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Description of *Karaganops* n. gen. *perratus* (Daniltshenko 1970) with otoliths in situ, an endemic Karaganian (Middle Miocene) herring (Clupeidae) in the Eastern Paratethys

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Abstract *Karaganops* is established as a new fossil genus of the family Clupeidae, subfamily Clupeinae, to encompass the nominal species *Sardinella perrata* Daniltshenko 1970 from the Karaganian of southern Russia. *Karaganops* belongs to the group of genera characterized by the presence of two elongated rays at the end of the anal fin, which further includes *Sardinella, Clupeonella, Sardina, Sardinops*, and *Harengula*. It differs from *Sardinella* amongst others in the absence of tooth plates on the palatines and pterygoids, the presence of seven branchiostegal rays (vs. six), the presence of two epurals (vs. three) and the presence of nine pelvic fin rays (vs. 7–8). Otoliths found in situ further support the separation of *Karaganops* from *Sardinella* and related genera and add evidence for a second, otolith-based species—*Karaganops komochtitziensis* (Strashimirov 1985)—from the Middle Sarmatian of Bulgaria. *Karaganops* is thought to represent an endemic clupeid genus of the Eastern Paratethys that evolved during the mid-Miocene Karaganian ecological crisis in the basin. An otolith found in situ in a skeleton of *Sarmatella doljeana* (Kramberger 1883) from the Early Sarmatian of Belgrade, Serbia and an otolith interpreted to be associated with another fossil clupeid genus and species—*Sarmatella tsurevica* (Baykina 2012)—from the Early Sarmatian of the Caucasus facilitates correlation with previously described otolith-based species. It demonstrates that *Sarmatella* may not represent a primary endemic of the Paratethys and that its fossil record reaches back in time to Early Miocene and possibly Late Oligocene in the North Sea Basin.

Keywords Ichthyology · Teleost · Clupeidae · Paleontology · Russia · Bulgaria · North Sea Basin

Introduction

The Karaganian stage of the Eastern Paratethys corresponds to the Early Serravallian of the Mediterranean region and the Middle Badenian of the Central Paratethys (Popov et al. 2009). It represents a pivotal event in the geological history of the Eastern Paratethys with specific physical and hydrological developments in the basin. Desalination spread across the basin during the Middle Chokrakian from the northern periphery of the Tethys and encompassing the entire basin during the Karaganian. Reduced water circulation led to establishment of a hydro-sulphidic zone in the deeper parts of the sea and pushed the fish fauna into the upper, brackish layers of the pelagic zone (Mikerina and Pinchuk 2014). As a result, the ichthyofauna became much impoverished. Fishes of the families Gadidae, Scombridae, Sphyraenidae and bathyal Phosichthyidae disappeared. The following fishes have been identified from the semi-marine Karaganian deposits: silversides—*Atherina prima* Switchenska 1959, mullets—*Mugil karaganicus* Switchenska 1973, lefteye flounders—*Arnoglossus ovalis* Switchenska 1981, as well as the endemic euryhaline herring *Karaganops perratus* (Daniltshenko 1970) n. gen.

Articulated skeletons of this clupeid species were described from the Middle Miocene deposits of the Tambov region by P. G. Daniltshenko as *Sardinella perrata*. In

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addition to Tambov, further specimens were described from locations in the Caucasus. In the original description of *S. perrata*, Daniltshenko clearly separated these two forms. He noted differences in the number of vertebrae and the number of fin rays as distinctive features, but without further specifications. Later in the article the author pointed out that "… Karaganian representatives of *Sardinella* in the Caucasus form a separate species, the description of which… will be devoted to a special work" (Daniltshenko and Iosifova 1970, p. 165). However, such paper has never been published.

We compared material from both locations (the Tambov material from literature, since Daniltshenko's original collection could not be located) and found that there are no obvious differences between specimens from both regions other than small differences in the body measurements and the number of vertebrae. Given the high degree of variability of these characters in clupeid fishes, we conclude that distinction of two separate species does not appear to be warranted with the data currently available.

Materials and methods

The material described herein was collected in 2011 during an expedition headed by Dr. A. F. Bannikov (Borisyak Paleontological Institute RAS). The locality is situated on the right bank of the Pshekha river near the southern limit of the Tsurevsky village, western North Caucasus. At this location, the river bank is very low, and the outcropping Karaganian rocks are composed of moderately thick grey calcareous clays with intercalations of light-grey marl and argillaceous limestone (Beluzhenko 2002) of the Middle Tsurevsky Formation. The fish fauna is dominated by articulated skeletons of *Karagnops perratus* associated with some specimens of mugilids.

Due to the physical and hydrological conditions that prevailed in the Karaganian basin, skeletal remains are relatively poorly preserved while fish otoliths are nearly perfectly preserved and are often found in situ.

The fossils collected in 2011 comprise 11 complete and fragmentary skeletons of *Karaganops perratus* (Daniltshenko 1970) (collection PIN 5509). Otoliths in situ were found in 3 specimens. Special attention was paid to the morphology of large bones of the visceral skull, particularly the jaw and opercular bones, as well as the morphological structure of the otoliths.

Courtesy to A. F. Bannikov and G. Carnevale, we were also able to study a well preserved isolated otolith found associated with skeletal remains of *Sarmatella tsurevica* (Baykina 2012) collected from a nearby location higher up in the stratigraphic section in sediments of Early Sarmatian (Volhynian) age. Since *S. tsurevica* is very abundant in the respective middle Tsurevsky Formation and represents the dominant clupeid fish recorded [the only other clupeid being a rare large species of the genus *Sardina* recently described by Baykina (2015)] we associate the otolith with this species and include its description herewith. Courtesy to L. Rundić and K. Bradić we were also able to study a further species of *Sarmatella* with otoliths in situ (*S. doljeana*) from the Early Sarmatian of excavations made in the 60s during the renovation of the 'Red Star' Belgrade football stadium.

The material referring to *Karaganops* and *Sarmatella tsurevica* is stored in Borisyak Paleontological Institute (PIN) of the Russian Academy of Sciences; the specimen studied of *Sarmatella doljeana* is part of the collection of the late J. Andjelković housed at the Faculty of Mining and Geology of the University of Belgrade, Serbia (RGF).

Comparative otoliths were used from the Middle Miocene of the North Sea Basin [*Sarmatella pulchra* (Smigielska 1966) from Schwarzhans (2010)] and the Sarmatian of Bulgaria [*Karaganops komochtitziensis* (Strashimirov 1985)] from the Museum of Geology and Paleontology of the University of Mining and Geology "St. Ivan Rilski" at Sofia, Bulgaria (UMG).

