

Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part V: Bothidae and Soleidae

Werner Schwarzhans¹ · Giorgio Carnevale² · Sanja Japundžić³ · Katarina Bradić-Milinoić⁴

Received: 18 December 2016 / Accepted: 3 February 2017 / Published online: 3 March 2017
© Akademie der Naturwissenschaften Schweiz (SCNAT) 2017

Abstract In the final section of our series of studies on Sarmatian fishes from the Paratethys with otoliths in situ, we deal with three pleuronectiform species. Each species is re-defined based on the type material plus additional specimens not previously described. Their generic allocation has been reviewed. Two of these species belong to the Bothidae: *Arnoglossus bassanianus* (Kramberger 1883) and *Bothus parvulus* (Kramberger 1883). The third species was originally described as *Rhombus serbicus* Anđelković 1966 and is now placed within the Soleidae. It is placed herein with the newly established fossil genus *Parasolea*, which is thought to be related to the extant *Solea* and *Vanstraelenia* and is considered to represent an extinct endemic Paratethyan taxon. Two of the three species described herein can be linked to isolated otoliths. The otolith-based species—*Arnoglossus? tenuis* (Schubert 1906)—is synonymized with a skeleton-based species—*Arnoglossus bassanianus* (Kramberger 1883). Isolated otoliths and comparison with related extant species indicate that the species described here must have reached sizes of at least twice those of the largest articulated skeletons.

Keywords Bothidae · Soleidae · *Arnoglossus* · *Bothus* · *Parasolea* · Croatia · Serbia

Introduction

Here, we present a study of three species of pleuronectiforms representing the last of a series of studies dealing with otoliths in situ from Sarmatian fishes of the Paratethys. The articulated skeletal remains described herein are remarkably well preserved and complete but in many cases of very small size and possibly representing juveniles or subadult individuals belonging to the families Bothidae and Soleidae. Skeletal remains of pleuronectiforms are not uncommon in Dolje near Zagreb, Croatia and somewhat less common in the locality studied in Belgrade, Serbia. Isolated otoliths regularly occur in the Middle Miocene deposits of the Paratethys (Bratishko et al. 2015). Pleuronectiform otoliths often exhibit some degree of side dimorphism and are characterized by a circumsulcal depression, which is considered to represent a synapomorphy of the group (Schwarzhans 1999). However, they are also known for showing only few and delicate diagnostic traits as well as a high degree of variability, thereby making species identification sometimes very difficult. The preservation of the otoliths in situ in the specimens of Dolje is varying, affected by the soft nature of aragonite in the diatomitic matrix. Nevertheless, through careful extraction and reconstruction it was possible in two of the three skeletal-based species to correlate otoliths in situ with isolated findings of otoliths.

Materials and methods

Seven complete or partially complete articulated skeletons from the collection of the Croatian Natural History Museum, Zagreb (CNHM) are described, of which five had

Editorial handling: Daniel Marty.

✉ Werner Schwarzhans
wswschwarz@aol.com

- ¹ Natural History Museum of Denmark, Zoological Museum, Universitetsparken 15, 2100 Copenhagen, Denmark
- ² Dipartimento di Scienze della Terra, Università degli Studi di Torino, via Valperga Caluso 35, 10125 Turin, Italy
- ³ Department of Geology and Paleontology, Croatian Natural History Museum, Demetrova 1, 10000 Zagreb, Croatia
- ⁴ Faculty of Mining and Geology, Department of Paleontology, University of Belgrade, Kamenička 6, 11000 Belgrade, Serbia

otoliths in situ, and a single additional incomplete articulated skeleton with an otolith in situ from the collection of the Chair of Historical Geology, Department of Regional Geology, Faculty of Mining and Geology, University of Belgrade (RGF), and indicated with the collection acronym AJ (referring to the collection of Jelena Anđelković). All the specimens with otoliths in situ housed at the CNHM are from the Sarmatian s. s. (Volhynian) deposits cropping out near Dolje, north of Zagreb. The single RGF specimen with an otolith in situ documented herein was collected from temporary excavations in 1961–62 during the renovation of the Rajko Mitić football stadium (formerly ‘Red Star’) in Belgrade. For a detailed description of the localities see Schwarzhans et al. (2016a).

