 5274/73b). **b1** Head with right sagitta and both lapilli preserved in situ, a well preserved T-shaped palatine (arrows indicate ethmoid and maxillary processes) and the articulation of branchiostegal rays 1–5 to the hyoid bar; **b2** pectoral and pelvic girdles and fins (arrows indicate point of bifurcation of pelvic-fin rays); **b3** scales on the flank (below insertion of D2) with well-preserved ctenii; **b4** caudal skeleton exhibiting a single, large epural and 17 segmented caudal-fin rays. Abbreviations: bp, basipterygium; br, branchiostegal ray; ce, ceratohyal; cl, cleithrum; de, dentary; ect, ectopterygoid; eh, epihyal; ep, epural; hh, hypohyal; hyp, hypural plate; lap, lapillus; mx, maxilla; orb, orbit; pal, palatine; pectR, pectoral-fin rays; pelvR, pelvic-fin rays; pelv<sup>sp</sup>, pelvic-fin spine; pmx, premaxilla; pop, preopercle; ps, parasphenoid; q, quadrate; ra, radials of pectoral girdle; sag, sagitta; sy, symplectic; uh, urohyal; v, vomer

size (23–27% SL), eyes 6–8% of SL, body depth at origin of D1 c. 17–21% SL, caudal peduncle slightly tapering towards caudal fin and relatively short (16–17% SL), caudal fin fan-shaped and moderately long (24.3% SL). For further body proportions and meristic counts, see Table 1.

**Neurocranium.** The neurocranium is preserved either in lateral (holotype, paratypes PIN 1306/68a, b) or dorsoventral view (paratype PIN 1306/68c). The frontal bones are long, narrow above the orbit and broad posteriorly. The parasphenoid is exposed at the lower margin of the orbit; it is straight, relatively narrow, with a broad posterior portion. The vomer has a broad, rounded anterior portion and a slender, pointed posterior process (Fig. 2a). Other details of the neurocranium are not recognizable. Scales are not present on the head.

**Jaws.** The mouth gape is moderately wide; the lower jaw articulation is situated more or less under the middle of the orbit (Fig. 2a). The dentary is narrow and long (9–10% SL); the angulo-articular is relatively massive and has a short, but relatively deep retroarticular process. The maxilla is slender and elongate, being slightly broader posteriorly and somewhat bent. The relatively long premaxilla is straight in lateral view; it has a thin and relatively long ascending process, a massive, rounded articular process and a well-developed, somewhat rounded postmaxillary process (Fig. 2a). Both the dentary and premaxilla bear large and small conical teeth, arranged in several rows; outer-row teeth are bigger than inner-row teeth. In specimen PIN 1306/68a, blunt teeth seem also to be present on the dentary. In the holotype, the bases of two enlarged teeth at the anterior portion of the premaxilla are recognizable.

**Suspensorium, opercular apparatus and hyoid arch.** The symplectic is a robust long rod; the metapterygoid is

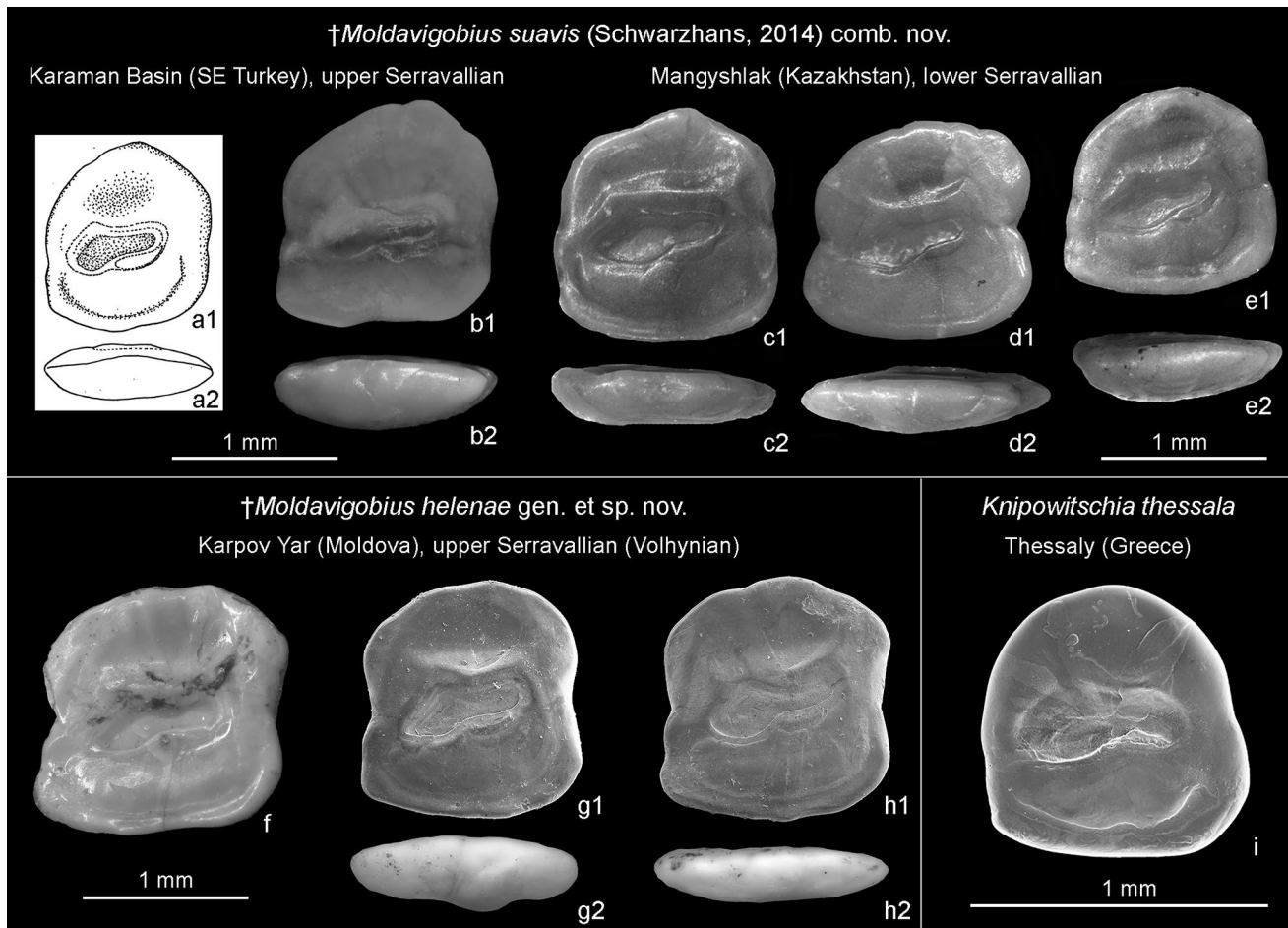
moderately long and slender (Fig. 2a). The quadrate is a roughly triangular bone with a deep and wide indentation in its posterior portion and a robust, thick and pointed posterior process (Fig. 2a). The palatine is T-shaped (indicated by arrows in Fig. 2b1); its proximal portion is not clearly detectable, but it seems to be short. The ectopterygoid is long, straight, somewhat broadened proximally and slender distally; it reaches the head of the palatine (Fig. 2b1). No entopterygoid is present. The preopercle, opercle and subopercle are poorly preserved, while the interopercle is not visible. The ceratohyal shows a relatively straight and slender anterior portion and a broadened posterior part; the epihyal is triangular (Fig. 2b1). The interhyal is not recognizable. Remains of the hypohyal and urohyal are preserved in the holotype (Fig. 2a); the latter is a thin, flat bone with a concave upper margin, a convex lower margin and an indented posterior margin. The number of branchiostegal rays is five; the first ray is slender, whereas rays 2–5 are relatively robust (Fig. 2a, b1). Branchiostegal ray 1 is attached slightly behind the middle of the slender part of the ceratohyal, rays 2–4 articulate with its broadened posterior part, and ray 5 inserts at the anteriormost edge of the epihyal (Fig. 2b1).