The fish measurements used in the present study in general 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; (lP) length of pectoral fin rays; (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 palaeontology

Order Clupeiformes Bleeker 1859.
Suborder Clupeoidei Bleeker 1859.
Family Clupeidae Cuvier 1817.

Subfamily Clupeinae Cuvier 1817.

Genus *Karaganops* gen. nov.
1970 *Sardinella* Valenciennes 1847—sensu Daniltshenko and Iosifova, p. 164.

Etymology: referring to the Karaganian regional stage of the Eastern Paratethys; gender masculine.

Type species: *Sardinella perrata* Daniltshenko 1970; Middle Miocene, Karaganian regional stage; Russia, Tambov region.

Diagnosis: skull narrow; two auditory capsules present, bulla prootica 2–2.5 times larger than bulla pterotica; frontals with longitudinal ridges on their caudal parts; maxilla narrow, saber-shaped bone, with slightly convex, serrated ventral margin, reaching vertical axis extending through orbital center; hypomaxilla absent; lower jaw long, high, and toothless; mandibular joint located posterior to the vertical extending through orbital center; subopercle with moderately developed process; preopercle high, its vertical ramus higher and wider than the horizontal; opercle smooth, with sloped posteroventral angle and distinct incision at posterior margin; branchiostegal membrane with seven rays; posterodorsal end of last ray transformed into short blade; body low, spindle-shaped; vertebral column consisting of 44–46 vertebrae; dorsal fin with 18 rays, subtriangular, originating anterior to midlength of body; pelvic fins with nine rays, located on vertical axis extending through the front of dorsal fin or 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 elongated; caudal skeleton with two epurals; ventral scutes very robust.

Two species: *K. perratus* (Daniltshenko 1970) from the Karaganian regional stage of the Eastern Paratethys and *K. komochtitziensis* (Strashimirov 1985), an otolith-based species from the Middle Sarmatian (Bessarabian) of Bulgaria.

Comparison: *Karaganops* differs from all extant genera of the subfamily Clupeinae, except for *Sardinella, Clupeonella, Sardina, Sardinops*, and *Harengula*, in the presence of two elongated rays at the end of the anal fin. In addition, it differs from *Clupea* in the relatively shorter maxilla, the presence of seven branchiostegal rays (versus eight) and well developed ventral scutes. It differs from *Sardinella* in the narrower frontals, more posterior position of the mandibular joint, absence of tooth plates on the palatines and pterygoids, the weaker development of the subopercular process, the presence of seven branchiostegal rays (*Sardinella* has six), the presence of two epurals (*Sardinella* has three) and the presence of nine rays in the pelvic fins (instead of 7–8). The absence of sculpture on the opercle distinguishes *Karaganops* from *Sardina* and *Sardinops*, and the absence of a hypomaxilla distinguishes it from *Harengula* (Whitehead et al. 1985). It differs from *Clupeonella* in the presence of two auditory capsules (*Clupeonella* lacks bulla pterotica), a more posterior position of the mandibular joint, the longer dorsal fin (18 rays vs. 14–15) and the presence of nine rays in the pelvic fins (instead of 8).

It differs from the extinct genus *Sarmatella* in a longer and serrated maxillary bone, the presence of longitudinal ridges on the frontals, a more posterior position of the mandibular joint, a more anterior position of the pelvic fins, a longer postanal length and also in the robust ventral scutes.

The otolith found in situ in *Karaganops perratus* differ from otoliths of Recent species of *Sardinella* and *Sardinops* in the lack of a deep excisura and antirostrum, a shorter rostrum and in being generally more compressed. Otoliths of *Clupeonella* in turn are even more compressed compared to those of *Karaganops* and have an even shorter rostrum. Otoliths of *Harengula* and *Sardina* are similar in proportion to those of *Karaganops*, but again with a deeply incised excisura. Those of *Harengula* differ additionally in the relatively short rostrum, which is less than twice as long as the antirostrum.

Karaganops perratus (Daniltshenko 1970)

Figures 1, 2, 3, 5.1

1970 *Sardinella perrata* Daniltshenko 1970—Daniltshenko and Iosifova, p. 164, Fig. 3.

1980 *Sardinella perrata* Daniltshenko 1970—Daniltshenko, p. 11.

Holotype: PIN, no. 2181-22, complete skeleton imprint; Russia, Tambov Region, close to the village of Sosnovka; Middle Miocene, Karaganian regional stage, Upper Lamka Formation.

Material: Eleven complete skeletons and fragments of moderate preservation; collection PIN 5509, no. 1, 2, 4, 5, 7, 9, 11–15; Karaganian, locality on Pshekha River near the southern limit of the Tsurevsky village.

Description (Figs. 1, 2, 3): Small fishes, with an elongated body, up to 90–100 mm of standard length (SL). The dorsal outline is almost straight, the abdomen is moderately convex. The body depth at the anterior margin of the dorsal fin base is 19–25 % of SL. The minimum body depth is 35–42 % of the maximum body depth, i.e. 8–10 % of SL. The head is large, 25–29 % of SL, and its height at the occiput is 19–23 % of SL.

The roof of the skull is straight along the dorsal profile. The snout is pointed. The skull is narrow. The bulla prootica is 2–2.5 times as large as the bulla pterotica. The parasphenoid is almost straight in the anterior part; within the orbit, it curves slightly ventrally and projects in its