The morphological terminology of otoliths was established by Koken (1891) modified by Weiler (1942) and Schwarzhans (1978). Abbreviations: general: vs = versus, HT = holotype, PT = paratype; skeletons: SL = standard length, TL = total length, HL = head length; A = anal-fin rays, B = branchiostegal rays, C = principal caudal-fin rays, D = dorsal-fin rays, P = pectoral-fin rays, V = pelvic-fin rays; AR = angulo-articular, CH = ceratohyal, CL = cleithrum, COR = coracoid, DENT = dentary, ECT = ectopterygoid, EP = epural, IOP = interopercle, MX = maxilla, OP = opercle, P = parasphenoid, PB = pelvic bone, PH = parahypural, PMX = premaxilla, PO = preopercle, Q = quadrate, SOP = subopercle, UH = urohyal; otoliths: OL = otolith length, OH = otolith height, OT = otolith thickness, SuL = sulcus length, OsL = ostium length, CaL = cauda length, OsH = ostium height, CaH = cauda height.

The term “otolith” refers to the saccular otolith (=sagitta). Lagenar otoliths are described as lapilli.

Systematic paleontology

Order Pleuronectiformes Bleeker 1859

Family Bothidae Regan 1910

Genus *Arnoglossus* Bleeker 1862

Arnoglossus bassanianus (Kramberger 1883)

(Figures 1a–c, 2a–g)

1883 *Rhombus bassanianus* Kramberger.—Kramberger: pl. 8, figs. 1–2

1906 *Solea tenuis* Schubert.—Schubert: pl. 20, fig. 9 (otolith-based species)

1954 *Rhombus corius miocenicus* Pobedina.—Pobedina: pl. 1, fig. 1 (otolith-based species)

1954 *Rhombus corius foliformis* Pobedina.—Pobedina: pl. 1, fig. 3 (otolith-based species)

?1969 *Rhombus bassanianus* Kramberger 1883.—Anđelković: pl. 13, figs. 1–2 (not verified)

?1970 *Rhombus bassanianus* Kramberger 1883.—Anđelković: pl. 25, fig. 2 (not verified)

?1989 *Rhombus bassanianus* Kramberger 1883.—Anđelković: pl. 20, fig. 3 (not verified)

2006 *Rhombus corius foliformis* Pobedina 1954.—Djafarova: pl. 24, fig. 2 (otoliths)

2015 *Arnoglossus? tenuis* (Schubert 1906).—Bratishko, Schwarzhans & Reichenbacher: figs. 12-1 - 12-3 (otoliths)