**Branchial arches.** Indistinct remains of gill arches are preserved in the holotype. The pharyngeal dentition includes both thick and slender conical teeth of multiple sizes.

**Vertebral column.** Total number of vertebrae is 27, of which 10 are abdominal. Vertebral centra are constricted in the middle; the centra of the abdominal vertebrae are relatively elongate. The length of the abdominal part of the vertebral column is 64–66% of the length of the caudal part (Table 1). The posteriormost abdominal vertebrae display relatively strong parapophyses. Thin ribs extend from vertebra 3 to vertebra 10; ribs of the last three pairs become successively shorter, with the last rib pair being much shorter than the preceding one. The haemal spines are more or less equally inclined posteriorly.

**Pectoral girdle and fins.** Only one of the anterior processes of the post-temporal is recognizable as a slender rod. The supracleithrum is a moderately elongate bone. The cleithrum is sturdy, long and slightly curved (Fig. 2a); scapula and coracoid are not preserved. Three radial bones are visible in the holotype, the fourth is obscured by the bones of the basipterygium (Fig. 2b2). The pectoral fin is slightly shorter than the pelvic fin and contains up to 17 rays (Fig. 2b2).

**Pelvic girdle and fins.** The pelvic fins are very close to each other and were probably united (Fig. 2b2); pelvic fin length is c. 15–19% SL. The pelvic spine is slender, its length is c. 3.8% SL. There are five pelvic-fin soft rays, which terminate distant from the anal-fin origin; each ray is bifurcated after



**Fig. 3** a–e Otoliths of †*Moldavigobius suavis* (Schwarzahns 2014) comb. nov. (shown in medial and dorsal views, dorsal view with lateral side down). **a** Holotype, right sagitta, Karaman Basin, SE Turkey (re-figured from Schwarzahns 2014: pl. 10, fig. 7). **b** Left sagitta (mirrored for better comparison), Karaman Basin, SE Turkey (re-figured from Schwarzahns et al. 2015: fig. 7.9). **c–e** Left sagittae (c, d, mirrored) and right sagitta (e) from Mangyshlak, Kazakhstan

(re-figured from Bratishko et al. 2015: figs. 10.7, 10.8, 10.10). **f–h** †*Moldavigobius helenae* gen. et sp. nov.; **f** right sagitta preserved in situ in holotype PIN 5274-73a; **g, h** right sagittae extracted from paratypes PIN 1306/68a and PIN 1306/68c. **i** *Knipowitschia thessala* (Vinciguerra, 1827), right sagitta, Karla Lake, Greece (collection BR). Figures **g–i** are SEM images. All other figures are stereoscopic images

26–34% of its total length (Figs. 1a1, 2b2). Almost straight (very gently curved) elongate basipterygii are visible in the holotype (Fig. 2b2).

**Dorsal fins.** The first dorsal fin contains six long and slender spines terminating in short filaments (best seen in the paratype PIN 1306/68b; Fig. 1b). The second spine seems to be the longest (but the first spine is not completely preserved), spine V is clearly shorter, spine VI inserts after a small gap (Table 1). The first dorsal-fin pterygiophore inserts behind the neural spine of the third vertebra; the pterygiophore formula is most probably 3-22110 (based on holotype and paratype PIN 1306/68b), with the vacant interneural space (=interneural gap) located between the neural spines of vertebrae 7 and 8 (uncertainty in the pterygiophore formula

is due to post-mortem distortion of the pterygiophores or neural spines).

The second dorsal fin originates above the last abdominal (holotype, paratype PIN 1306/68b) or first caudal vertebra (paratype PIN 1306/68a). It consists of a long, slender spine (8–10% SL) and 11 soft segmented rays. The rays display a comparatively long, undivided proximal portion before they begin to branch, and do not reach the dorsal procurrent caudal-fin rays (Fig. 1b). The first D2-ptyerygiophore inserts into the interneural space of vertebrae 8 and 9.

**Anal fin.** The anal fin comprises a moderately long spine (4–6% SL) and 11 soft rays. Rays are not completely preserved posteriorly, but appear to end distant from the beginning of the ventral procurrent caudal-fin rays. As observed in the D2 rays, the anal-fin rays also possess a comparatively



**Table 1** Body morphometry, meristic traits and squamation of †*Moldavigobius helenae* gen. et sp. nov. from Karpov Yar, Naslavcea, northern Moldova

	PIN 5274/73 holotype (part + counterpart)	PIN 1306/68b paratype	PIN 1306/68a paratype	PIN 5274/69 referred specimen
SL (mm)	34.2	*24.2	*29.0	29.5
<b>Measurements (in mm), in brackets standardized values (in % of SL, if not indicated otherwise)</b>				
Head length	9.2 (26.9)	6.5 (26.9)	7.5 (25.8)	6.9 (23.4)
Length eye	c. 2.0 (21.7 % HL)	c. 1.6 (24.6% HL)	c. 2.2 (29.3% HL)	c. 1.8 (26.1% HL)
Length lower jaw	c. 3.3 (35.9% HL)	2.2 (33.8% HL)	–	c. 2.8 (40.6% HL)
Predorsal distance to D1	12.4 (36.2)	8.3 (34.2)	9.3 (32.1)	9.7 (32.9)
Predorsal distance to D2	19.9 (58.2)	13.1 (54.1)	14.3 (49.3)	–
Distance end of D2 to first procurrent ray	4.6 (13.4)	4.5 (18.4)	–	–
Preanal distance	20.5 (59.9)	13.4 (55.4)	–	16.2 (54.9)
Caudal peduncle length	5.9 (17.2)	3.9 (16.1)	–	–
Minimum caudal peduncle depth	3.9 (11.4)	2.7 (11.1)	–	c. 2.7 (9.1)
BD at origin of D1	c. 7.2 (21.0)	4.8 (19.8)	c. 5.0 (17.2)	–
BD at origin of A	7.6 (22.2)	5.0 (20.7)	–	–
D1 base	3.6 (10.5)	2.5 (10.3)	2.7 (9.3)	–
D2 base	8.2 (24.0)	4.8 (19.8)	–	–
Distance insertion D1-spine VI to begin of D2	2.3 (6.7)	2.2 (9.1)	2.2 (7.6)	–
Distance insertion D1-spine V to VI	1.4 (4.1)	1.06 (4.4)	1.1 (3.8)	–
Distance insertion D1-spine IV to V	0.8 (2.3)	0.5 (2.1)	c. 0.5 (c. 1.7)	–
Ratio distance D1-spines V–VI to IV–V	1.7	2.1	c. 2.2	–
D2 spine length	2.8 (8.2)	2.5 (10.3)	2.8 (9.6)	–
A base	7.5 (21.9)	5.3 (21.9)	–	–
A spine length	1.4 (4.1)	1.5 (6.2)	–	–
A spine length in % of next ray	c. 46%	60%	–	–
Caudal fin length	8.3 (24.3)	–	–	–
Pectoral fin length	c. 5.5 (16.1)	c. 3.3 (13.6)	–	–
Pelvic fin length	6.6 (19.3)	c. 3.6 (14.9)	–	–
Pelvic fin spine length	c. 1.3 (3.8)	–	–	–
Abdominal vertebral column length	9.9 (28.9)	Distorted	–	8.7 (29.5)
Caudal vert. column length	14.9 (43.6)	Distorted	–	13.6 (46.1)
Abd. vert. column in % of caudal vert. column	66.4	–	–	63.9
<b>Meristic counts</b>				
Vertebrae (abdominal + caudal)	27 (10 + 17)	27 (10 + 17)	–	27 (10 + 17)
D1 spines	VI	VI	VI	VI
D1 pterygiophore formula	Probably 3–22110	Pobably 3–22110	Unclear	Unclear
D2 elements	I,11	I,11	–	–
A elements	I,11	I,11	–	–
AP	2?	2 or 3?	–	–
Caudal fin rays, segmented (dorsal/ventral)	9/8	–	–	–
Caudal procurrent rays (dorsal/ventral)	9/8	8 or 9/–	–	–
Pectoral fin rays	17	c. 15	–	–

