Swiss J Palaeontol (2017) 136:141–149
DOI 10.1007/s13358-016-0121-6

Review of "*Clupea humilis*" from the Sarmatian of Moldova and description of *Moldavichthys switshenskae* gen. et sp. nov.

E. M. Baykina[1] · **W. W. Schwarzhans**[2]

Received: 12 August 2016 / Accepted: 23 September 2016 / Published online: 12 October 2016

Abstract *Moldavichthys switshenskae* is established as a new fossil genus and species of the family Clupeidae, subfamily Alosinae, to encompass the specimens from the Sarmatian of Moldova, which hitherto have been recorded as *Clupeonella humilis* (v.Meyer, 1851). Specimens from the type area and strata (Ottnangian of the Western Paratethys) differ from the Moldovan ones in a greater number of vertebrae, the more posterior position of dorsal fin and a greater number of postventral scutes. Their generic allocation requires review. *Moldavichthys* resembles the recent genus *Alosa*, known from the northern Atlantic, NE Pacific, the Mediterranean and the Ponto-Caspian Sea. *Moldavichthys* differs from *Alosa* in the shape of the jaw and the opercular bones and the otolith morphology and is thought to represent an extinct Paratethyan endemic lineage. Otolith in situ was found in three skeletons of *Moldavichthys switshenskae*. They are unusually compact and compressed when compared to Recent *Alosa* otoliths, with the caveat however, that very little is known of otoliths from the extant Ponto-Caspian *Alosa* species. There are no isolated fossil otoliths known, which would correspond to *M. switshenskae*, although recently *Alosa paulicrenata* Bratishko, Schwarzhans & Reichenbacher 2015 has been described from the Konkian of Kazakhstan. A review of Sarmatian otoliths from Bulgaria has revealed a species, which we tentatively assign as *Moldavichthys*? *gomotartziensis* (Strashimirov, 1985).

Keywords Ichthyology · Teleost · Clupeidae · Alosinae · Paleontology · Moldova · Bulgaria

Introduction

The clupeid subfamily Alosinae, or shads, include some of the largest herrings, most of which are marine and anadromous species. They include seven recent genera with thirty-one species living in warm temperate and subtropical to tropical waters of the northern hemisphere (Whitehead et al. 1985). Fossil alosins are well known since the early Oligocene (Daniltshenko 1960, 1980; Grande 1985). However, in the Paleogene and Neogene deposits of the Eastern Paratethys, they are much less common than representatives of the Clupeinae. This may partly be caused by the preservation of potential fossil alosin material lacking many important features, such as the medial notch of the upper jaw or dentition of jaw bones, which can easily lead to confusion with certain Clupeinae. For example, *Clupeonella* is similar to alosins in its body shape, the position of the fins, and a full range of robust ventral scutes. *Sardina* and *Sardinops* have opercular bones sculptured with radial ridges and grooves like *Alosa*. Thus, many of the Oligocene–Miocene clupeids of the Eastern Paratethys require review for proper subfamilial allocation.

Here, we describe a new genus and species from the Sarmatian of Northern Moldova, which has been regarded as a member of the Clupeinae in the past having been assigned to *Clupea humilis* v.Meyer, 1851 or *Clupeonella humilis* (v.Meyer, 1851) following Daniltshenko (1980),

Editorial handling: L. Cavin and D. Marty.

✉ W. W. Schwarzhans
wwschwarz@aol.com

E. M. Baykina
baikina.eug@mail.ru

[1] State Darwin Museum, Moscow 119991, Russia

[2] Natural History Museum of Denmark, Zoological Museum, Universitetsparken 15, 2100 Copenhagen, Denmark

respectively, and which we now relocate to the subfamily Alosinae.

Since the middle of the nineteenth century, numerous findings of *Clupeonella humilis* (v.Meyer, 1851) have been recorded from the lower Sarmatian marls of Karpov Yar, Northern Moldova, Naslavcea village. In literature, these fishes were first mentioned and briefly described as *Clupea humilis* v.Meyer, 1851 (Ionko 1954), because Ionko considered it to be identical with this species, which was first described from the Ottnangian of the Western Paratethys. Later, Daniltshenko (1980) placed the species in the genus *Clupeonella* following a review of Menner (1949), who had described similar skeletons from Chokrakian deposits of Western Ciscaucasia. However, our studies conclude that despite the overall similarity with *Clupeonella*, the Moldovan fishes show a number of significant differences, such as: two auditory bullae (instead of one), teeth-bearing premaxilla, opercle sculptured with radial ridges and last rays of the anal fin normally developed, not extended. We consider these features to diagnostically satisfy a position within Alosinae. Additional characters typically found in the Alosinae are a medial notch on the premaxilla, a straight or slightly curved parasphenoid, projected near the middle of the orbit and a full range of highly developed ventral scutes.

The specific shape of the jaw and opercle and the morphology of the otolith differ from other alosin genera and have led us to view the Moldovan fishes as representing an extinct genus, *Moldavichthys* n.gen., possibly endemic to the Paratethys. We would like to stress though that the reinterpretation of the fishes from the Sarmatian of Moldova hitherto recorded as *Clupeonella humilis* and now described as *Moldavichthys switshenskae* n.gen. n.sp. does in no way indicate that the type-specimens of *Clupeonella humilis* would necessarily belong to the same genus. In fact we would like to emphasize that those specimens from the Ottnangian of the Western Paratethys certainly represent a distinct species (see below) and require in depth review of its systematic position.