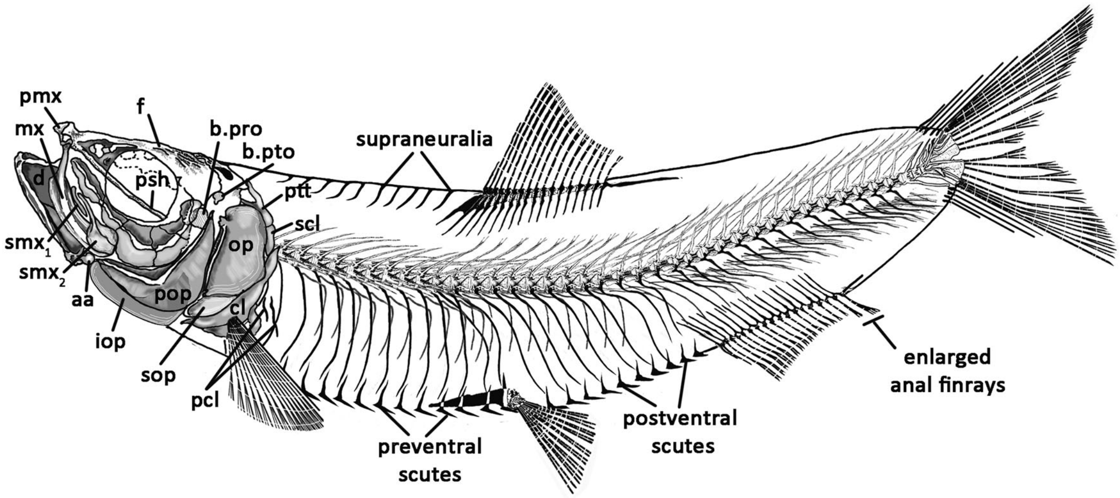

Fig. 1 Generalized reconstruction of skeleton of *Karaganops perratus* (Daniltshenko 1970) from several specimens in the collection PIN 5509 (Krasnodar region; Karaganian stage). Designations of bones (after Grande 1985): (*aa*) anguloarticular, (*b.pro*) prootic bulla, (*b.pto*) pterotic bulla, (*cl*) cleithrum, (*d*) dentary, (*f*) frontal, (*iop*) interopercle, (*mx*) maxilla, (*op*) opercle, (*pcl*) postcleithra, (*pop*) praeopercle, (*pmx*) praemaxilla, (*psh*) parasphenoid, (*ptt*) posttemporal, (*scl*) supracleithrum, (*sop*) subopercle, (*smx*) supramaxilla, (*sph*) sphenotic

lower third. The frontals are sculptured with few, very distinct longitudinal ridges on its posterior part.

The mouth is terminal. The premaxilla is short, narrow and subtriangular. The maxilla is narrow and saber-shaped (Fig. 2mx). Its ventral margin is moderately convex and serrated for almost the entire length of the bone; the posterior end is pointed upwards and reaches to the middle of the orbit or slightly posterior of it. The articular process is long, thin, positioned at an angle of about 140° to the bone axis. The supramaxillae are well developed. The anterior supramaxilla is large, long, moderately wide and wedge-shaped. The dorsal and ventral margins of the posterior supramaxilla are convex, its ventral arch being wide and smooth (Fig. 2smx).

A hypomaxilla is absent. The outline of the mandible is regular trapezoidal, with a rounded dorsal margin. The mandible projects slightly beyond the upper jaw and is articulated with the skull just behind the middle of the orbital level. The anguloarticular is subtriangular, short, with a moderately developed articular process (Fig. 2aa). The anterior margin is concave in the upper part and convex in the lower. The dentary is deep and toothless (Fig. 2d). The symphyseal region is moderately long and low; the anteroventral angle is rounded. The anterodorsal dentary margin has a long subrectangular recess. Its posterior margin is mostly concave. The axial rays at the margin of the anterior dentary are positioned at an angle of 40°. The dorsal margin of the quadrate is not incised.

The preopercle is moderately large and deep (Fig. 2-pop). Its horizontal ramus is shorter than the vertical ramus and significantly narrower. The rami of the preopercles are positioned at an angle of about 100°. The opercle is moderately high, wide and smooth (Fig. 2op). The posterior margin has a deep incision and the lower half of the bone is wider than the upper half. The postero-ventral angle of the opercle is sloped and pointed. The subopercle is long, narrow, wedge-shaped or rhomboidal, with a moderately developed process (Fig. 2sop). The interopercle is long, curved, with a high and wide posterior end. The anterior tip is narrow, with a low ledge directed anteriorly (Fig. 2iop); and it bears a longitudinal ridge.

The branchiostegal membrane has seven rays. The last ray is saber-shaped, with an almost straight ventral margin and the dorsal margin curved (Fig. 2r.br). The posterodorsal corner of the last ray is turned into a narrow, short, curved and pointed blade.

The vertebral column extends slightly above the longitudinal trunk axis. It consists of 44–46 vertebrae, including 25–26 abdominal vertebrae, the anterior-most 4 or 5 of which are covered by the opercle. The abdominal vertebrae are less elongate than the caudal vertebrae. The neural spines of the abdominal vertebrae are long (as long as four or five vertebrae), narrow, curved and positioned at an angle of approximately 60° to the vertebral centrum; they are not fused until the beginning of the caudal region. The longest neural spines are observed just posterior to the dorsal fin. The caudal region consists of 18 or 19 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 23–24 rib