**Table 1** (continued)

	PIN 5274/73 holotype (part + counterpart)	PIN 1306/68b paratype	PIN 1306/68a paratype	PIN 5274/69 referred specimen
Pelvic fin elements	I,5	Probably I,5	–	–
<b>Other fin related characters</b>				
D2 spine shape	Slightly curved	Straight	Slightly curved	–
Insertion of D2 opposite to	Vertebra 10	Vertebra 10	Vertebra 11	–
Insertion of A opposite to	Vertebra 11	Vertebra 11	–	Vertebra 11
A spine shape	Straight	Slightly curved	–	–
Caudal fin shape	Fan-shaped	–	–	Fan-shaped
<b>Squamation</b>				
Flank scales	Aliform, ctenoid, thick margins	Ovate–aliform, ctenoid, thick margins	Ovate–aliform, ctenoid, thick margins	–
Radii number	8	c. 8	–	–
Scales in longitudinal row	< 30	–	–	–
Belly scales	Cycloid, weak radii	Present	–	–
Predorsal scales	Present	–	–	–

Note that the paratype PIN 1306/68c and the referred specimen PIN 5274/49 are not included due to their inappropriate preservation. Abbreviations: A, anal fin; AP, number of anal-fin pterygiophores inserting before haemal spine of first caudal vertebra; BD, body depth; D1, first dorsal fin; D2, second dorsal fin; –, not preserved; \*, SL was calculated based on the length of the sagitta preserved in situ (PIN 1306/68a, PIN 5274/69) or based on the head length (PIN 1306/68b) (see methods for details)

**Table 2** Measurements of otoliths preserved in situ in †*Moldavigobius helenae* gen. et sp. nov. from Karpov Yar, Naslavcea, northern Moldova

Species	PIN 5274/73 holotype	PIN 1306/68c paratype	PIN 1306/68a paratype	PIN 5274/69 referred specimen	PIN 5274/49 referred specimen
SL (mm)	34.2	*30.6	*29.0	29.5	*27.9
<i>Otolith (left, right) measurements in mm</i>					
Sag-l	–, 1.57 (4.6% SL)	1.45, 1.40	–, 1.35	–, 1.38 (4.7% SL)	–, 1.30
Sag-h	–, 1.49	1.51, 1.49	–, 1.45	–, 1.39	–, 1.40
Sag-t	–	0.31, 0.31	–, 0.39	–, 0.39	–
Sag-l/sag-h	–, 1.05	0.96, 0.94	–, 0.93	–, 0.99	–, 0.93
sag-h/sag-t	–	4.9, 4.8	–, 3.7	–, 3.6	–
Sulcus inclin. angle	15.7	15.8, 17.8	18.9	16.5	15.0
Lap-h	0.61	–	0.59, –	–	–
Lap-w	0.41	–	0.45, –	–	–
Lap-t	–	–	0.21	–	–
Lap-h/lap-w	1.49	–	1.31, –	–	–
Lap-h/lap-t	–	–	2.8	–	–

Abbreviations: lap-h, lap-t and lap-w, lapillus height, thickness and width; sag-h, sag-l and sag-t, sagitta height, length and thickness; –, not preserved. \*, SL was calculated based on the length of the sagitta preserved in situ (see methods for details)

long, undivided proximal portion before they begin to branch (Fig. 1a1). The point of insertion of the anal fin is one vertebra behind the origin of D2, i.e., below the first caudal vertebra (visible in holotype and paratype PIN 1306/68b) (Fig. 1a1, b). Two or three anal-fin pterygiophores insert anterior to the haemal spine of the first caudal vertebra.

**Caudal endoskeleton and fin.** The caudal fin is moderately long (24.3% of SL) and fan-shaped (Fig. 1a1). It is composed of 17 segmented principal rays; the number of principal rays in the upper lobe is 9 (Fig. 2b4). Ten procurrent rays are present dorsally and nine ventrally (visible in the holotype). The caudal skeleton is covered by large scales, which obscure its details. However, it is clear that the terminal centrum is



fused with HYP3 + 4 and that a long slender hypural plate 5 is present (Fig. 2b4). A single large epural can clearly be seen, whose distal portion is roughly triangular (Fig. 2b4). The contour of the parhypural cannot be discerned. One or two vertical rows of relatively small ctenoid scales cover the proximal portion of the principal caudal-fin rays (Fig. 2b4).

**Otoliths.** The sagitta is squarish-to-rectangular in shape, length/height index 0.93–1.05 (Table 2). Dorsal margin weakly curved; no marked posterodorsal projection; anterior and posterior margins slightly incised in the middle (Figs. 1, 3f–h). Predorsal angle distinct, sharp, and positioned almost as high as posterodorsal angle, preventral and posteroventral angle pronounced. Sulcus shoe sole-shaped, relatively slender, moderately inclined ( $\alpha = 15.0^\circ$ – $18.9^\circ$ ), cauda adjoined by crista inferior with well-developed subcaudal iugum terminating slightly before the end of the cauda.

Lapillus ovate, with rounded medial margin, relatively straight lateral margin and distinct sulculus (Fig. 1d3).

**Scales.** The body is densely covered with scales (Figs. 1a1, b, c1, 2b3), which are also present on the proximal part of the caudal fin (Fig. 2b4). Flank scales are ctenoid, with thickened posterior margin and about eight radii; the ctenii are sharp and relatively small and slender (Fig. 2b3). The number of longitudinal scales is about 30. Small cycloid belly scales and predorsal scales are also present.

## Discussion

### Assignment of †*Moldavigobius* gen. et sp. nov. at the family level

The presence of five branchiostegal rays, as seen in †*Moldavigobius helenae* gen. et sp. nov. (Fig. 2a), is regarded as a synapomorphy for the families Gobiidae and Oxudercidae (Wang et al. 2001; Gill and Mooi 2012). Further characteristic traits of the Gobiidae and Oxudercidae (although exceptions may occur) include a T-shaped palatine, absence of the endopterygoid, and presence of an interneural gap between the two dorsal fins (Akihito et al. 1984; Hoese 1984; Hoese and Gill 1993). Each of these traits can be clearly discerned in †*M. helenae* gen. et sp. nov. (see species description). Accordingly, †*Moldavigobius* gen. nov. can be classified as a member of the Gobiidae + Oxudercidae.