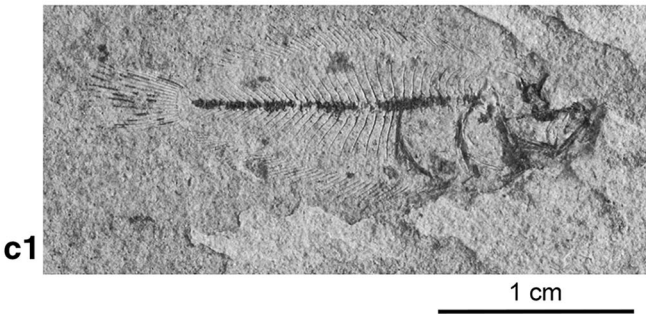
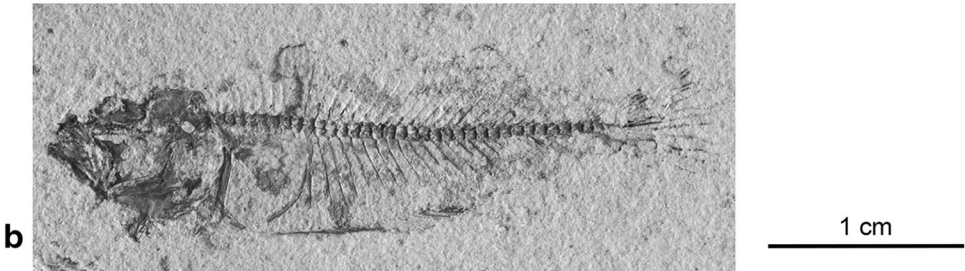
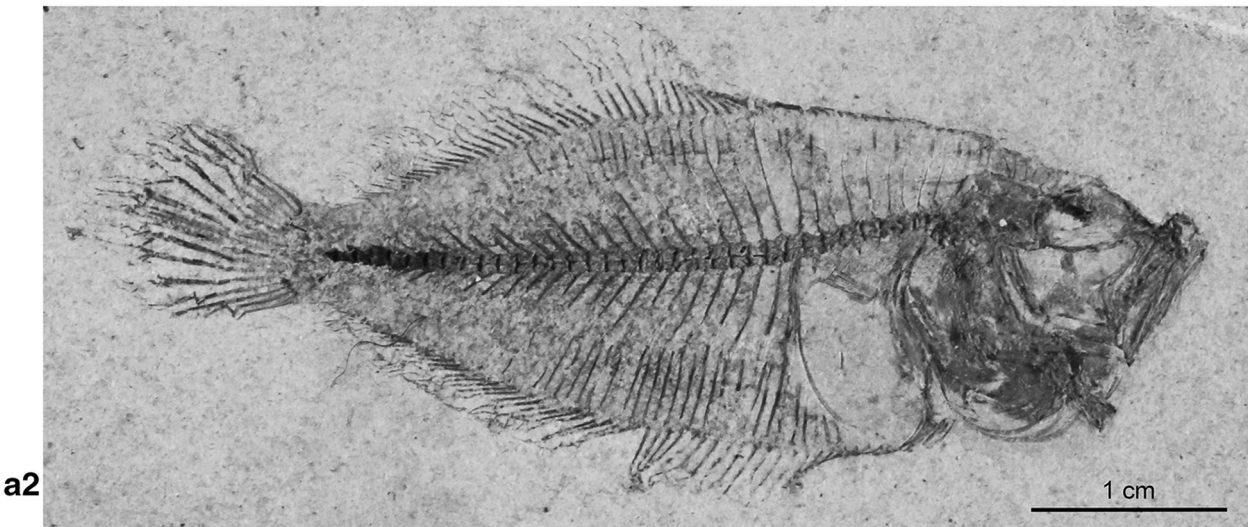
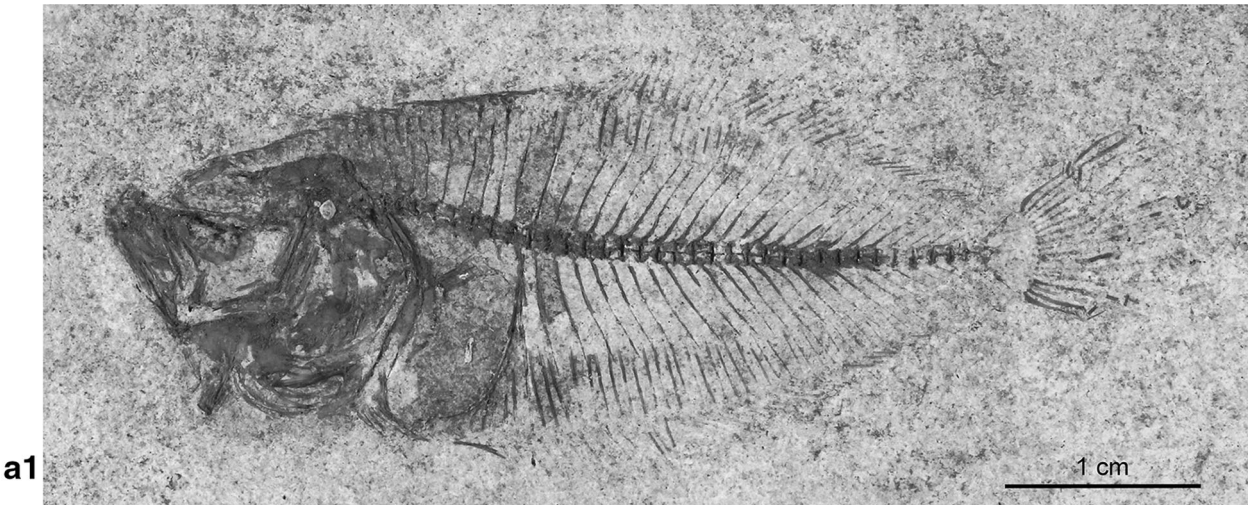
Material: Three complete or nearly complete articulated skeletons from Dolje, Croatia, Sarmatian s.s. (Volhynian), two of which in plate and counterplate; CNHM 154.1 + 2, holotype, 45 mm SL (Figs. 1a, 2a, b, d), CNHM 258.1 + 2, 21.5 mm SL (Fig. 1c), CNHM 274, 29.5 mm SL (Figs. 1b, 2c, e); two specimens (CMHN 154 and 274) contain otoliths in situ (Fig. 2d–e). Three isolated otoliths from the Konkian of Karaigaly, Mangishlak, Kazakhstan, described by Bratishko et al. (2015), from the National Museum of Natural History of the National Academy of Sciences of Ukraine, NMNH 2532/093, 095 and 096.