In modern literature, the name giving genus *Alosa* is one of the largest genera with 15 species according to Whitehead et al. (1985). This account includes *Pomolobus* and *Caspialosa* in subgeneric ranking. Due to the high species diversity, which we consider somewhat problematical, the spectrum of morphological features that characterize this genus is greatly expanded. It thus also affects the taxonomy of fossil Alosinae. The outcome in our view is a somewhat distorted picture, where we see the Clupeinae having intensively evolved during Oligocene–Miocene time with numerous, partly extinct lineages, but the Alosinae having been represented during the same time frame mainly by a widely defined genus *Alosa*. In consequence, the revision of fossil Alosinae may be a necessary and challenging task, but it can only be satisfyingly resolved after a review of the extend species of the genus *Alosa*.

Materials and methods

The material described herein comprises articulated skeletons from the collection of the Borisyak Paleontological Institute (PIN) of the Russian Academy of Sciences. A total of 30 complete and fragmentary skeletons were examined of *Moldavichthys switshenskae* n.gen. et n.sp. (PIN 1306 and PIN 5274, Karpov Yar, Naslavcea village, Northern Moldova). Otoliths in situ were found in three specimens (PIN 1306/114, 1306/118, and PIN 5274/10 A&B).

The fish measurements used in this study follow the scheme proposed by Svetovidov (1952) with some modifications: (SL) standard body length; (Ar) preorbital distance; (rs) orbital diameter; (sp) postorbital distance; (Ap) head length; (tu) head depth at the occiput; (lmx) maxillary length; (lmd) mandibular length; (H) maximum body depth; (h) minimum body depth; (aD) predorsal distance; (D_1C) postdorsal distance; (aV) preventral distance; (aA) preanal distance; (PV) pectoventral distance; (VA) ventroanal distance; (A_1C) postanal length; (lD) dorsal fin base length; (hD) dorsal fin height; (lA) anal fin base length; (hA) anal fin depth; (lC) length of middle caudal fin rays.

The terminology employed here for the morphological description of the otoliths follows Koken (1891), Weiler (1942) and Schwarzhans (1978). The following abbreviations are used for the morphometric measurements: otolith length = OL; otolith height = OH; otolith thickness = OT; ostium length = OsL; cauda length = CaL; sulcus length = SuL. The rostrum length is measured from the tip of the rostrum to the level of the deepest point of the excisura and is calculated as percentage of OL. The length of the dorsal rim is measured from the tip of the antirostrum to the tip of the posterior rim and is calculated as percentage of OL.

Systematic paleontology

Order Clupeiformes Bleeker, 1859.
Suborder Clupeoidei Bleeker, 1859.
Family Clupeidae Cuvier, 1817.
Subfamily Alosinae Svetovidov, 1953.
Genus *Moldavichthys* gen. nov.

1954 Clupea Linnaeus, 1758—sensu Ionko, p. 111, Tab. I, fig. 1.
1980 Clupeonella Kessler, 1877—sensu Daniltshenko, p. 12.

Etymology Named after the Latin transliteration Moldavia for the state of Moldova, which harbors the type-locality.

Type species Moldavichthys switshenskae sp. nov.; Middle Miocene, Serravallian, Early Sarmatian (Volhynian); Karpov Yar, Naslavcea village, Moldova. *Moldavichthys* is a monotypic genus.

Diagnosis Two auditory capsules present, bulla prootica 1,5–2 times larger than bulla pterotica; parasphenoid straight or almost straight, projects into lower half of orbit; premaxilla with teeth; maxilla moderately wide, saber-shaped, with slightly convex, serrated ventral margin, reaching vertical axis extending through orbital center; hypomaxilla absent; lower jaw high and tooth-bearing; mandibular joint located near vertical extending through orbital center; subopercle with well developed process; preopercle moderately high, its vertical ramus higher and wider than the horizontal; opercle sculptured with thin, but well developed radial ridges, with slight incision at posterior margin; branchiostegal membrane with seven or eight rays; posterodorsal end of last ray transformed into curved blade; body moderately high; vertebral column consisting of 39–44 vertebrae; dorsal fin with 15–16 rays, subtriangular, originating anterior to midlength of body; pelvic fins with eight (?) rays, located within anterior one-third of dorsal fin base; anal fin originating at boundary between anterior and middle thirds of postdorsal distance; two last anal fin rays not elongated; caudal skeleton with two epurals; ventral scutes very robust; otolith compressed (OL:OH = 1.35–1.40), with a short, blunt rostrum, a deeply but irregularly curved ventral rim and ostium being just slightly longer than cauda (OsL:CaL = 1.20–1.30).

Comparison Of all recent alosin genera of the northern hemisphere, *Alosa* resembles most, but *Moldavichthys* differs significantly in the compressed otolith morphology with the short and blunt rostrum and convex ventral rim, the shape of the jaw and the opercular bones (Figs. 2, 4).

Moldavichthys switshenskae sp. nov.
Figures 1, 2, 3

1954 *Clupea humilis* v.Meyer, 1851—Ionko, p. 111, Tab. I, fig. 1.
1980 *Clupeonella humilis* (v.Meyer, 1851)—Daniltshenko, p. 12.

Holotype PIN, no. 1306-112, skeleton imprint without caudal fin; northern Moldova, Naslavcea village, Karpov Yar locality; Middle Miocene, Serravallian, Early Sarmatian (Volhynian).
Etymology Named in honor of the late A. A. Switshenska (Moscow), who collected much of the type-material and in recognition of her contribution to the knowledge of fossil fishes from Russia.