In deciding whether †*Moldavigobius* gen. nov. belongs to the Gobiidae or Oxudercidae, the configuration of the ‘palatopterygoquadrate complex’, the D1 pterygiophore formula and the number of epural bones are useful (Birdsong et al. 1988; Harrison 1989). The palatopterygoquadrate complex is made up of the palatine, ectopterygoid and quadrate bones, whose size and arrangement differ in certain respects

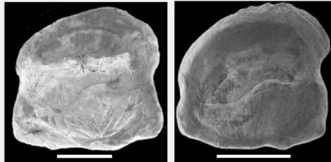
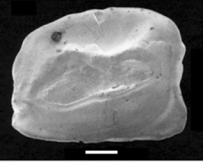
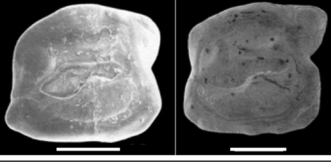
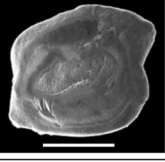
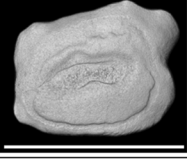
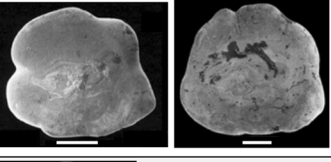

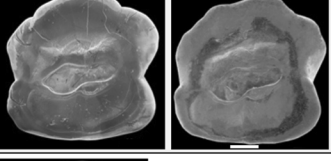
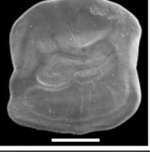
between the two families (Harrison 1989; Thacker 2013; Reichenbacher et al. 2018). Characteristic for many Gobiidae is a short palatine (whose ventral tip ends with some distance from the quadrate) and a relatively long ectopterygoid (which extends almost to the head of the palatine) (Harrison 1989). This condition is found in †*M. helenae* gen. et sp. nov. (Fig. 2a, b1). Furthermore, Oxudercidae have a derived D1 pterygiophore formula sequence, which is 3-12210 (Harrison 1989). This configuration is not present in †*Moldavigobius* gen. nov.; its (probable) D1 pterygiophore formula sequence is 3-22110, which is a common D1 pterygiophore formula for the Gobiidae, albeit not a derived character (Birdsong et al. 1988). The number of epural bones is usually two in Oxudercidae (plesiomorphic condition) and one in Gobiidae (derived) (Birdsong et al. 1988; Harrison 1989). †*Moldavigobius helenae* gen. et sp. nov. shows a single epural (Fig. 2b4). In summary, †*Moldavigobius* gen. nov. can be assigned to the Gobiidae.

### Possible assignment to an extant gobiid lineage and genus?

The Gobiidae can be divided into 14 lineages based on molecular data (Agorreta et al. 2013; Thacker 2015). However, little is known about the morphological synapomorphies that define each of these lineages and, as mentioned in Reichenbacher and Bannikov (2022), a phylogenetic matrix based on morphology that includes members of all 14 lineages is not available. Hence, the ‘best-fit’ approach sensu Penk et al. (2019) is used in the following to analyse whether †*Moldavigobius* gen. nov. can be assigned at the level of lineage.

We first chose the vertebral count seen in †*Moldavigobius* gen. nov. to explore possibly related extant lineages among the Gobiidae. The use of this specific trait is based on the available evidence, which indicates that vertebral counts are relatively constant within gobiid lineages (Birdsong et al. 1988). The choice is additionally justified because the 10 + 16 count is the plesiomorphic state; hence, the 10 + 17 count seen in †*Moldavigobius* gen. nov. is a derived condition (Reichenbacher and Bannikov 2022). Among the extant Gobiidae, a regular 10 + 17 vertebrae count occurs in *Bathygobius*, *Glossogobius* and *Grallenia* (all of which belong to the *Glossogobius* lineage), in both genera of the *Aphia* lineage (*Aphia*, *Lesueurigobius*), and in four genera of the highly diverse *Gobius* lineage (in *Caffrogobius*, *Coryogobius*, *Heteroleotris*, *Sufflogobius*) (Fig. 4).

In the second step, we used (i) the number of soft rays in the anal fin, and examined whether it contains one ray more or less than the second dorsal fin, and (ii) the otolith morphology. These characters have been shown to be taxonomically informative in previous publications (although exceptions occur). The number of soft rays in the anal fin is a

Lineage	Genus	Meristic and otolith characters	Otolith figures
<b>Glossogobius</b>	<i>Bathygobius</i> circumtropical, marine	Vert 10+17 A 1,8 (1 ray less than in D2) <sup>1</sup> Otolith rectangular, no or small postero- dorsal projection Shown otoliths: <i>B. curacao</i> , Belize, IRSNB (left); <i>B. burtoni</i> , tropical E Atlantic (right)	
	<i>Glossogobius</i> freshwater, estuarine	Vert 10+17 (variable) A 1,7–9 (1–2 rays less than in D2) <sup>2</sup> Otolith rectangular, no or small postero- dorsal projection Shown otolith: <i>G. callidus</i> , S Africa, ex Smale et al. (1995, pl. 129A)	
	<i>Grallenia</i> marine, associated to coral reefs	Vert 10+17, 10+18 A 1,6–10(11) (0–1 ray less than in D2) <sup>3–5</sup> No otolith data < 23 mm SL, very slender body, 15 segmented caudal fin rays <sup>4</sup>	-
<b>Gobius</b>	<i>Caffrogobius</i> marine, Indian Ocean, S-Atlantic	Vert 10+17, 11+16 A 1,8–12 (1–2 rays less than in D2) <sup>6</sup> Otolith square to rectangular, marked posterodorsal projection Shown otoliths: <i>C. agulhensis</i> (left), <i>C.</i> <i>gilchristi</i> (right), S Africa, ex Smale et al. (1995, pl. 128B1, D1)	
	<i>Coryogalops</i> marine, Indian Ocean, SE Atlantic	Vert 10+17 A 1,8–11 (1–2 (3) rays less than in D2) <sup>7</sup> Otolith square to rhomboid, marked posterodorsal projection Shown otolith: <i>C. tessellatus</i> , Persian Gulf	
	<i>Heteroleotris</i> marine, Indian Ocean, W Pacific	Vert 10+17 A 1,8–11 (0–1 ray less than in D2) <sup>8</sup> Otolith rectangular, marked posterodorsal projection Shown otolith: <i>Heteroleotris</i> sp., Arabian Sea, ZSM	
	<i>Sufflogobius</i> marine, pelagic, SE Atlantic	Vert 10+17 A 1,12–13 (as in D2) <sup>5,9</sup> Otolith rectangular-trapezoid, small posterodorsal projection Shown otoliths: <i>S. bibarbatus</i> , S Africa, ex Smale et al. (1995, pl. 129J1, J2)	
<b>Aphia</b>	<i>Aphia</i> marine, pelagic, NE Atlantic, Mediterranean Sea, Black Sea	Vert 10+17 A 1, 11–15 (0–1 ray more than in D2) <sup>10</sup> Otolith slightly rounded to ovate, no posterodorsal projection Shown otolith: <i>A. minuta</i> , Portugal, IRSNB	
	<i>Lesueurigobius</i> marine, E Atlantic, Mediterranean Sea	Vert 10+17, lanceolate caudal fin <sup>10</sup> A 1,12–17 (0–1 ray more than in D2) <sup>10</sup> Otolith squarish-rounded, with postero- dorsal projection Shown otoliths: <i>L. friesii</i> , NE Atlantic, Galicia (left), <i>L. sueri</i> , IRSNB (right)	
<b>Aphia (?)</b>	† <i>Moldavigobius</i> marine, Eastern Paratethys, SE Mediterranean	Vert 10+17 A 1,11 (as in D2) otolith ± squarish, no marked posterodorsal projection Shown otolith: Paratype PIN 1306-68c	



**Fig. 4** Compilation of gobiid genera that share with *Moldavigobius* gen. nov. the count of 10 abdominal and 17 caudal vertebrae (vertebral counts compiled from Reichenbacher and Bannikov 2022: table 2). Numbers of anal- and second dorsal-fin rays and otolith morphology compiled from different literature sources (indicated with superscript numbers), otolith images for *Glossogobius*, *Caffrogobius*, *Sufflogobius* were refigured from Smale et al. (1995). Some additional morphological information is provided for *Grallenia* for which no otolith data were available. References: <sup>1</sup>Miller and Stefanni (2001), Tornabene et al. (2010); <sup>2</sup>Hoese and Allen (2009), Hoese et al. (2015); <sup>3</sup>Shibukawa and Iwata (2007); <sup>4</sup>Allen and Hammer (2018); <sup>5</sup>Froese and Pauly (2022); <sup>6</sup>Goren (1996); <sup>7</sup>Kovačić et al. (2014); <sup>8</sup>Hoese (1986a), Hoese and Larson (2005), Kovačić and Bogorodsky (2014); <sup>9</sup>Hoese (1986b); <sup>10</sup>Miller (1986). Scale bars for otoliths = 0.5 mm

diagnostic trait at the level of genus and species (e.g., Miller 1986; Kovačić 2020), and the relationship between the numbers of rays in the anal fin and second dorsal fin is phylogenetically informative, with the presence of an extra ray in the anal fin (relative to the second dorsal fin) being the derived condition (Pezold 2004). The overall shape of a gobioid otolith, and particularly the shape and morphology of its sulcus (= ostium and cauda), are important diagnostic characters at the level of the genus, and are also of taxonomic value at the level of lineages (Gierl et al. 2018; Lombarte et al. 2018; Schwarzahns et al. 2020a, b).