Description: The body is relatively slender, with a large head and a dorsally protruding snout. The length of the head is larger than its depth. The mouth is oblique. The gape of the mouth is large, measuring between 10.5 and 14.3% SL. The scales are not preserved. Counts and measurements are summarized in Table 1.

Neurocranium. The overall outline of the neurocranium is recognizable, although individual bones cannot be recognized because of inadequate preservation. The supraoccipital crest is flat and straight and shows no dorsal expansion below the anterior dorsal-fin pterygiophores (Figs. 2a, b). The dorsal margin of the neurocranium above and in front of the left eye is elevated above the supraoccipital crest, but similarly straight and inclined; the anterior dorsal-fin pterygiophores appear to be not supported by the dorsal margin of the neurocranium. The parasphenoid is long, slender and almost straight.

Jaws and suspensorium. Premaxilla, maxilla, ectopterygoid, dentary, angulo-articular and quadrate are discernible in the eyed-side plate of the holotype (CNHM 154.2; Fig. 2b). The premaxilla shows a long and slender ascending process and a broad articular process. There is evidence of very small and short, closely spaced conical teeth on the dentary of CNHM 274.

Urohyal and branchiostegal rays. The urohyal is well exposed in the holotype (CNHM 154.2; Fig. 2b) and in CNHM 274 (Fig. 2c) in a position slightly inclined downwards anteriorly (Amaoka 1969). It is fishhook-shaped as described in Amaoka (1969), with the two branches forming an angle of 45°–50°. The upper branch is slightly to distinctly longer than the lower branch; a bony



◀**Fig. 1** Articulated skeletal remains of *Arnoglossus bassanianus* (Kramberger 1883). **a** CNHM 154, holotype; **a1** CNHM 154.2; **a2** CNHM 154.1; **b** CNHM 274; **c** CNHM 258; **c1** CNHM 258.2; **c2** CNHM 258.1

lamina stretches across the full length of the upper branch above the inner ridge and it is slightly expanded at its midlength and slightly restricted in front of the large cardiac apophysis (see Amaoka 1969 for explanation); the sciatic part is truncated and tapering to the lower tip. The hyoid bar supports six or seven branchiostegal rays.

Opercular series. The opercle, subopercle, interopercle and preopercle are partially recognizable in the holotype (CNHM 154), but are incomplete and poorly preserved not allowing a detailed description (Fig. 2b).