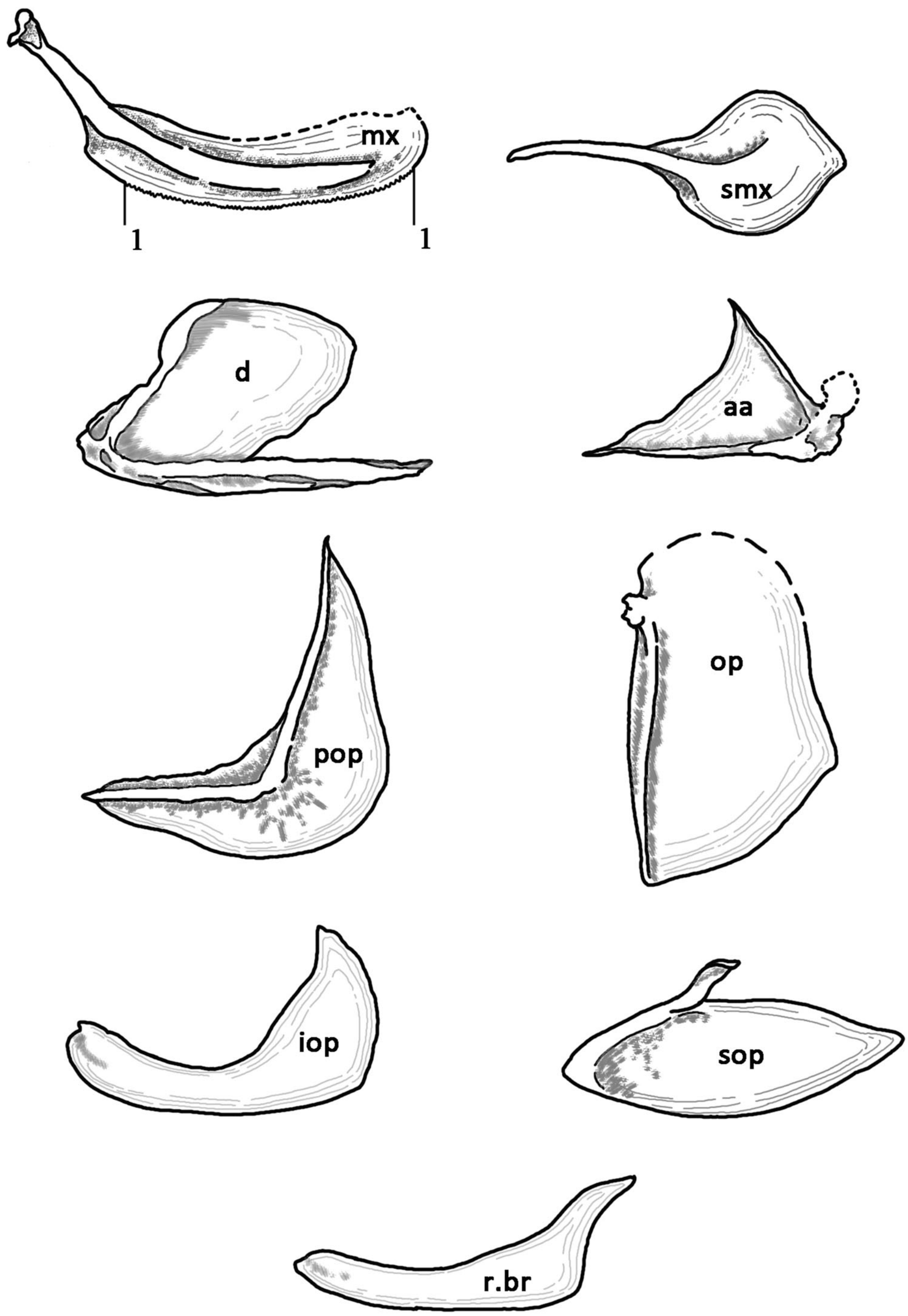

Fig. 2 Shape of selected bones of the visceral skull of *Karaganops perratus* (Daniltshenko 1970); *dotted lines* designate reconstructed bone parts; 1–1—serration along ventral margin of maxillary. Designations of bones: (*aa*) anguloarticular, (*d*) dentary, (*mx*) maxilla, (*smx*) posterior supramaxilla, (*iop*) interopercle, (*op*) opercle, (*pop*) preopercle, *(r.br)* posterior branchiostegal ray, (*sop*) subopercle

pairs, which are very thin, long, and reach the abdominal outline.

The dorsal fin is high, its height being equal to the length of approximately 5 vertebrae, with the third and the fourth rays being the longest; and it originates above the 17th or 18th abdominal vertebra. The dorsal fin base is 11–15 % of SL. The dorsal fin contains 17–18 rays supported by 18–19 pterygiophores (the first pterygiophore is free). About 10 supraneurals are present.

The anal fin is displaced strongly caudally. The origin of the anal fin is positioned opposite to the third caudal vertebra and it terminates under the 10th or 11th caudal vertebra. The anal fin base is 14–16 % of SL. The anal fin consists of 17–19 rays supported by 17–18 pterygiophores. The two posteriormost rays are elongated and attached to a single pterygiophore.

The pectoral fins are long (17 % of SL). They are pointed and attached at a low position just slightly above

Table

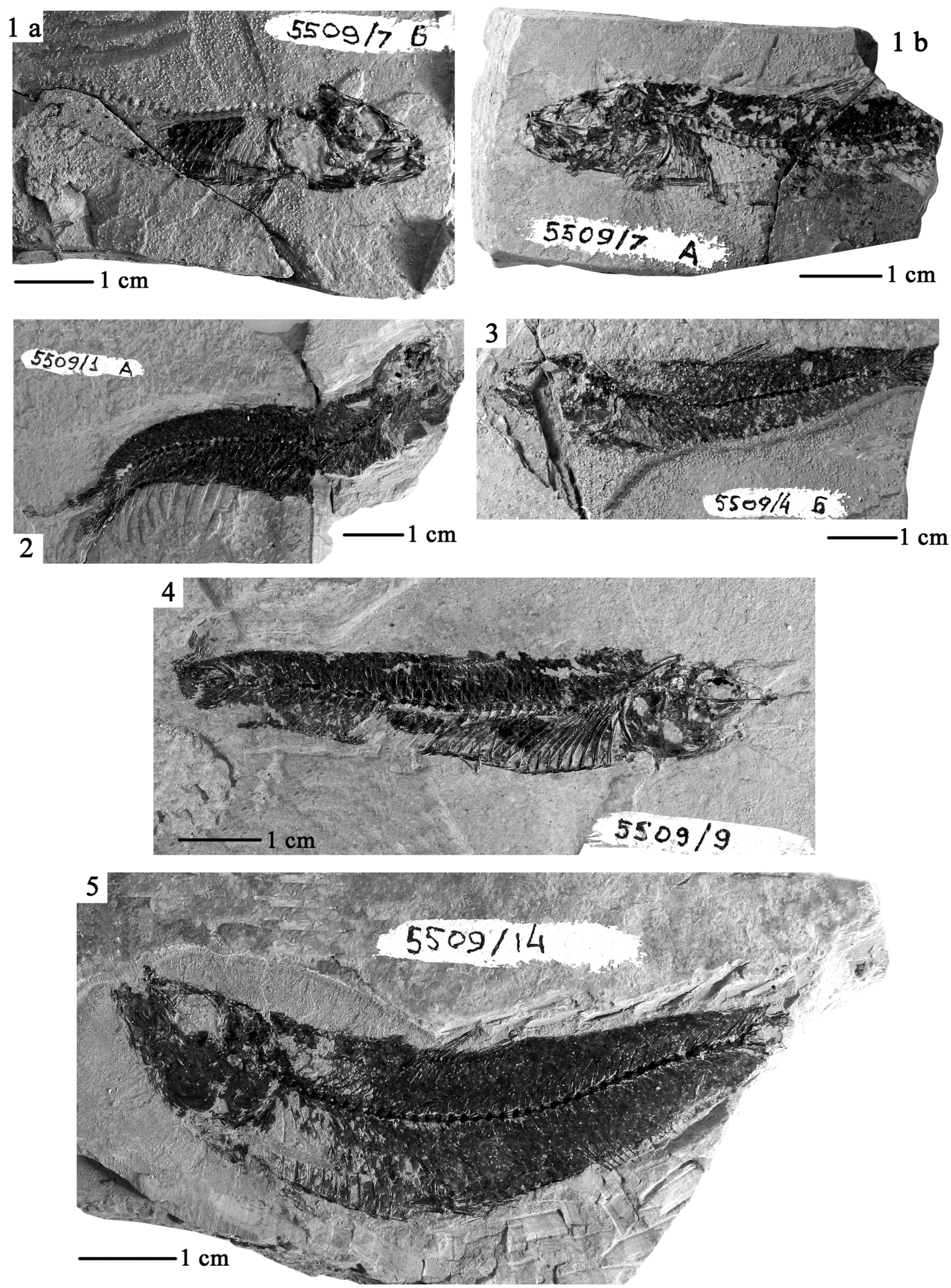

Fig. 3 *Karaganops perratus* (Daniltshenko 1970). **1a**, **b** PIN 5509/7, skeleton without caudal fin, plate and counter-plate; **2** PIN 5509/1, skeleton; **3** PIN 5509/4, skeleton with mechanical damage marks from preparation; **4** PIN 5509/9, skeleton; **5** PIN 5509/14, skeleton without caudal fin. Krasnodar Region, right bank of the Pshekha river, at southern limit of the Tsurevsky village; Karaganian, Tsurevsky Formation

the abdominal outline. The fin contains 15 rays, with the second and third being the longest.