### Comparison with the *Glossogobius* lineage

Three genera of the *Glossogobius* lineage, i.e., *Bathygobius*, *Glossogobius* and *Grallenia* possess a regular 10 + 17 vertebrae count (Fig. 4).

*Bathygobius* and *Glossogobius* have lower ray counts in the anal fin than †*Moldavigobius* gen. nov. does ( $\leq 9$  vs. 11), and one or two rays less in the anal fin than in the second dorsal fin (vs. equal counts). In addition, the sulcus shapes of their otoliths are clearly distinct from the sulcus of †*Moldavigobius* gen. nov. In *Bathygobius*, the cauda is almost horizontal (vs. inclined in †*Moldavigobius* gen. nov.); in *Glossogobius*, the lower sulcus margin is straight (vs. indented at the junction of ostium and cauda in †*Moldavigobius* gen. nov.). In addition, the subcaudal iugum is positioned at the transition between ostium and cauda in both *Bathygobius* and *Glossogobius* (vs. along the cauda) and is relatively weakly developed (vs. prominent) (Fig. 4). There is a superficial similarity between the overall shapes of the otoliths of *Bathygobius*, *Glossogobius*, and †*Moldavigobius* gen. nov., owing to the absence of a marked posterodorsal projection. However, this character state represents a plesiomorphic condition, since the otoliths of the Thalasseleotridae, to which the (more derived) Gobiidae + Oxudercidae are sister (Gill and Mooi 2012; Thacker et al. 2015), also do not show a marked posterodorsal projection (see

Schwarzahns 2019: figs. 99.9–11 for otoliths of *Thalasseleotris iota*; see also Gierl et al. 2022).

In *Grallenia*, up to 11 anal-fin rays can occur, and the number of soft rays in the anal fin can be the same as (or one less than) in the second dorsal fin (Fig. 4). As no otolith data are available for *Grallenia*, we investigated whether *Grallenia* and †*Moldavigobius* gen. nov. share other characteristic traits. This is obviously not the case as *Grallenia* is of very small size (< 23 mm SL vs. up to 34.2 mm in †*Moldavigobius* gen. nov.), always associated with coral reefs (vs. not), has a very slender body resembling that of a ‘sand goby’ (vs. compact body), and 15 segmented caudal-fin rays (vs. 17) (data for *Grallenia* from Allen and Hammer 2018). Taking all differences together, we do not consider †*Moldavigobius* gen. nov. to be closely related to the *Glossogobius* lineage (Fig. 4).

### Comparison with the *Gobius* lineage

Four genera of the highly diverse *Gobius* lineage, namely, *Caffrogobius*, *Coryogalops*, *Heteroleotris* and *Sufflogobius* have a regular 10 + 17 vertebrae count (Fig. 4).

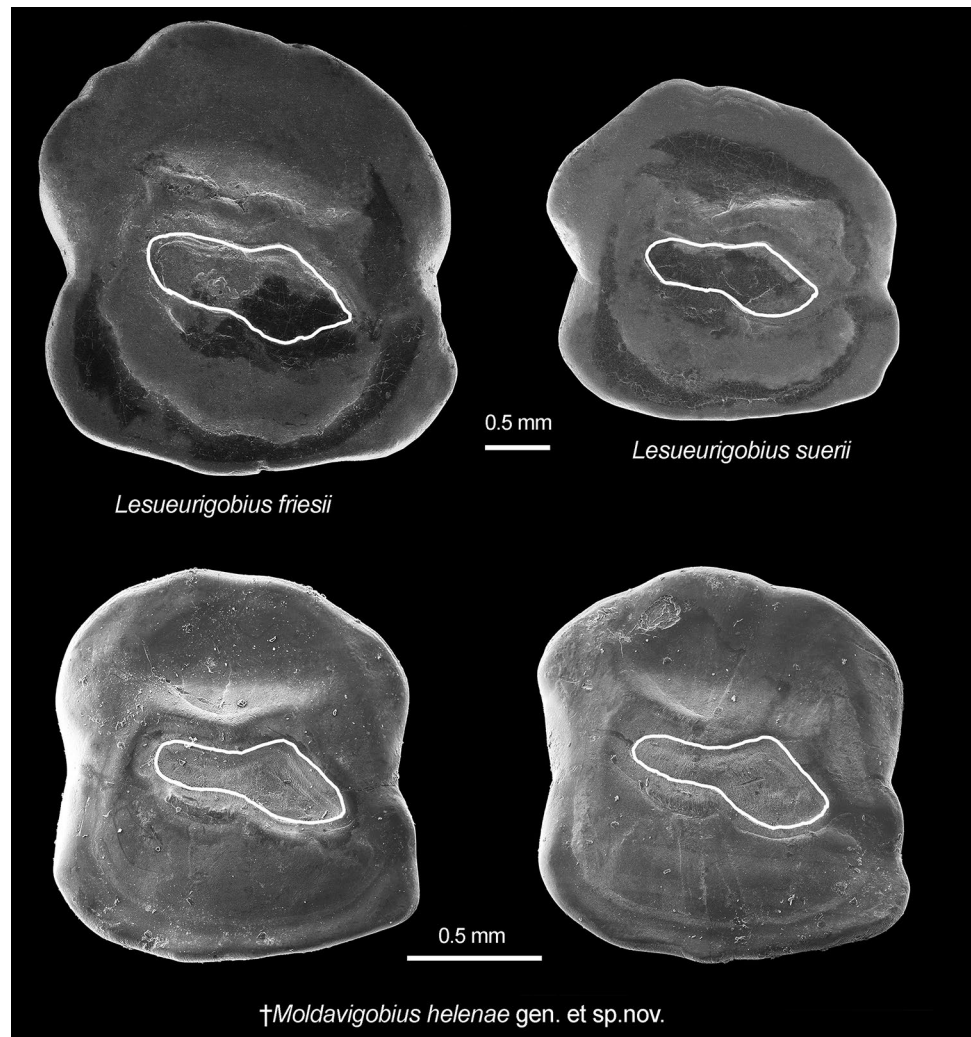
The monotypic genus *Sufflogobius* has 12–13 rays in both the second dorsal and the anal fin (vs. 11 in †*Moldavigobius* gen. nov.). The otoliths of *Sufflogobius* differ from those of †*Moldavigobius* gen. nov. in their irregular to trapezoid shape (vs. squarish) (Fig. 4). This is a rather unusual shape for a gobioid otolith, and may be related to the pelagic lifestyle of *Sufflogobius*.