Material Thirty skeletons including plates and counterplates and fragments; two collections: PIN 1306, no. 101–104, 107, 108, 110–112, 114, 116, 117, 119–121, 123–126, 129, 130, 132–134, 137, 139 (by A. A. Switchenska) and PIN 5274, no. 6, 9, 12, 16 (by A. F. Bannikov); Sarmatian, Karpov Yar, Naslavcea village at Dnestr River, Moldova.

Description (Figs. 1, 2, 3) Small fishes, with moderately high, not elongated body, up to 70 mm of standard length (SL). The dorsal profile is almost straight, the abdomen is significantly convex. The body depth at the anterior margin of the dorsal fin base is 27–33 % of SL. The minimum body depth is 28–42 % of the maximum body depth, i.e., 8–12 % of SL. The head is large and high, 30–36 % of SL, and its height at the occiput is 25–30 % of SL.

The roof of the skull is straight along the dorsal profile. The snout is pointed. The bulla prootica is 1.5–2 times as large as the bulla pterotica. The parasphenoid is straight or almost straight along its entire length; its visible part is below the central axis of the orbit, but not as low as is usually found in clupeins. Details of the frontals are not discernable in our material.

The mouth is terminal. The premaxilla is wide, tooth-bearing, with a long posterior process and a medial notch. The maxilla is saber-shaped, thin and moderately wide (Fig. 2b, mx). Its ventral margin is slightly convex and serrated for almost the entire length of the bone; the posterior end is rounded, pointed upwards and reaches to the middle of the orbit or slightly anterior of it. The articular process is long, thin, positioned at an angle of about 140° to the axis of the bone. The supramaxillae are very well developed. The anterior supramaxilla is large, long, wide, slightly convex, with a small longitudinal ridge. The dorsal and ventral margins of the posterior supramaxilla are convex; the bone is rhomboid (Fig. 2b, smx). The anterior process is long and thin.

A hypomaxilla is absent. The outline of the mandible is rounded trapezoidal, with a straight dorsal margin. The mandible projects significantly beyond the upper jaw and is articulated with the skull near the middle of the orbital level. The anguloarticular is subtriangular, with a moderately developed articular process (Fig. 2b, aa). The anterior margin is deeply concave in the upper part and convex in the lower. The dentary is likely tooth-bearing, with a long and low anterodorsal margin (Fig. 2b, d). The symphysal region is low; the anteroventral angle is rounded. Its posterior margin is concave in the lower half. The axial rays at the margin of the anterior dentary are positioned at an angle of 40°–50°. The dorsal margin of the quadrate can bear a wide and gentle notch.

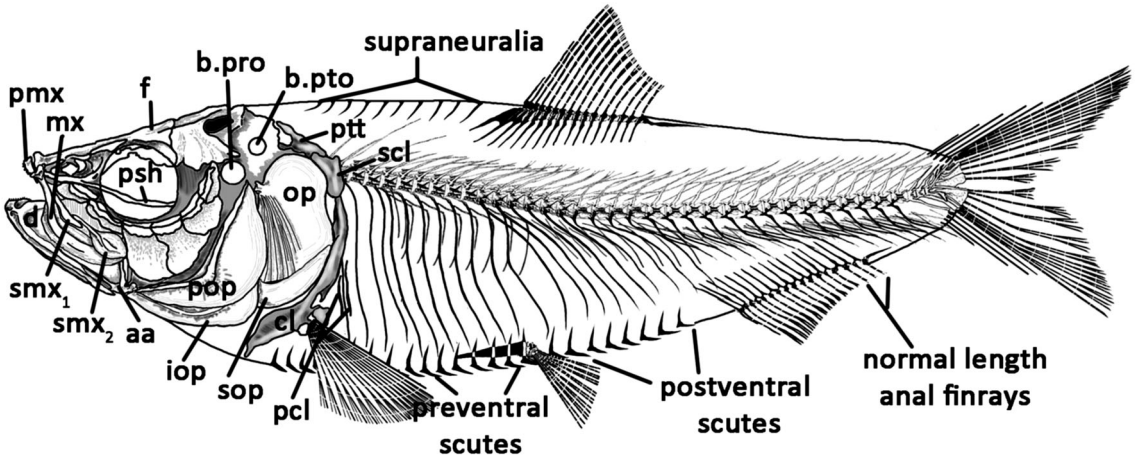


Fig. 1 Generalized reconstruction of skeleton of *Moldavichthys switshenskae* gen. et sp. nov. from several specimens in the collections PIN 1306 and 5274 [Naslavcea village, Karpov Yar; Early Sarmatian (Volhynian)]. Designations of bones (after Grande 1985): *aa* anguloarticular, *b.pro* prootic bulla, *b.pto* pterotic bulla, *cl* cleithrum, *d* dentary, *f* frontal, *iop* interopercle, *mx* maxilla, *op* opercle, *pcl* postcleithra, *pop* preaopercle, *pmx* premaxilla, *psh* parasphenoid, *ptt* posttemporal, *scl* supracleithrum, *sop* subopercle, *smx* supramaxilla

The preopercle is moderately large and low (Fig. 2b, pop). Its horizontal ramus is about 1.5 times shorter than the vertical ramus and 2–2.5 times narrower. The rami of the preopercles are positioned at an angle of about 100°–110°. The opercle is high, wide, and sculptured with 5–8 thin radial ridges (Fig. 2b, op). The posterior margin may have a gentle incision, and the lower half of the bone is much wider than the upper half. The postero-ventral angle of the opercle is sloped and pointed. The subopercle is long, narrow, wedge-shaped and with a high developed process (Fig. 2b, sop). The interopercle is long, slightly curved, with a high and wide posterior end and a robust longitudinal ridge (Fig. 2b, iop).