The pelvic fins are short, approximately as long as three to four vertebrae. They originate under the 20ies vertebra, under to the anterior margin or the anterior third of the dorsal fin. The pelvic fins contain eight or nine rays.

The caudal fin is notched very deeply. The middle rays of the caudal fin are about 8 % as long as SL. The outermost rays are approximately 2–2.5 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 35–40 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 13–15 scutes in front of the pelvic fins and 10 behind.

Measurements from 11 specimens of *K. perratus:* SL ranges from 57 to 80 mm, but there are fragments of apparently larger specimens. Morphometric data in % of SL: Ap—25–29, tu—19–23, H—19–25, h—8–10, aD—47–52, D_1C—37–45, aV—48–52, aA—70–73, A_1C—12–16, lD—11–15, lA—14–16, lP—17, PV—20–26, VA—19–24, lC—8–9; в % от Ap: Ar—18–26, rs—25–32, sp—36–50, lmx—35, lmd—49–61.

Otolith (Fig. 5.1): three of the eleven specimens studied show otoliths in situ, and in one case (PIN 5509-7) it is well enough exposed on plate and counter-plate to warrant detailed description.

Otolith length (OL) 1.65 mm (right otolith) and 1.75 mm (left otolith). The otolith is moderately elongate (OL:OH = 1.65–1.75). Its dorsal rim is nearly straight and horizontal, slightly ascending towards rear, considerably shorter than the otolith length (65 % of 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 in the rear half of the otolith. The anterior part of the ventral rim is shallow below the rostrum, nearly straight, with an indention below the rear part of the ostium towards the posterior part of the ventral rim. The ventral rim is coarsely and irregularly undulating. The rostrum is moderately long (25–27 % of OL), with a blunt tip. The excisura is wide, not incised, and forms an angle of 100°–120°. The antirostrum is high, not projecting. The posterior rim is regularly curved, with its strongest projection at its middle.

The inner face is slightly convex with a wide, deep, long sulcus (OL:SuL = 1.20–1.25). The ostium is distinctly longer than the cauda (Osl:CaL = 1.65–1.75), not widened, and with a shallow ventral rim underpinned by a distinct furrow ventrally below the ostium. The cauda shows less distinct margins and is slightly widened dorsally. The dorsal depression is narrow. The outer face is not visible since the otolith is embedded in the rock.

Comparison There are some slight differences in quantitative features between specimens from the Caucasus and Tambov of *K. perratus*. The specimens from the Caucasus differ in a greater number of vertebrae (44–46 vs. 40–42), a greater number of dorsal fin rays (17–18 vs. 15–16), as well as a smaller number of anal fin rays (17–19 vs. 21–22). For the time being, we have refrained in this article to formally distinguish the Caucasian and Tambov specimens of *Karaganops* as two separate species, because the type material has been unavailable for study and the original images of *K. perratus* do not allow a reliable evaluation.

Occurrence Middle Miocene, Karaganian regional stage, Lamka Formation of the Tambov Region and Tsurevsky Formation, Northern Caucasus.

Isolated otoliths

No isolated otoliths are known that would correlate with the otoliths in situ found in *K. perratus* on the species level, which is due to the poor overall knowledge of Karaganian otoliths. However, Strashimirov (1985) described a number of clupeid otoliths from the Middle Sarmatian (Bessarabian) of Bulgaria and we interpret one of these species as representing a species of *Karaganops*—*Karaganops komochtitziensis* (Strashimirov 1985). It was originally described as *Clupea komochtitziensis*, and we consider *Gobius latirostratus sarmaticus* Strashimirov 1985 to represent a junior synonym. The type specimens of Strashimirov were not retrieved and are probably lost, but other material collected by him and kindly made available for review by his son Strashimir Strashimirov (Sofia) and Ms Dimka Sinnyovska (Museum of Geology and Paleontology of the University of Mining and Geology "St. Ivan Rilski", Sofia) contained a specimen that can be attributed to *K. komochtitziensis* (Fig. 5.2) as described by Strashimirov (1985). It is very similar to *K. perratus* in outline and proportions differing only in the even more obtuse angled excisura, the prominent dorsally positioned posterior tip of the otolith and the slightly longer rostrum (33 % of OL vs 25–27 %). In the light of *Karaganops perratus* skeleton finds being restricted to the Karaganian we regard *Karaganops komochtitziensis* as a separate species, subject, however, to review should more otolith specimens become available of both species.

Genus *Sarmatella* Menner, 1949

Sarmatella doljeana **(Kramberger 1883).**
Figures 4, 5.3

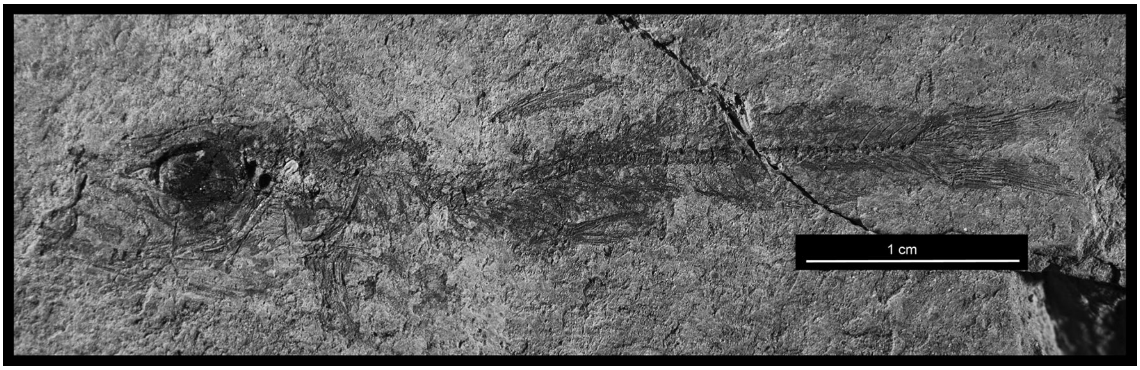

Fig. 4 *Sarmatella doljeana* (Kramberger 1883). RGF AJ 23; Belgrade, excavations made during the renovation of the 'Red Star' football stadium; lower Sarmatian s.s

1883 *Clupea* (*Meletta*) *doljeana* Kramberger 1883—Pl. 14, Fig. 4.

??1985 *Clupea viola* Strashimirov 1985—Pl. 1, Figs. 1, 2, 3, 4.
2013 *Sarmatella doljeana* (Kramberger 1883)—Baykina, p. 525.