Axial skeleton. The vertebral column contains 35 or 36 (9 + 26 or 27) vertebrae. The first vertebra is often hidden under some of the bones of the head skeleton; it is scarcely recognizable in CNHM 154.2 (Fig. 2b) and bears no neural spine. The vertebral centra are subrectangular, longer than high, except for those of the first six or seven vertebrae, which are higher than long. The neural spines of most of the abdominal vertebrae are long, almost entirely straight or only slightly bent; they are nearly vertically except for the anteriormost three, which are slightly inclined forwards. Parapophyses are visible on the posterior four to five abdominal vertebrae, increasing in length backward. The caudal vertebrae show long neural and haemal spines that are increasingly more inclined posteriorly in the series. The first haemal spine is fragmented in the holotype, but complete in the two other specimens and does not appear to be longer than the subsequent haemal spine. Myorhabdoi are visible along the anterior-dorsal trunk of the fish between the neural spines of the abdominal vertebrae (Fig. 2b).

Caudal skeleton. The caudal skeleton is scarcely preserved in all the examined specimens thereby preventing a detailed analysis of its skeletal structure. There are 17 principal caudal-fin rays.

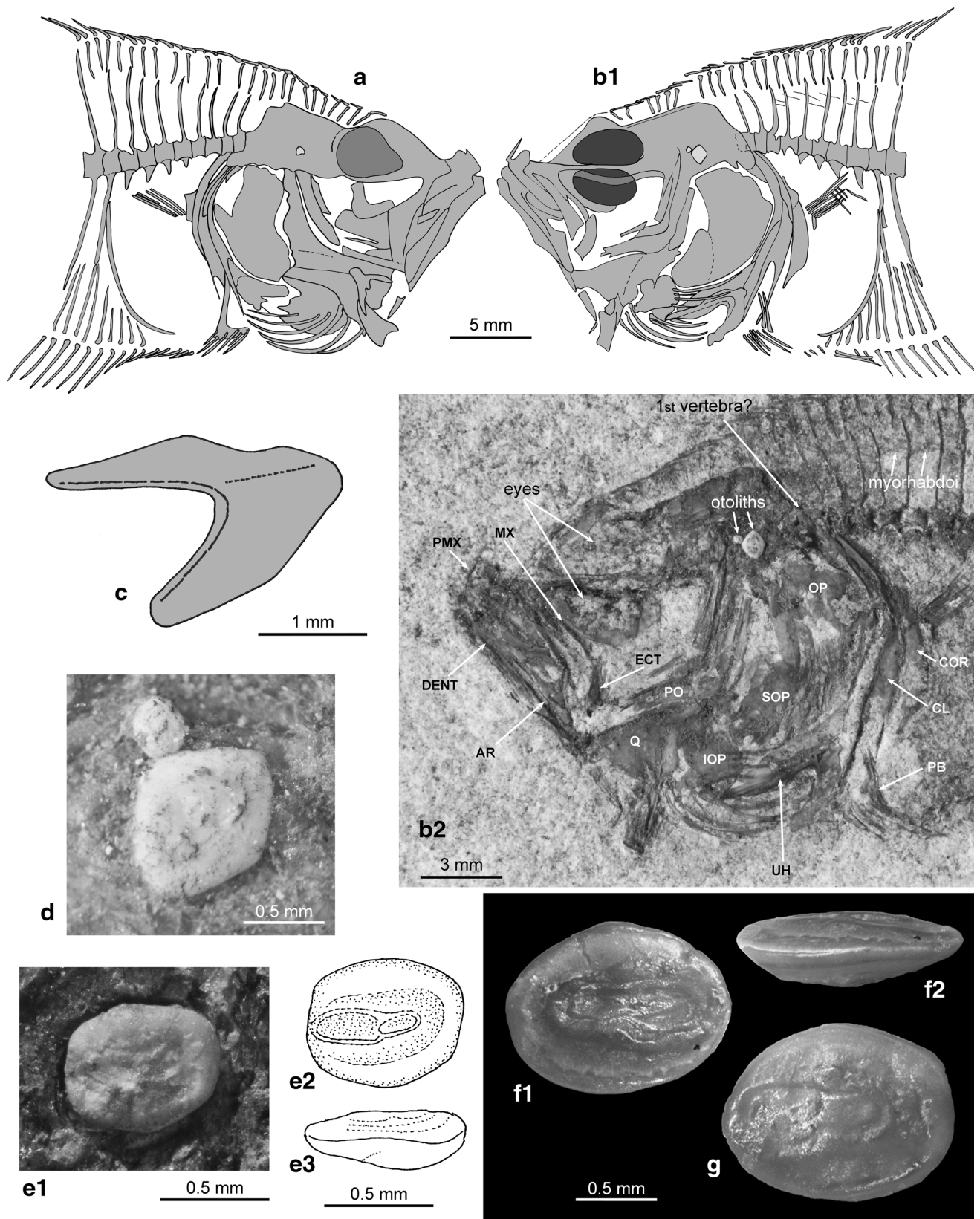
Median fins. The dorsal fin seems to originate above the eye approximately at the level of the anterior tip of the supraoccipital crest and comprises 65 rays in CNHM 154 and 258; however, it cannot be excluded that it extended more anteriorly in origin with very short rays and pterygiophores like in Recent species of *Arnoglossus*. Eight dorsal-fin pterygiophores are positioned nearly vertically above the supraoccipital crest to which they are connected; the succeeding three dorsal-fin pterygiophores are insert in the first interneural space (between the first and the second abdominal vertebrae); there is no evidence of dorsal-fin pterygiophores in the ethmoid region. Therefore, the anterior dorsal-fin pterygiophore formula is 0 – 8 – 3. The anal fin contains 48–55 rays. The first anal-fin