The branchiostegal membrane has seven or eight rays. The last ray is saber-shaped, with a straight ventral margin and a curved dorsal margin. The posterodorsal corner of the last ray is subtriangular, wide, without a clear blade.

The vertebral column extends slightly above the longitudinal trunk axis. It consists of 39–44 vertebrae, including 22–27 abdominal vertebrae, the anterior-most 4 or 5 of which are covered by the opercle. The abdominal vertebrae are slightly elongated. The caudal region consists of 17 vertebrae. Their neural spines are approximately as long as the haemal spines and positioned at an angle of approximately 45°–50° to the vertebral centrum. Intermuscular bones are numerous, observed throughout the vertebral column, except for the region of the caudal fin. There are 20–25 rib pairs, which are very thin, long, and reach to the abdominal outline.

The dorsal fin is subtriangular. It originates above the 15th–17th abdominal vertebra and terminates above the 21st–23rd vertebrae. The dorsal fin contains 15–16 rays supported by 16–17 pterygiophores (the first pterygiophore is free). About 9–10 supraneurals are present.

The anal fin is displaced caudally. The origin of the anal fin is positioned opposite to the third or fourth caudal vertebra and terminates under the 11th caudal vertebra. The anal fin base is 13–18 % of SL. The anal fin height is 8–11 % of SL. The anal fin consists of 17–18 rays. The two posteriormost rays are not elongated.

The pectoral fins are moderately long, pointed, and attached at a low position just slightly above the abdominal outline. The fin contains 14–16 rays, with the second and third being the longest.

The pelvic fins are long, approximately as long as five to six vertebrae. They originate under the 17th–20th vertebra, under the anterior third of the dorsal fin base. The pelvic fins contain eight (?) rays.

The caudal fin is very deeply notched. The middle rays of the caudal fin are about 7–13 % as long as SL. The outermost rays are approximately three times as long as the middle rays. The skeleton of the caudal fin contains two elongated epurals, six autogenic hypurals, and one parhypural, which is fused with the first preural vertebra.

About 38–40 transverse rows of scales are present. The row of ventral scutes forms a very distinct keel. Anteriorly, it reaches onto the throat and posteriorly terminates just before reaching the anal fin. There are 15–16 scutes in front of the pelvic fins and 8 behind.

Measurements from 30 specimens of *Moldavichthys switshenskae*: SL ranges from 31 to 65 mm. Morphometric data in % of SL: Ap—30–36, tu—25–30, H—27–33, h—8–12, aD—46–53, D1C—35–40, aV—51–59, aA—72–82, A1C—9–15, lD—12–15, hD—15–22, lA—13–18, hA—8–11, PV—24–32, VA—20–27, lC—7–13; in % of Ap: Ar—16–26, rs—27–35, sp—41–53, lmx—30–58, lmd—47–61.