*Caffrogobius*, *Coryogalops* and *Heteroleotris* share their anal-fin ray counts with †*Moldavigobius* gen. nov., but *Caffrogobius* and *Coryogalops* have at least one ray less in the anal fin than in the second dorsal fin (vs. equal in †*Moldavigobius* gen. nov.). The otoliths of *Caffrogobius*, *Coryogalops* and *Heteroleotris* are characterized by the presence of a marked posterodorsal projection (vs. absent in †*Moldavigobius* gen. nov.) (Fig. 4). It seems justified to assume that the presence of this projection is a derived character state for the *Gobius* lineage, because almost all its members have it, whereas it is lacking or at least much less developed in the other lineages of the Gobiidae (Gut et al. 2020; Schwarzahns et al. 2020a, b; unpublished data of BR). The otoliths of †*Moldavigobius* gen. nov. do not show this derived character state, and we, therefore, consider a close relationship of the new fossil taxon to the *Gobius* lineage to be unlikely.

### Comparison to the *Aphia* lineage

A regular 10 + 17 vertebrae count occurs in both genera of the *Aphia* lineage (*Aphia*, *Lesueurigobius*) (Fig. 4). The number of the anal-fin rays in †*Moldavigobius* gen. nov. is at the lower limit of the corresponding counts in *Aphia* (11–15)

**Fig. 5** Otoliths of the extant gobiid *Lesueurigobius* Whitley (IRSNB, collection Chaîne), and the extinct gobiid †*Moldavigobius* gen. nov. (PIN 1306/68a, PIN 1306/68c) with the contour of the sulcus highlighted. Otoliths of †*Moldavigobius* are mirrored for better comparison. All figures are SEM images and show the medial view



and one ray less than the lower bound in *Lesueurigobius* (12–17) (Fig. 4). Both *Aphia* and *Lesueurigobius* can have one ray more in the anal fin than in the second dorsal fin, but the counts can also be the same (as in †*Moldavigobius* gen. nov.).

The otolith of *Aphia* is ovate and very different from the otolith of †*Moldavigobius* gen. nov. (Fig. 4). In contrast, the otoliths of *Lesueurigobius* resemble those of †*Moldavigobius* gen. nov. in their almost square shape and also in the length and inclination of the sulcus (Fig. 4). However, the cauda width is greater in *Lesueurigobius* than in †*Moldavigobius* gen. nov., while the dorsal lobe of the ostium is more pronounced in †*Moldavigobius* gen. nov. than in *Lesueurigobius* (Fig. 5). Further differences concern the overall otolith shape, which is characterized by the expanded, rounded posterodorsal region in both *L. friesii* and *L. suerii*, whereas the same region is angular and not expanded in †*Moldavigobius* gen. nov. Essentially, the otolith of †*Moldavigobius* gen. nov. gives the impression that it is ‘on the

way’ to becoming a true *Lesueurigobius* otolith, i.e., is at a very early stage in such an evolutionary trajectory. Interestingly, Schwarzhans (2014) found that some otoliths of †*M. suavis* from the Karaman Basin are similar to juvenile otoliths of fossil *Lesueurigobius* from the same beds.

There are further similarities between †*Moldavigobius* gen. nov. and *Lesueurigobius*, e.g., in general body morphometry (see Supplementary Table in Reichenbacher and Bannikov 2022 for data on *Lesueurigobius*) and in the presence of large ctenoid scales. Nevertheless, †*Moldavigobius* gen. nov. is clearly not a member of the genus *Lesueurigobius*, because not only its otoliths, but also its fan-shaped caudal fin clearly differs from the lanceolate or longish caudal-fin shape of the extant species of *Lesueurigobius* (Maul 1971; Miller 1986). Taking all similarities and differences into account, †*Moldavigobius* gen. nov. may represent an ancient relative of *Lesueurigobius* and a possible member of the *Aphia* lineage.



## Conclusions

The new gobioid genus and species †*Moldavigobius helenae* gen. et sp. nov. described in this paper represents a further contribution to the characterization of the unusually rich record of gobies recovered from the upper Serravalian deposits near Naslavcea in northern Moldova. Together with those reported in our previous study (Reichenbacher and Bannikov 2022), this new find is the fifth genus and the seventh species of gobioids from the locality, and their biodiversity at this site is far from being fully explored. †*Moldavigobius helenae* gen. et sp. nov. definitely belongs to the Gobiidae, and probably to the *Aphia* lineage.

Furthermore, the otoliths of †*Moldavigobius* gen. nov. revealed that an otolith-based species previously described as *Knipowitschia suavis* Schwarzhans, 2014 represents a second species of †*Moldavigobius* gen. nov. This is especially remarkable, because the extant genus *Knipowitschia* belongs to the family Oxudercidae (=Gobionellidae sensu Thacker 2013), whereas †*Moldavigobius* gen. nov. is an extinct genus of the Gobiidae. †*Moldavigobius* gen. nov. thus underlines the role of otoliths preserved in situ in elucidating the taxonomic diversity of ancient Gobioidae. Re-assignment of the ‘*Knipowitschia*’ *suavis* otoliths to the new genus also implies that the range of †*Moldavigobius* gen. nov. extended from the SE Mediterranean (presence of †*M. suavis*, see Schwarzhans 2014) to the western sector of the Eastern Paratethys (presence of †*M. helenae* gen. et sp. nov., this study) and the easternmost Eastern Paratethys (presence of †*M. suavis*, see Bratishko et al. 2015).

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## References

- Agorreta, A., D. San Mauro, U. Schlieven, J.L. Van Tassell, M. Kovačić, R. Zardoya, and L. Rüber. 2013. Molecular phylogenetics of Gobioidae and phylogenetic placement of European gobies. *Molecular Phylogenetics and Evolution* 69 (3): 619–633. <https://doi.org/10.1016/j.ympev.2013.07.017>.
- Akihito, M., T. Hayashi, K. Yoshino, T. Yamamoto, Shimada, and H. Senou. 1984. Suborder Gobioidae. In *The fishes of the Japanese archipelago*, ed. H. Masuda, K. Amaoka, C. Araga, T. Uyeno, and T. Yoshino, 236–289. Tokyo: Tokai University Press.
- Allen, G.R., and M.P. Hammer. 2018. *Grallenia larsonae*, a new species of sandgoby (Pisces: Gobiidae) from northern Australia. *Journal of the Ocean Science Foundation* 31: 87–96.
- Arratia, G. 1999. The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements. In *Mesozoic fishes 2 - Systematics and fossil record*, ed. G. Arratia and H.-P. Schultze, 265–334. München: Verlag Dr. Friedrich Pfeil.
- Bannikov, A.F. 2009. On early Sarmatian fishes from the Eastern Paratethys. *Paleontological Journal* 43 (5): 569–573. <https://doi.org/10.1134/s003103010905013x>.
- Bannikov, A.F. 2010. *Fossil vertebrates of Russia and adjacent countries. Fossil acanthopterygians fishes (Teleostei, Acanthopterygii)*. Moscow: GEOS.
- Bannikov, A. F. 2017. New data on the distribution of the fossil gobiiform fishes in the Miocene of the Eastern Paratethys. In *The 10th Indo-Pacific Fish Conference, Tahiti – 2–6 October 2017, Book of Abstracts*, p. 138.
- Bannikov, A. F. 2018. New data on the distribution of the gobiiform fishes (Gobioidae) in the Eastern Paratethys [Novye dannye o rasprostraneni bychkovidnykh ryb (Gobioidae) v Vostochnom Paratetise]. In *Basic and Applied Paleontology. Materials of LXIV session of the Paleontological Society*, 175–176. St. Petersburg: VSEGEI.
- Betancur-R, R., E.O. Wiley, G. Arratia, A. Acero, N. Bailly, M. Miya, G. Lecointre, and G. Ortí. 2017. Phylogenetic classification of bony fishes. *BMC Evolutionary Biology* 17 (1): 162. <https://doi.org/10.1186/s12862-017-0958-3>.
- Birdsong, R.S., E.O. Murdy, and F.L. Pezold. 1988. A study of the vertebral column and median fin osteology in gobioid fishes with comments on gobioid relationships. *Bulletin of Marine Science* 42 (2): 174–214.
- Bratishko, A., W. Schwarzhans, B. Reichenbacher, Y. Vernyhorova, and S. Čorić. 2015. Fish otoliths from the Konkian (Miocene, early Serravalian) of Mangyshlak (Kazakhstan): Testimony to an early endemic evolution in the Eastern Paratethys. *Paläontologische Zeitschrift* 89 (4): 839–889. <https://doi.org/10.1007/s12542-015-0274-4>.
- Carnevale, G., A.F. Bannikov, W. Landini, and C. Sorbini. 2006. Volhynian (early Sarmatian sensu lato) fishes from Tsurevsky, North Caucasus, Russia. *Journal of Paleontology* 80 (4): 684–699. [https://doi.org/10.1666/0022-3360\(2006\)80\[684:vesslf\]2.0.co;2](https://doi.org/10.1666/0022-3360(2006)80[684:vesslf]2.0.co;2).
- Cuvier, G. 1816. *Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Tome II, Les reptiles, les poissons, les mollusques et les annélides*. Paris: A. Belin.