Material: RGF AJ 23. A right otolith found in situ in a nearly complete fish skeleton from the 'Red Star' football stadium, Belgrade, Early Sarmatian. The specimen with the otolith in situ is shown in Fig. 4 for documentary purposes.

Otolith description (Fig. 5.3): Otolith length (OL) 0.85 mm. The otolith is thin and moderately elongate (OL:OH = 1.6). Its dorsal rim is moderately high, nearly flat and horizontal, with marked though rounded pre- and postdorsal angles at its edges; it is considerably shorter than the otolith length (70 % of OL). The ventral rim is similarly deeply curved as the dorsal rim, particularly its rear portion, but without prominent angles. The anterior part of the ventral rim is slightly shallower at the rostrum, with a strong indention below the rear part of the ostium, followed by a moderate shift downwards of the ventral rim. The rostrum is moderately long (27 % of OL), and distinctly tapering to the pointed tip. The excisura is very wide, slightly incised at an angle of about 100°. The antirostrum is high, angular, not projecting. The posterior rim is blunt, nearly vertically cut.

The inner face is very slightly convex, nearly flat, with a moderately wide, deep and long sulcus (OL:SuL = 1.2). The ostium is longer than the cauda (Osl:CaL = 1.5), somewhat widened and with a shallow ventral rim. The cauda shows less distinct margins are not widened and with a tapering posterior tip. The dorsal depression is narrow. The ventral field shows an indistinct depression below the central part of the sulcus. The outer face is flat, somewhat depressed at the rostrum, resulting in a very thin rostrum (which in fact did break during the excavation).

Discussion: Strashimirov (1985) described the otolith-based species *Clupea viola* from the Sarmatian s.l. (probably Middle to Late Sarmatian s.l.) of Bulgaria. Unfortunately, it was not possible to retrieve the relevant type material. Judging from his photographs it appears that *Clupea viola* could represent a junior synonym of *S. doljeana*.

***Sarmatella tsurevica* (Baykina 2012)**
Figure 5.4

1968 *Otolithus* (*Clupeidarum*) *longirostris* Suzin 1968 (in Zhizhchenko)—Pl. 18, Fig. 5 [name not available: ICZN article13.1.1].

2012 *Illusionella tsurevica* Baykina 2012—p. 305.
2013 *Sarmatella tsurevica* (Baykina 2012)—Baykina, p. 524.

Material: PIN no. 5073/200. A single isolated clupeid otolith was found on a slab containing disintegrated clupeid bones from Early Sarmatian (Volhynian) rocks of the middle Tsurevsky Formation near Tsurevsky in the northern Caucasus. The same location has provided many well preserved articulated skeletons with *Sarmatella tsurevica* as the dominant clupeid species (Baykina 2012) and another very rare clupeid—*Sardina tarletskovi* Baykina 2015. We, therefore, conclude that the isolated clupeid otolith retrieved from this formation and described here in all likelihood represents *S. tsurevica*.

Otolith description (Fig. 5.4): Otolith length (OL) 1.0 mm. The otolith is elongate (OL:OH = 1.8). Its dorsal rim is shallow, gently and regularly curved, considerably shorter than the otolith length (70 % of OL) and without prominent angles. The ventral rim is more deeply curved than the dorsal rim at its rear half of otolith. The anterior part of the ventral rim is shallow below the rostrum and less strongly curved, with a strong indention below the rear part of the ostium, and it is here where the ventral rim is considerably