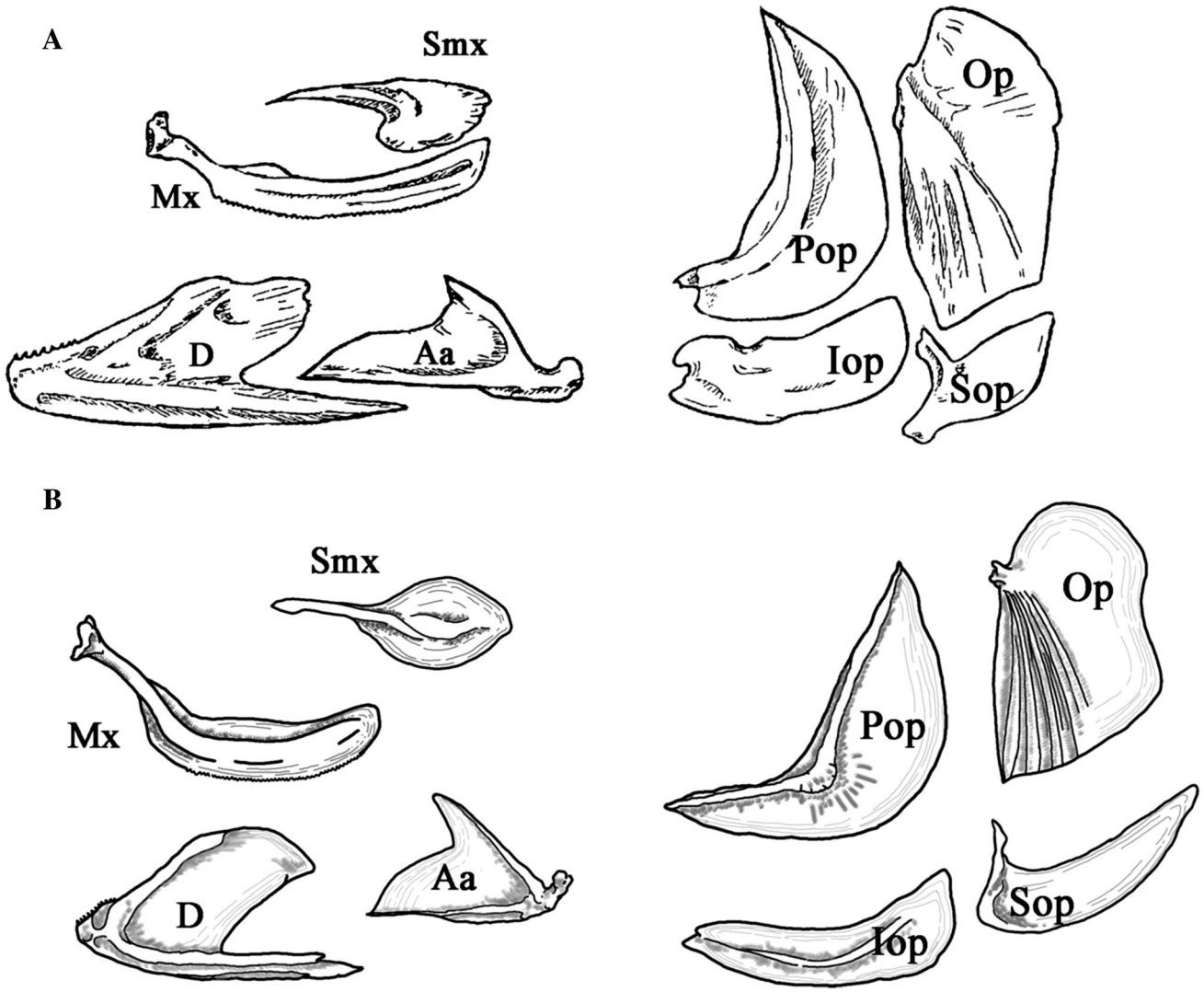
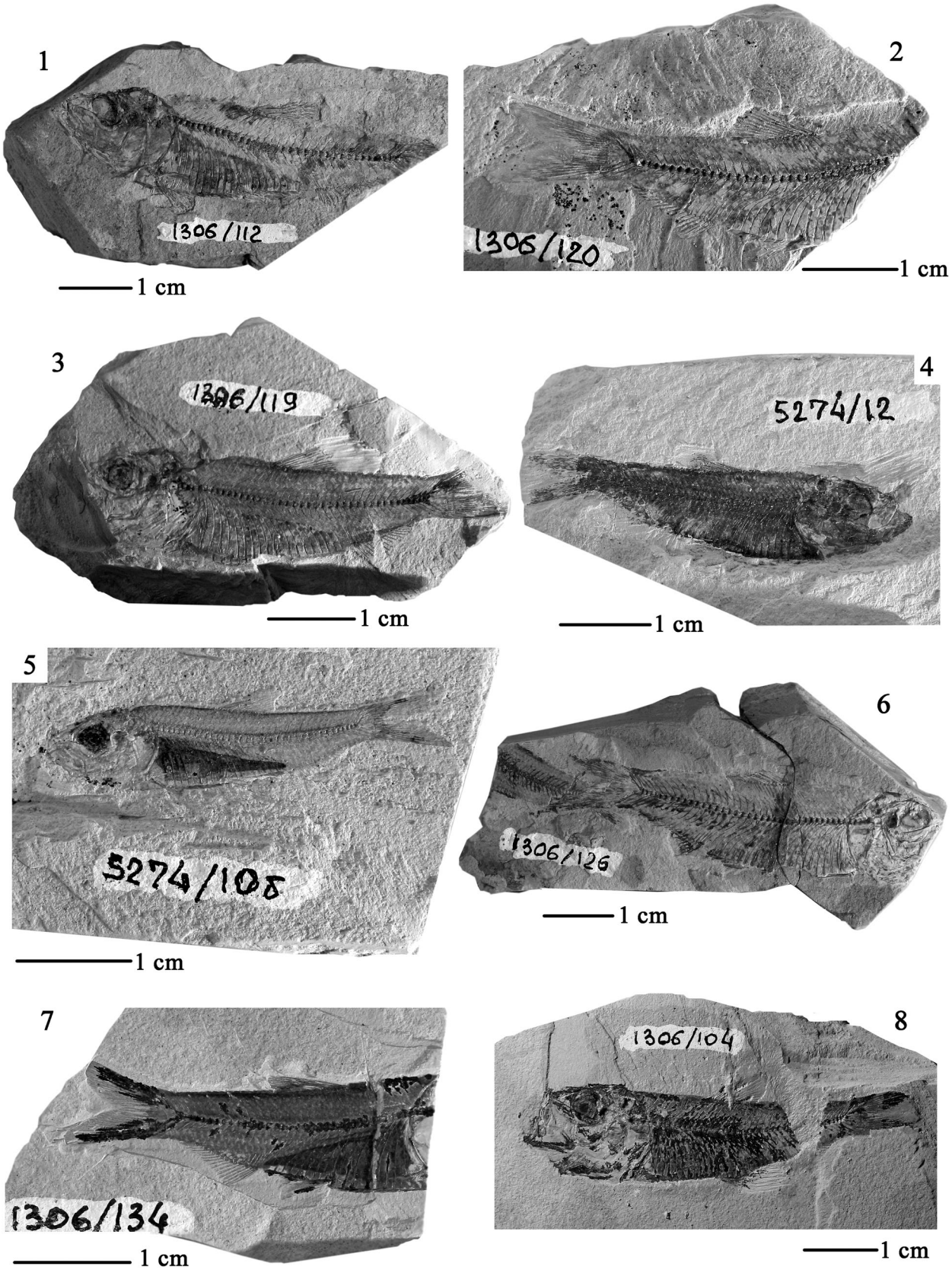


Fig. 2 Shape of selected bones of the visceral skull: **a** typical alosin—Recent *Alosa pontica* (Eichwald) (after Vasil'eva 1996, with modifications), **b** *Moldavichthys switshenskae* gen. et sp. nov. Designations of bones: *aa* anguloarticular, *d* dentary, *mx* maxilla, *smx* posterior supramaxilla, *iop* interopercle, *op* opercle, *pop* preopercle, *sop* subopercle

Otolith (Fig. 4, 1): Three specimens studied showed otoliths in situ, and in one case (PIN 5274/10), it is well enough exposed on plate and counter-plate to warrant a detailed description.