- Froese, R., and D. Pauly. 2022. FishBase. World Wide Web electronic publication. [www.fishbase.org](http://www.fishbase.org), version (12/2020).
- Gierl, C., and B. Reichenbacher. 2015. A new fossil genus of Gobiiformes from the Miocene characterized by a mosaic set of characters. *Copeia* 103 (4): 792–805. <https://doi.org/10.1643/ci-14-146>.
- Gierl, C., D. Liebl, R. Šanda, J. Vukić, H.R. Esmaili, and B. Reichenbacher. 2018. What can goby otolith morphology tell us? *Cybium* 42 (4): 349–363. <https://doi.org/10.26028/cybium/2018-424-006>.
- Gill, A.C., and R.D. Mooi. 2012. Thalasseleotrididae, new family of marine gobioid fishes from New Zealand and temperate Australia, with a revised definition of its sister taxon, the Gobiidae (Teleostei: Acanthomorpha). *Zootaxa* 3266 (1): 41–52. <https://doi.org/10.11646/zootaxa.3266.1.3>.
- Gierl, C., M. Dohrmann, P. Keith, M. Humphreys, H.R. Esmaili, J. Vukić, R. Šanda, and B. Reichenbacher. (2022). An integrative phylogenetic approach for inferring relationships of fossil gobioids (Teleostei: Gobiiformes). *PLOS ONE* 17(7), e0271121. <https://doi.org/10.1371/journal.pone.0271121>
- Goren, M. 1996. A review of the southern African gobioid fish genus *Caffrogobius* Smitt, 1900. *The J.L.B. Smith Institute of Ichthyology Special Publication* 57:1–28.
- Günther, A. C. L. G. 1880. *An introduction to the study of fishes*. Edinburgh: Adam and Charles Black.
- Gut, C., J. Vukić, R. Šanda, T. Moritz, and B. Reichenbacher. 2020. Identification of past and present gobies: Distinguishing *Gobius* and *Pomatoschistus* (Teleostei: Gobioidae) species using characters of otoliths, meristics and body morphometry. *Contributions to Zoology* 89: 282–323. <https://doi.org/10.1163/18759866-bja10002>.
- Harrison, I.J. 1989. Specialization of the gobioid palatopterygoquadrate complex and its relevance to gobioid systematics. *Journal of Natural History* 23 (2): 325–353. <https://doi.org/10.1080/00222938900770211>.
- Hoese, D.F. 1984. Gobioidae: relationships. In *Ontogeny and systematics of fishes*, ed. H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall, and S.L. Richardson, 588–591. Gainesville, Florida: American Society of Ichthyologists and Herpetologists.
- Hoese, D.F. 1986a. Descriptions of two new species of *Heteroleotris* (Pisces: Gobiidae) from the western Indian Ocean, with discussion of related species. *The J.L.B. Smith Institute of Ichthyology Special Publication* 41: 1–25.
- Hoese, D.F., and G.R. Allen. 2009. Description of three new species of *Glossogobius* from Australia and New Guinea. *Zootaxa* 1981: 1–14.
- Hoese, D.F., and A.C. Gill. 1993. Phylogenetic relationships of eleotridid fishes (Perciformes, Gobioidae). *Bulletin of Marine Science* 52 (1): 415–440.
- Hoese, D.F., and H.K. Larson. 2005. Description of two new species of *Heteroleotris* (Gobiidae) from the south Pacific, with a revised key to species and synonymization of the genus *Pascua* with *Heteroleotris*. *Zootaxa* 1096: 1–16.
- Hoese, D.F., R.K. Hadiaty, and F. Herder. 2015. Review of the dwarf *Glossogobius* lacking head pores from the Malili lakes, Sulawesi, with a discussion of the definition of the genus. *Raffles Bulletin of Zoology* 63: 14–26.
- Hoese, D. F. 1986b. Family No. 240: Gobiidae. In *Smiths' Sea Fishes*, eds. M. M. Smith, and P. C. Heemstra, 774–807. Johannesburg: Macmillan South Africa.
- Iglésias, S.P., J. Vukić, D.Y. Sellos, T. Soukupová, and R. Šanda. 2021. *Gobius xoriguer*, a new offshore Mediterranean goby (Gobiidae), and phylogenetic relationships within the genus *Gobius*. *Ichthyological Research*. <https://doi.org/10.1007/s10228-020-00797-9>.
- Ijlin, B.S. 1927. Keys to the gobies (Fam. Gobiidae) of the Sea of Azov and the Black Sea. Preliminary Communication. *Trudy Azovsko-Cernomorskoj Naučno-Promyslovoj Ékspedicii* 2: 128–143.
- Ionko, V.I. 1954. O nakhodke iskopayemykh ryb v nizhnesarmatskikh otlozheniyakh MSSR. *Trudy Odesskogo Universiteta. Sbornik Geologo-Geograficheskogo Fakul'teta* 2: 109–119.
- Jordan, D.S., and B.W. Evermann. 1896. The fishes of North and Middle America: A descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, North of the Isthmus of Panama Part I. *Bulletin of the United States National Museum* 47: 1–1240.
- Kessler, K. F. 1877. *The Aralo-Caspian Expedition. IV. Fishes of the Aralo-Caspio-Pontine ichthyological region*. St. Petersburg.
- Kovačić, M. 2020. Checklist of gobies (Teleostei: Gobiidae) of the Mediterranean Sea and a key for species identification. *Zootaxa* 4877 (1): 75–101. <https://doi.org/10.11646/zootaxa.4877.1.3>.
- Kovačić, M., and S.V. Bogorodsky. 2014. A new species of *Heteroleotris* (Perciformes: Gobiidae) from the Red Sea. *Zootaxa* 3764 (4): 475–481. <https://doi.org/10.11646/zootaxa.3764.4.7>.
- Kovačić, M., S.V. Bogorodsky, and A.O. Mal. 2014. Two new species of *Coryogalops* (Perciformes: Gobiidae) from the Red Sea. *Zootaxa* 3881 (6): 513–531. <https://doi.org/10.11646/zootaxa.3881.6.2>.
- Liu, H.T.H., H. Ahnelt, G.A.C. Balma, and G.B. Delmastro. 2009. First record of *Gobius roulei* (Gobiidae) in the Ligurian Sea. *Cybium* 33 (3): 253–254.
- Lombarte, A., M. Miletic, M. Kovačić, J.L. Otero-Ferrer, and V.M. Tuset. 2018. Identifying sagittal otoliths of Mediterranean Sea gobies: Variability among phylogenetic lineages. *Journal of Fish Biology* 92 (6): 1768–1787. <https://doi.org/10.1111/jfb.13615>.
- Maul, G.E. 1971. On a new goby of the genus *Lesueurigobius* from off the Atlantic coast of Morocco and Madeira (Perciformes, Gobioidae). *Bocagiana* 29: 1–7.
- Miller, P.J. 1986. Gobiidae. In *Fishes of the north-eastern Atlantic and the Mediterranean (FNAM)*, ed. P.J.P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen, and E. Tortonese, 1019–1085. Paris: UNESCO.
- Miller, P.J., and S. Stefanni. 2001. The Eastern Pacific species of *Bathygobius* (Perciformes: Gobiidae). *Revista De Biología Tropical* 49: 141–156.
- Miller, P. J. 2004. The freshwater fishes of Europe. Vol. 8/II. Gobiidae 2. Wiebelsheim: AULA-Verlag.
- Müller, J. 1845. Über den Bau und die Grenzen der Ganoiden, und über das natürliche System der Fische. *Physikalisch-Mathematische Abhandlungen Der Königlich Akademien Der Wissenschaften Zu Berlin* 1845: 117–216.
- Nelson, J.S., T.C. Grande, and M.V.H. Wilson. 2016. *Fishes of the World*, 5th ed. Hoboken: Wiley.
- Penk, S.B.R., M. Altner, A.F. Cerwenka, U.K. Schliewen, and B. Reichenbacher. 2019. New fossil cichlid from the middle Miocene of East Africa revealed as oldest known member of the Oreochromini. *Scientific Reports* 9 (10198): 1–24. <https://doi.org/10.1038/s41598-019-46392-5>.
- Pezold, F. 2004. Phylogenetic analysis of the genus *Gobionellus* (Teleostei: Gobiidae). *Copeia* 2004 (2): 260–280. <https://doi.org/10.1643/CI-02-218R3>.
- Reichenbacher, B., and A.F. Bannikov. 2022. Diversity of gobioid fishes in the late middle Miocene of northern Moldova, Eastern Paratethys – part I: An extinct clade of *Lesueurigobius* look-alikes. *PalZ* 96: 67–112. <https://doi.org/10.1007/s12542-021-00573-8>.
- Reichenbacher, B., R. Gregorová, K. Holcová, R. Šanda, J. Vukić, and T. Přikryl. 2018. Discovery of the oldest *Gobius* (Teleostei, Gobiiformes) from a marine ecosystem of Early Miocene age. *Journal of Systematic Palaeontology* 16 (6): 493–513. <https://doi.org/10.1080/14772019.2017.1313323>.
- Reichenbacher, B., S. Filipescu, and A. Miclea. 2019. A unique middle Miocene (Sarmatian) fish fauna from coastal deposits in the