pterygiophore is very long and curved and inserts in front of the first haemal spine to which it is closely associated. The subsequent seven or eight anal-fin pterygiophores insert in the first interhaemal space and the successive two to three in the second interhaemal space, resulting in an anterior anal-fin pterygiophore formula of 1 – 7 or 8 – 2 or 3. The dorsal- and anal-fin rays reach their maximum length at about mid-length of the body, measuring about 9.4–11.4% SL.

Paired fins and girdles. The pectoral fin and girdle are incompletely preserved. At least six to seven short pectoral-fin rays can be observed, measuring about 7% SL. The well-developed cleithrum and coracoid are clearly exposed in CNHM 154.2 (Fig. 2b). The basipterygia are slender and bear six short pelvic-fin rays each.

Otolith (Fig. 2d–g). The sagitta and lapillus are preserved in situ in the holotype CNHM 154.2 (Fig. 2d) and in CNHM 274 (Fig. 2e). The lapillus is very small, less than one-third of the sagitta and regularly oval in outline. The outer surface of the left sagitta is exposed in CNHM 154.2; it slightly exceeds 1 mm in length, and shows a smooth, slightly convex surface and a rounded parallelogram-like outline. In CNHM 274 the inner face of the sagitta is exposed measuring 0.73 mm in length. The index OL:OH is 1.2, the index OH:OT 2.2. The otolith has a rounded rectangular outline with broad, obtuse, suppressed mediodorsal and medioventral angles. The anterior rim is nearly vertical, just slightly inclined backwards towards dorsal, and the posterior rim is similarly nearly vertical and inclined backwards dorsally. The rims are smooth lacking an excisura and antirostrum at the anterior rim. The inner face is slightly convex with the sulcus and the area surrounding it up to the broad circumsulcal depression being somewhat elevated above the level of the face itself. The sulcus has no clear opening towards the anterior rim; it is slightly inclined and relatively shallow. The ostium is much larger and wider than the cauda (OsL:CaL = 1.6; OsH:CaH = 1.7), whereas the cauda is slightly shifted dorsally. Ostial and caudal colliculi are indistinctly separated.