Otolith length (OL) 0.75 mm (right otolith) and 0.73 mm (left otolith). The otolith is compressed, compact (OL:OH = 1.35–1.40). Its dorsal rim is nearly straight and horizontal, slightly ascending toward rear, somewhat shorter than the otolith length (80 % OL), with the predorsal angle marking the tip of the antirostrum and the postdorsal angle at the junction with the posterior rim. The ventral rim is more deeply curved than the dorsal rim, but in a very irregular manner. The anterior part of the ventral rim is not reduced below the rostrum. The rostrum is moderately short (20 % OL), with a blunt, vertically cut tip. The excisura is wide, only slightly incised, and forms an angle of 100°–110°. The antirostrum is high, slightly projecting. The posterior tip is broad, blunt, characterized by a regularly curved rim, with its strongest projection dorsally, above the level of the sulcus.

The inner face is slightly convex with a wide, deep, long sulcus (OL:SuL = 1.15). The ostium is poorly separated from the cauda and only slightly longer (Osl:CaL = 1.20–1.30), not or only slightly widened, and with a shallow ventral margin and a feeble furrow below. The cauda shows less distinct margins and shows a tapering tip. The dorsal depression is narrow and shallow. The outer face is not visible, since the otolith is embedded in the rock.


1
1306/112
1 cm
2
1306/120
1 cm
3
1306/119
1 cm
4
5274/12
1 cm
5
5274/108
1 cm
6
1306/126
1 cm
7
1306/134
1 cm
8
1306/104
1 cm

◀**Fig. 3** *Moldavichthys switshenskae* gen. et sp. nov. **1** PIN 1306/112, skeleton without caudal fin, holotype; **2** PIN 1306/120, skeleton imprint without skull; **3** PIN 1306/119, skeleton with damaged skull; **4** PIN 5274/12, skeleton; **5** PIN 5274/10b, skeleton imprint; **6** PIN 1306/126, skeleton with damaged skull; **7** PIN 1306/134, skeleton without skull; **8** PIN 1306/104, skeleton with preparation damage. Moldova, right bank of the Dnestr river, Naslavcea village, Karpov Yar; Middle Miocene, Serravallian, Early Sarmatian (Volhynian)

Comparison Many meristic parameters of *Moldavichthys switshenskae* are coincident with specimens of *Clupea humilis* v.Meyer, 1851 (*Clupeonella humilis* after Menner 1949) from the Ottnangian of the Western Paratethys. *Moldavichthys switshenskae* differs in the longer articular process of the maxilla (about 50 % of the length of the bone vs. 20–30 %), the smaller number of vertebrae (39–40 vs. 42–44), the more anterior position of the dorsal fin (fin base inserted above the 15th vertebra vs. the 17th in *C. humilis*) and the smaller number of postventral scutes (8 vs. 10).

Otoliths in situ have been described from *C. humilis* from the Ottnangian of the type-locality Unter-Kirchberg in Bavaria by Weiler (1955) and isolated otoliths from the area were extensively studied by Reichenbacher (1988), who also described a related otolith-based species (*Clupeonella cornuta* Reichenbacher 1988) from the same strata. These otoliths differ significantly from *M. switshenskae* in a much more elongate shape (OL:OH = 1.7–2.1 vs. 1.35–1.40), a longer rostrum and the tendency of the posterior part of the ventral rim being reduced and the anterior, rostral part being massive, just opposite to the development observed in *M. switshenskae*.

The Chokrakian fishes described by Menner (1949) as *Clupeonella humilis* from Western Ciscaucasia were not available for investigation.

Otolith comparison The compressed shape with the blunt rostrum and the convex ventral rim characterizes *Moldavichthys switshenskae* otoliths and distinguishes them from Recent *Alosa* otoliths, with the caveat, however, that only a single, poorly preserved recent otolith is known from an endemic Ponto-Caspian species, i.e., *A. pontica* (Eichwald, 1838), which is also very elongate and shows a long rostrum (not figured). In addition, small otolith specimens of recent *Alosa* species may at times be similarly compressed as *Moldavichthys* otoliths, as, for instance, is shown by a small otolith of *A. aestivalis* (Mitchill, 1814) (Fig. 4, 4) when compared to a "normal" sized *Alosa fallax* (Lacepède, 1803) (Fig. 4, 5). Both differ though from *Moldavichthys* in the straight ventral rim and the inferior tip of the ostium. (For figures of further recent *Alosa* otoliths, see Campana 2004 and Lombarte et al. 2006). Similarly compressed and compact otoliths are found in the endemic Caspian clupein *Clupeonella cultriventris* (Nordmann, 1840) (Fig. 4, 6), which, however, shows more rounded dorsal and ventral rims and, most importantly, a deep incision at the ventral rim just before the commencement of the rostrum below the rear part of the ostium, which is not matched anywhere in alosin otoliths. Except for *Clupeonella humilis* (v.Meyer, 1850), which we consider subject to review in its generic position, the earliest fossil otoliths of the genus are *Clupeonella pliocenica* (Klein, 1960) from the Apsheronian (Early Pleistocene) of Azerbaijan.