- eastern Pannonian Basin (Romania). *Palaeobiodiversity and Palaeoenvironments* 99 (2): 177–194. <https://doi.org/10.1007/s12549-018-0334-3>.
- Sauvage, M.H.E. 1875. Notes sur les poissons fossiles. *Bulletin De La Société Géologique De France* 3 (3): 631–642.
- Schneider, C.A., W.S. Rasband, and K.W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9 (7): 671–675. <https://doi.org/10.1038/nmeth.2089>.
- Schwarzahns, W. 2014. Otoliths from the middle Miocene (Serravalian) of the Karaman Basin, Turkey. *Cainozoic Research* 14 (1): 35–69.
- Schwarzahns, W. 2017. A review of otoliths collected by W. Weiler from the Badenian of Romania and by B. Strashimirov from Badenian equivalents of Bulgaria. *Cainozoic Research* 17 (2): 167–191.
- Schwarzahns, W., K. Bradić, and L. Rundić. 2015. Fish-otoliths from the marine-brackish water transition from the Middle Miocene of the Belgrade area, Serbia. *Paläontologische Zeitschrift* 89 (4): 815–837. <https://doi.org/10.1007/s12542-015-0272-6>.
- Schwarzahns, W., H. Ahnelt, G. Carnevale, S. Japundžić, K. Bradić, and A. Bratishko. 2017. Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part III: tales from the cradle of the Ponto-Caspian gobies. *Swiss Journal of Palaeontology* 136 (1): 45–92. <https://doi.org/10.1007/s13358-016-0120-7>.
- Schwarzahns, W., K. Agiadi, and G. Carnevale. 2020a. Late Miocene–Early Pliocene evolution of Mediterranean gobies and their environmental and biogeographic significance. *Rivista Italiana Di Paleontologia e Stratigrafia* 126 (3): 657–724.
- Schwarzahns, W., R. Brzobohatý, and U. Radwańska. 2020b. Goby otoliths from the Badenian (middle Miocene) of the Central Paratethys from the Czech Republic, Slovakia and Poland: A baseline for the evolution of the European Gobiidae (Gobiiformes; Teleostei). *Bollettino Della Società Paleontologica Italiana* 59 (2): 125–173. <https://doi.org/10.4435/bspi.2020.10>.
- Shibukawa, K., and A. Iwata. 2007. *Grallenia*, a new goby genus from the western Pacific, with descriptions of two new species (Perciformes: Gobiidae: Gobiinae). *Bulletin of the National Museum of Nature and Science Series a, Supplement* 1: 123–136.
- Smale, M. J., G. Watson, and T. Hecht. 1995. Otolith atlas of southern African marine fishes. In *Ichthyological Monographs*. Grahams-town: J. L. B. Smith Institute of Ichthyology.
- Thacker, C.E. 2013. Phylogenetic placement of the European sand gobies in Gobiionellidae and characterization of gobiionellid lineages (Gobiiformes: Gobioidei). *Zootaxa* 3619 (3): 369–382.
- Thacker, C.E. 2015. Biogeography of goby lineages (Gobiiformes: Gobioidei): Origin, invasions and extinction throughout the Cenozoic. *Journal of Biogeography* 42 (9): 1615–1625. <https://doi.org/10.1111/jbi.12545>.
- Thacker, C.E., T.P. Satoh, E. Katayama, R.C. Harrington, R.I. Eytan, and T.J. Near. 2015. Molecular phylogeny of Percomorpha resolves *Trichonotus* as the sister lineage to Gobioidei (Teleostei: Gobiiformes) and confirms the polyphyly of Trachinoidei. *Molecular Phylogenetics and Evolution* 93: 172–179. <https://doi.org/10.1016/j.ympev.2015.08.001>.
- Tornabene, L., C.C. Baldwin, L.A. Weigt, and F.L. Pezold. 2010. Exploring the diversity of western Atlantic *Bathygobius* (Teleostei: Gobiidae) with cytochrome c oxidase-I, with descriptions of two new species. *Aqua, International Journal of Ichthyology* 16 (4): 141–170.
- Wang, H.-Y., M.-P. Tsai, J. Dean, and S.-C. Lee. 2001. Molecular phylogeny of gobioid fishes (Perciformes: Gobioidei) based on mitochondrial 12S rRNA sequences. *Molecular Phylogenetics and Evolution* 20 (3): 390–408. <https://doi.org/10.1006/mpev.2001.0957>.
- Whitley, G.P. 1950. New fish names. *Proceedings of the Royal Society of New South Wales* 1948–49: 44.
- Więcaszek, B., A. Nowosielski, J. Dąbrowski, K. Górecka, S. Keszka, and A. Strzelczak. 2020. Fish size effect on sagittal otolith outer shape variability in round goby *Neogobius melanostomus* (Pallas 1814). *Journal of Fish Biology* 97 (5): 1520–1541. <https://doi.org/10.1111/jfb.14521>.