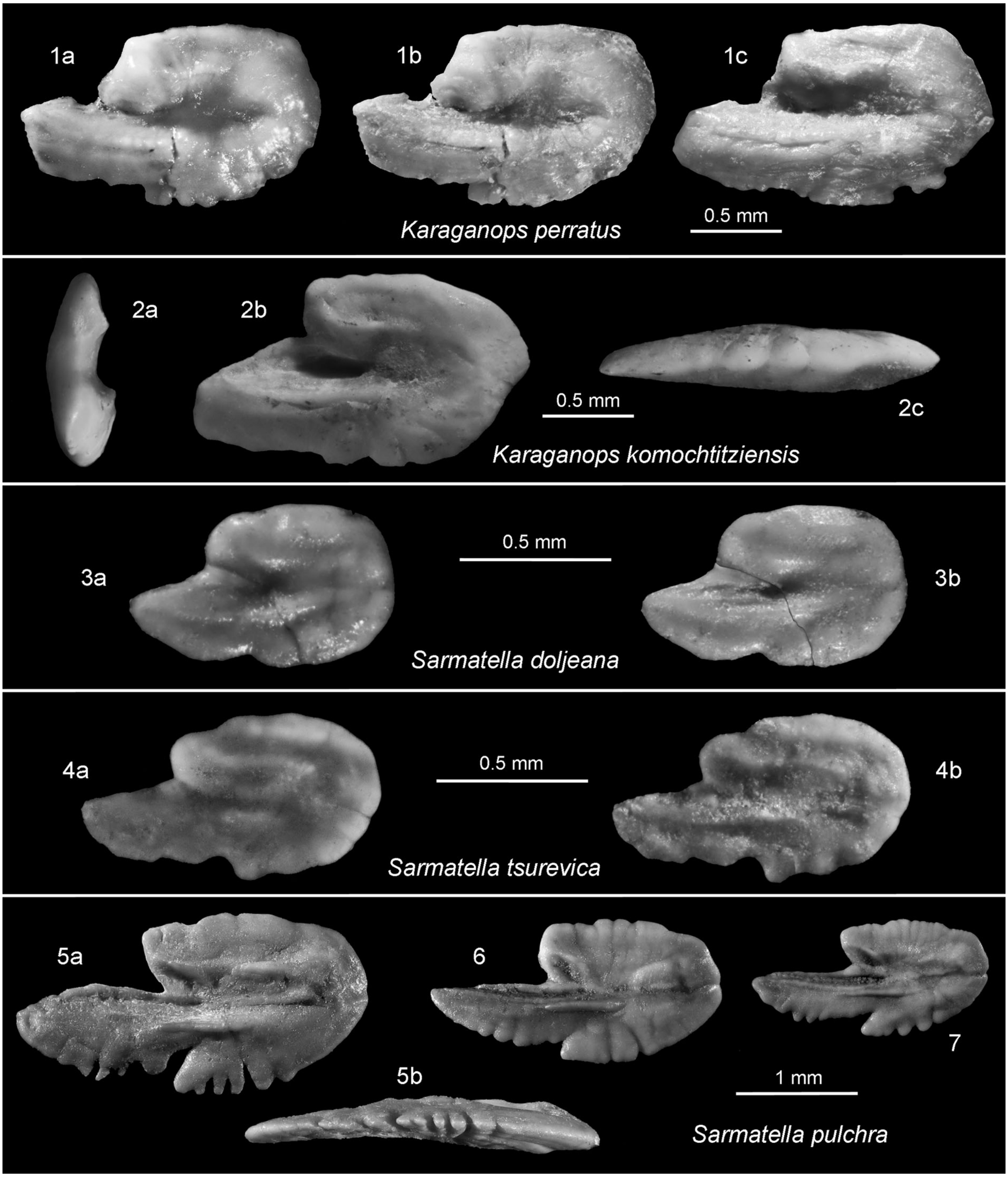

Fig. 5 *Karaganops perratus* (Daniltshenko 1970). Otoliths found in situ. **1a**, **b** PIN 5509-7 A; 1a water wet specimen; 1b dry specimen. **1c** PIN 5509-7 B, counter plate of PIN 5509-7 A, otolith figured mirror imaged, dry photograph. *Karaganops komchtitziensis* (Strashimirov 1985). Otolith found isolated; UMG-X 8583, Bulgaria, well Smirnenski B-4, Sarmatian s.l., Bessarabian, Krivodol Fm. **2a** View from anterior. **2b** Inner face. **2c** Ventral view. *Sarmatella doljeana* (Kramberger 1883). Otolith found in situ in specimen RGF AJ 23 (specimen broken into two halves during preparation). **3a** Water wet specimen; **3b** dry specimen. *Sarmatella tsurevica* (Baykina 2012). Otolith found isolated, but associated with skeletal remains of *S. tsurevica*; PIN no. 5073/200, Russia, Krasnodar district, Sarmatian, Volhynian, Tsurevsky 1 fish layer. **4a** water wet specimen; **4b** dry specimen (specimen broken into two halves during preparation). *Sarmatella pulchra* (Smigielska 1966). Otoliths found isolated; refigured from Schwarzhans (2010). **5**, **6** SMF PO 64613-14, Germany, Dingden, Reinbekian. **7**: SMF PO 64616, Germany, Hoerstgen shaft 32 m, upper Hemmoorian. **5b** ventral view

shifted downwards. The ventral rim is irregularly undulating. The rostrum is long (32 % of OL), slender, and with a pointed tip. The excisura is wide, slightly incised at about an angle of 90°. The antirostrum is moderately high and slightly projecting. The posterior rim is regularly curved, with the strongest projection at its middle.

The inner face is very slightly convex, nearly flat, with a rather narrow, deep, and long sulcus (OL:SuL = 1.25). The ostium is distinctly longer than the cauda (Osl:-CaL = 1.8), not widened, and with a shallow ventral rim. The cauda shows less distinct margins, is not widened, and with a rounded posterior tip. The dorsal depression is narrow. The ventral field shows an indistinct depression below the central part of the sulcus. The outer face is flat, with few radial furrows.

Discussion: The otolith of *S. tsurevica* is readily distinguished from the otolith found in situ in *S. doljeana* by the slightly more elongate shape (OL:OH = 1.8 vs 1.6), the rounded posterior rim, the shallow and rounded dorsal rim (vs angular) and the more reduced ventral rim below the rostrum. Both share, however, the distinct notch at the mid-ventral rim followed by a more strongly curved rear part of the ventral rim, the nearly flat inner face and a broad excisura combined with a rostrum that is moderately long when compared with otolith of other clupeid genera.

Suzin (1968, in Zhizhchenko) figured an otolith as *Otolithus* (*Clupeidarum*) *longirostris* from the Early Sarmatian of the Crimea and/or southern Russia, which according to his detailed drawing certainly represents the same species. However, Suzin never adequately described the species and, therefore, the name must be considered not available following article 13.1.1 of the ICZN.

Isolated otoliths

Otoliths of the otolith-based species *Clupea pulchra* Smigielska 1966 (placed in *Sardinops* by Schwarzhans 2010) from the Early and Middle Miocene of the Central Paratethys and the North Sea Basin (Fig. 5.5–5.7) closely resemble otoliths of *Sarmatella tsurevica*. Outline and proportions are strikingly similar as well as the presence of the distinct notch that sets off the sharp rostrum posteriorly from the rear half of the more deeply curving ventral rim, which we regard as of prime diagnostic value for the otoliths of this genus.

Clupea pulchra was originally described by Smigielska along with a second, much less common fossil otolith-based clupeid—*Clupea weileri* Smigielska 1966—from the early and late Badenian (then called lower and upper Tortonian) of Poland. These finds coincide with several skeleton-based clupeid records from the Badenian and Sarmatian of the Central Paratethys, of which *Sarmatella sardinites* (Heckel 1850) (see Baykina 2012, 2013) is amongst the most common. In fact, *Sarmatella sardinites* has also been recorded from early Miocene and Oligocene rocks in the Central Paratethys, but Schultz (2013, as *Sardinella sardinites*) commented that those earlier records require review and verification. Finds of otoliths of *Sarmatella pulchra* from the Hemmoorian and Reinbekian (late Burdigalian and Langhian) of the North Sea Basin (Schwarzhans, 2010, as *Sardinops pulcher*), however, indicate that the genus may be earlier in origin than the late Badenian to Sarmatian skeleton finds suggest and may have been more widely distributed geographically.

Schwarzhans (2010) discussed the generic relationship in comparison with Recent otoliths of *Sardinops* and *Spratelloides* figured in Rivaton and Bourret (1999), but also mentioned significant differences in proportions and outline. Nolf (2013) listed the species as a clupeid of unknown relationship in open generic nomenclature. Now, the otolith find of *Sarmatella doljeana* and even more the one attributed to *Sarmatella tsurevica* demonstrate that the specific form of the rostrum and its ventral margin and notch represent diagnostic valuable characters for generic definition. We, therefore, re-allocate the species with the genus *Sarmatella* as *Sarmatella pulchra*. *Sarmatella pulchra* differs from otoliths of *S. tsurevica* in the slightly more elongate shape (OL:OH = 2.0–2.1 vs 1.8), the considerably incised excisura and the more finely serrated ventral rim. A similar, probably related otolith-based species had been described from the Late Oligocene of the North Sea Basin as *Sardinops sagittalis* Schwarzhans 1994. This species most likely represents either another, earlier species of the genus *Sarmatella* or of a related fossil genus. We refrain here from a formal re-assignment of this species owing to ongoing research by one of us (Baykina) of clupeid skeletons from the Oligocene of the Paratethys.