There are no isolated fossil otoliths known, which would relate to *M. switshenskae*. The recently described *Alosa paulicrenata* Bratishko, Schwarzhans & Reichenbacher, 2015 from the Konkian of Kazakhstan differs in being considerably more elongate (OL.OH = 1.9–2.0 vs. 1.35–1.4) and showing a longer and inferiorly pointed rostrum (35–42 % SL vs. 20 % SL), both traits that clearly relate to extant *Alosa* otoliths. A review of Sarmatian otoliths from Bulgaria from the collection of the late Strashimirov from UMG has revealed the presence of another otolith-based species originally described as *Clupea gomotartziensis* Strashimirov, 1985 (Fig. 4, 3) that resembles *M. switshenskae* in the compressed shape and the short rostrum, but differs in the rostrum being pointed and narrowed below the ostium. We tentatively allocate the species with *Moldavichthys* and consider Ot. (Osmeridarum) *minimus* Djafarova, 2006 and Ot. (Osmeridarum) *wilhelmi* Djafarova, 2006 as likely synonyms.

Occurrence Middle Miocene, Serravallian, Early Sarmatian (Volhynian), Moldova.

Conclusions and outlook

Our study shows that a detailed review of articulated fossil clupeid skeletons from the Paratethys may result in a more diversified faunal assemblage than hitherto recognized. It also shows that the presence and analysis of otoliths in situ can contribute significantly to a better understanding of the systematic position of the studied fossil fish specimens. We realize that a continued and substantial effort will have to be invested to achieve a comprehensive review of the

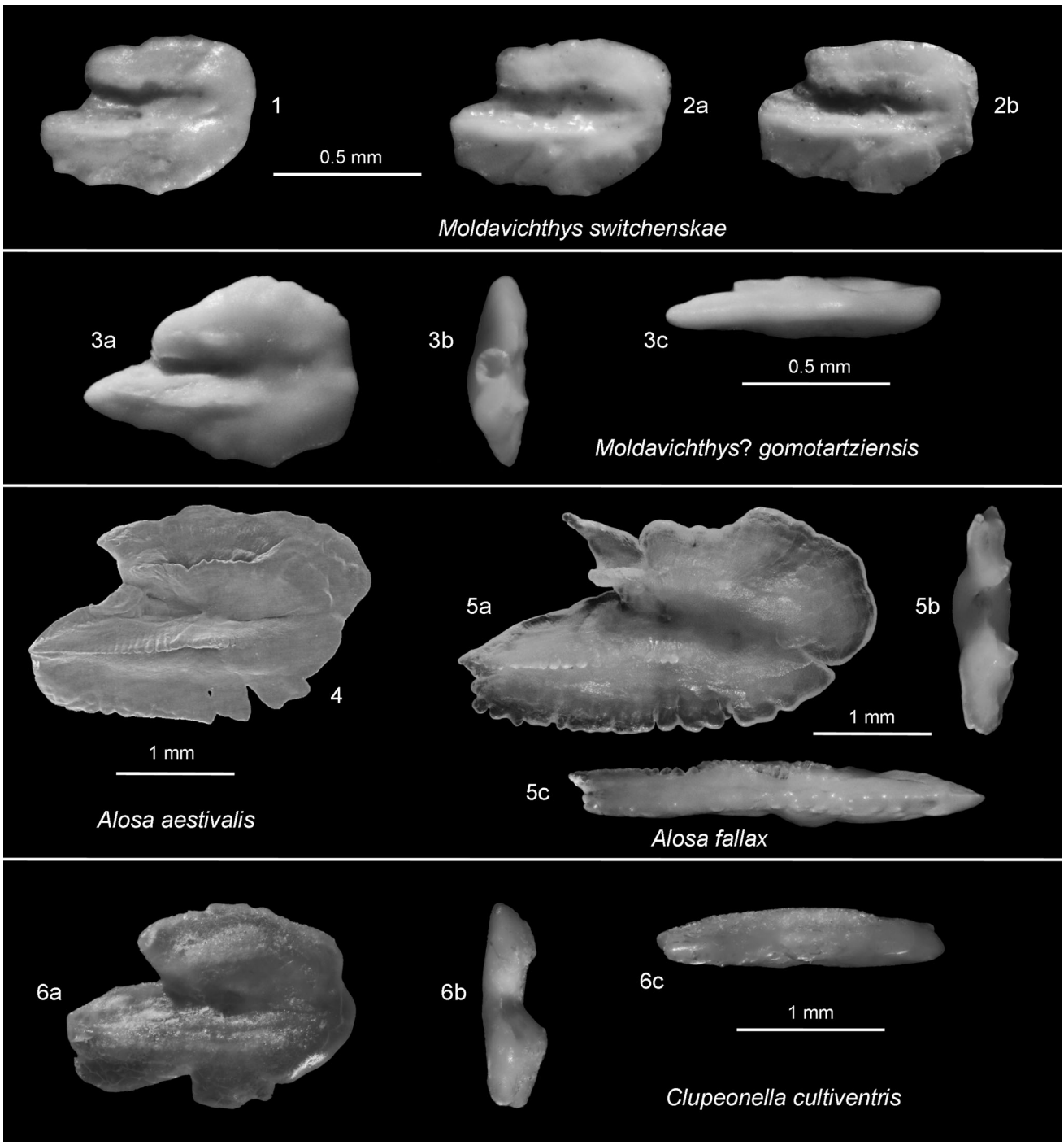


Fig. 4 Otoliths found in situ in *Moldavichthys switshenskae*. gen. et sp. and comparative specimens. **1–2** *Moldavichthys switshenskae* gen. et sp. nov., **1** PIN 5274-10b, water wet specimen; **2** counter-plate PIN 5274-10a, mirror imaged; **2a** water wet specimen; **2b** dry specimen. **3** *Moldavichthys*? *gomotartziensis* (Strashimirov 1985), otolith found isolated, UMG-X 8585, Bulgaria, well Simeonovo B-7, Sarmatian s.l., late Chersonian; **3a** inner face; **3b** anterior view; **3c** ventral view. **4** *Alosa aestivalis* (Mitchill 1814), Recent otolith, SEM photograph refigured from Campana (2004) and Lombarte et al. (2006). **5** *Alosa fallax* (Lacepède 1803), Recent otolith from commercial catch, coll. Schwarzhans; **5a** inner face; **5b** anterior view; **5c** ventral view. **6** *Clupeonella cultiventris* (Nordmann 1840), Recent otolith, BMNH 99.10.24.3-6, Kazakhstan, Caspian Sea off Mangyshlak Peninsula; **6a** inner face; **6b** anterior view; **6c** ventral view

Oligo-Miocene clupeids of the Paratethys, and we believe that in the course of such investigations, there will be ample more opportunities to find and analyze otoliths in situ in such fishes.

Acknowledgments We sincerely thank A. F. Bannikov and E. K. Sytchevskaya (Moscow, PIN RAS) for making available the specimens of *Moldavichthys switshenskae*. Comparative recent otoliths have been made available through the support of O. Crimmen and the late P. Whitehead (London, BMNH), T. Hecht (Grahamstown) and J. Nielsen (Copenhagen, ZMUC); fossil comparative otoliths were thankfully provided by A. Bratishko (Luhansk), D. Sinnyovska (Sofia, UMG) and A. Lord (Frankfurt, SMF). We thank A. Bratishko and R. Brzobohatý for their constructive reviews.

References

Bratishko, A., Schwarzhans, W., Reichenbacher, B., Vernihorova, Y., & Ćorić, S. (2015). Fish otoliths from the Konkian (Miocene, early Serravallian) of Mangyshalk (Kazakhstan)- testimony of an early endemic evolution in the Eastern Paratethys. *Paläontologische Zeitschift, 89*, 839–889.

Campana, S. E. (2004). *Photographic atlas of fish otoliths of the northwest Atlantic Ocean* (p. 284). Ottawa: NRC Research Press.

Daniltshenko, P. G. (1960). *Kostistye Ryby Maykopskih otlozenij Kavkaza.* Moscow: USSR Academy of Science, 78, p. 208 **(in Russian)**.

Daniltshenko, P. G. (1980). *The order Clupeiformes*. In *Iskopaemye kostistye ryby SSSR* (*Fossil Bone Fishes of the USSR*) (pp. 7–26). Moscow: Nauka **(in Russian)**.

Djafarova, J. D. (2006). *Otolity neogena Azerbaidjana* (*Neogene otoliths of Azerbaijan*) (p. 167). Baku: Nafta-Press **(in Russian)**.

Grande, L. (1985). Recent and fossil clupeomorph fishes with materials for revision of the subgroups of clupeoids. *Bulletin of the American Museum of Natural History, 181*, 231–372.

Ionko, V. I. (1954). O nakhodke iskopayemykh ryb v nizhnesarmatskikh otlozheniyakh MSSR. *Trudy Odesskogo Universiteta. Sbornik Geologo-Geograficheskogo Fakulteta, 2*, 109–119. **(in Russian)**.

Klein, L. N. (1960). Resultaty issledovaniya otolitov ryb iz pliocenovyh i postpliocenovyh otlozheniy Prikurinskoi nizmennosti Azerbaidjana. (Results of fish otoliths research in Pliocene and Postpliocene deposits of the Prikurin lowland). *Trudy AzNII po dobytche nefti, 10*, 101–121. **(in Russian)**.

Lombarte, A., Chic, O., Parisi-Baradad, V., Olivella, R., Piera, J., & Garcia-Ladona, E. (2006). A web-based environment for shape analysis of fish otoliths. The AFORO database. *Scientia Marina, 70*, 147–152.

Menner, V. V. (1949). *Class Pisces*. In *Atlas rukovodyashchikh form iskopaemykh faun SSSR* (*Atlas of Index Forms of Fossil Faunas of the USSR*) (Vol. 13, pp. 346–360). Neogen (Neogene). Moscow: Gosgeolitizdat **(in Russian)**.

Reichenbacher, B. (1988). Die Fischfauna der Kirchberger Schichten (Unter-Miozän) an der Typuslokalität Illerkirchberg bei Ulm. *Stuttgarter Beiträge zur Naturkunde B, 139*, 1–53.

Strashimirov, B. (1985). Otolity ot gornia sarmat na Severozapadna Bulgaria. *Annual of the Highest Institute of Mining and Geology Sofia, 31*, 21–36. **(in Russian)**.

Svetovidov, A. N. (1952). *Sel'devye* (*Clupeidae*). *Fauna SSSR. Ryby* (*Clupeids: Fauna of the USSR: Fishes*). Moscow: Akademia Nauk SSSR **(in Russian)**.

Vasil'eva, E. D. (1996). On divergence of shads of genus Alosa from the Azov Sea: cranyological findings. *Journal of Ichthyology, 36*(2), 139–145. **(in Russian)**.

Weiler, W. (1955). Untersuchungen an der Fischfauna von Unter- und Oberlirchberg bei Ulm vornehmlich an Hand von Otolithen in situ. *Paläontologische Zeitschrift, 29*, 88–102.

Whitehead, P. J. P., Nelson, G. J., & Wongratana, T. (1985). Clupeoid fishes of the world (Suborder Clupeoidei). Part 1—Chirocentridae, Clupeidae and Pristigasteridae. *FAO Fisheries Synopsis, FAO Species. Catalogue, 7*(1), 1–304.