Conclusions and outlook

Karaganops perratus is a new example of the forced rapid endemic evolution of the fish fauna in the Eastern Paratethys during the times of accelerated environmental fluctuations of the Middle Miocene, which were caused by the sequestration of the basin from the world oceans. Osteological finds of the genus *Karaganops* are restricted to the Karaganian of the Eastern Paratethys and the genus is therefore considered to represent an adaptation to the very specific environment that developed in the basin during this time interval. Detailed and conclusive relationships of *Karaganops* cannot be assessed at present including any relationships to the endemic living clupeids of the Caspian Sea of the genus *Clupeonella*.

The finding of otoliths in situ in *Karaganops perratus* and *Sarmatella doljeana* and another otolith find attributed to *Sarmatella tsurevica* add new evidence useful for the reconstruction of clupeid evolution in the Paratethys. The otoliths of all three species enhance the definition of the respective genera. The allocation of otolith-based species to either of the genera demonstrates the additional systematic and phylogenetic value that can be created by aligning skeletal and otolith-based taxonomies. In the case of *Karaganops* it shows the possible continuation of the lineage from Karaganian to Middle Sarmatian times in the Paratethys. Small basins with similar environments to the Karaganian sea may have persisted on Bulgarian terrain into Sarmatian times (Koleva-Rekalova 2001) and could have acted as locations for a continued thriving of fishes adapted to this specific environment such as *Karaganops*. In the case of *Sarmatella* it supports an origin of the genus earlier than late Badenian to Sarmatian and shows a wider geographical distribution than documented by skeleton finds, i.e. in the North Sea Basin, indicating that the genus was not a primary endemic of the Paratethys.

We believe that new excavations in the rich Miocene and Pliocene deposits of the Eastern Paratethys can contribute so much more to the understanding of the development of the unique endemic fish fauna of the Eastern Paratethys and the modern Caspian Sea. The fossilization potential of otoliths in situ appears to be particularly good in these rocks and, therefore, we expect more integrated skeletal and otolith studies in the future.

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References

Baykina, E. M. (2012). A new clupeid genus (Pisces, Clupeiformes, Clupeidae) from the Sarmatian of the Eastern Paratethys, Krasnodar region. *Paleontological Journal, 46*(3), 302–312.

Baykina, E. M. (2013). A revision of *Clupea doljeana* Kramberger and *Sarmatella vukotinovici* (Kramberger) (Pisces, Clupeidae) from the Sarmatian of Croatia. *Paleontological Journal, 47*(5), 523–532.

Baykina, E. M. (2015). A new species of the genus *Sardina* (Pisces, Clupeidae) from the Middle Miocene of the Eastern Paratethys. *Paleontological Journal, 49*(4), 402–406.

Beluzhenko, E. V. (2002). Stratigraphy of the Middle-Upper Miocene and Pliocene beds of the Psekups-Belaya Interfluve (Northwestern Caucasus): part 1. Middle Miocene. *Byull. Mosk. O–va Ispyt. PrirOtd. Geol., 77*, 47–59. **(in Russian)**.

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

Daniltshenko, P. G., & Iosifova, J. I. (1970). Findings of Miocene marine fishes from Tambov Region. *Dokl. Akad. Nauk USSR., 190*, 162–165. **(in Russian)**.

Grande, L. (1985). Recent and fossil clupeomorph fishes with materials for revision of the subgroups of clupeoids. *Bull. Amer. Mus. Natur. Hist., 181*, 231–372.

Koken, E. (1891). Neue Untersuchungen an tertiären Fischotolithen II. *Z. dtsch. Geol. Ges., 43*, 77–170.

Koleva-Rekalova, E. (2001). Attempt for correlation of the Miocene (Sarmatian) aragonite sediments from North Bulgaria. *Comptes rendus de l'Académie bulgare des Sciences, 54*, 67–72.

Kramberger, D. (1883). Die jungtertiäre Fischfauna Croatiens. *Beiträge zur Paläontologie Österreich-Ungarns und des Orients, 3*, 65–85.

Mikerina, T. B., & Pinchuk, T. N. (2014). Distribution and source of dispersed organic matter in the Karaganian–Konkian–Sarmatian deposits of the Eastern Paratethys. *Geology, Geography and global Energy, 4*(55), 20–33.

Nolf, D. (2013). The diversity of fish otoliths, past and present. Royal Belgian Institute of Natural Sciences.

Popov, S. V., Akhmetiev, M. A., Lopatin, A. V., Bugrova, E. M., Sytchevskaya, E. K., & Sherba, I. G. (2009). Paleogeography and biogeography of Paratethys basins. Part 1. Late Eocene—Early Miocene. *Trans. Paleontol. Inst., 292*, 1–178.

Rivaton, J. and Bourret, P. (1999). Otoliths of the Indo-Pacific fishes. Documents Sci. & Tech., Centre IRD de Nouméa.

Schultz, O. (2013). Band 3; Pisces. In (W.E. Piller, ed.): Catalogus Fossilium Austriae; Ein systematisches Verzeichnis aller auf österreichischem Gebiet festgestellten Fossilien. Verlag der österreichischen Akademie der Wissenschaften.

Schwarzhans, W. (1978). Otolith-morphology and its usage for higher systematical units, with special reference to the Myctophiformes s.l. *Meded. Wekgr. Tert. Kwart. Geol., 15*, 167–185.

Schwarzhans, W. (1994). Die Fisch-Otolithen aus dem Oberoligozän der Niederrheinischen Bucht. *Geologisches Jahrbuch, Reihe A, 140*, 1–248.

Schwarzhans, W. (2010). The otoliths from the Miocene of the North Sea Basin. Backhuys Publishers, Leiden, and Margraf Publishers, Weikersheim.

Smigielska, T. (1966). Otolity Ryb z Tortonu Południowej Polski. *Ann. Soc. geol. Pologne, 36*(3), 205–275. **(in Polish)**.

Strashimirov, B. (1985). Otolity ot gornia sarmat na Severozapadna Bulgaria. *Ann. Highest Inst. Min. Geol., 31*, 21–36. **(in Bulgarian)**.

Suzin, A. V. (1968). Otoliths. In B. P. Zhizhchenko (Ed.), *Micropaleontologicheskie metody stratigraficheskih postroeniy v neftegazonosnyh oblastiah (Micropalaeontological methods of stratigraphical research in the oil-and-gas bearing region)* (pp. 74–77). Moscow: Nedra. **(in Russian)**.

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

Weiler, W. (1942). Die Otolithen des rheinischen und nordwestdeutschen Tertiärs. Abh. Reichsamt Bodenfotsch. *NF, 206*, 1–140.

Whitehead, P. J. P., Nelson, G. J., & Wongratana, T. (1985). Clupeoid fishes of the world (suborder Clupeoidei): part 1. Chirocentridae. *Clupeidae and Pristigasteridae. FAO Fish. Synop., 7*, 305–579.