Isolated otoliths with morphology consistent to that described herein have been reported from the Konkian and Sarmatian strata of the Central and Eastern Paratethys under different genus and species names and were recently assigned to as *Arnoglossus? tenuis* (Schubert 1906) by Bratishko et al. (2015). Two specimens are refigured here from Bratishko et al. (2015; Fig. 2f, g). They show the same characteristic proportions of the sulcus and the regularly rounded outline without excisura and opening of the ostium. These characters were used by Bratishko et al. (2015) as rational for a tentative assignment to the genus



◀**Fig. 2** *Arnoglossus bassanianus* (Kramberger 1883). **a** CNHM 154.1, reconstruction of the head and abdominal region; **b1–2** CNHM 154.2, reconstruction of the head and abdominal region and photograph; **c** CNHM 274, interpretative drawing of the urohyal; **d** CNHM 154.1, photograph of the otolith *in situ*; **e1–3** CNHM 274, photograph of the otolith *in situ*; **e1–2** inner face; **e3** ventral view; **f–g** isolated otoliths from the Konkian of Karaigali, Mangyshlak, Kazakhstan (refigured from photographs from Bratishko et al. 2015); **f1, g** inner faces; **f2** ventral view; **g** reversed

Arnoglossus (see Schwarzhans 1999). The largest specimen (Fig. 2g) is about 1.4 mm long and was then considered to represent a small specimen. Based on the proportions observed in CNHM 154, it would correspond to a fish of about 60 mm SL. Extant *Arnoglossus* species usually reach 150 to 300 mm SL, even if Norman (1934) reported a size

of 47 mm for fully mature specimens of *Arnoglossus kessleri* Schmidt 1915 that can reach a maximum size of 66 mm. Therefore, it is quite possible that specimens of *A. bassanianus* of the size of 60 mm SL and with otoliths of 1.5 mm OL represent fully mature individuals.

Discussion: The holotype is the largest and best preserved specimen available in plate and counterplate. CNHM 274 is moderately well preserved, while CNHM 258 is poorly preserved and therefore is only tentatively assigned to *Arnoglossus bassanianus*. The presence of myorhabdoi and the absence of a neural spine on the first vertebra (although usually hidden under the head bones) are currently regarded as synapomorphic for the family Bothidae (e.g., Amaoka 1969; Chanet and Schultz 1994; Patterson and Johnson 1995; Chanet et al. 2004). The overall shape and

Table 1 Counts and measurements of *Arnoglossus bassanianus*

Meristics	<i>Arnoglossus bassanianus</i>		
	CNHM 154 (HT)	CNHM 274	CNHM 258
SL (mm)	45	29.5	21.5
HL (mm)	17	9.8	7.5
Otolith	Yes	Yes	
Vertebrae	9 + 27 = 36	9 + 26 = 35	9 + 27 = 36*
Abdominal vertebrae with parapophyses	4	5	5
D	65		65
A	55		48
P	6	7	6
V	6	6	6
C	17	17	17
B	6 or 7		7
Dorsal pterygiophore formula**	0 – 8 – 3		
Anal pterygiophore formula***	1 – 8 – 2 or 3		1 – 7 – 2
Morphometrics (% of SL)			
Head length (HL)	38.0	33.3	35.0
Max head height (HH)	36.0	27.0	32.0
HL:HH	HL > HH	HL > HH	HL > HH
Max. body depth	40.0	34.0?	37.0
Snout length	8.3	7.0	8.2
Angle of mouth	50°	40°–45°	50°
Mouth gape	14.3		10.5
Orbit diameter	6.0	6.4	6.7
Caudal peduncle Depth	11.0	9.5	11.8
Longest dorsal-fin ray	11.4		
Longest anal-fin ray	9.4		9.0
Pectoral length	7.0	7.0	7.0
Pelvic length	4.5	4.0	6.0

* First vertebra obscured

** Ethmoidal pterygiophores—neurocranial pterygiophores—additional pterygiophores prior to first neural spine

*** 1st anal pterygiophore—pterygiophores before 1st haemal spine—pterygiophores between 1st and 2nd haemal spines

position of the urohyal and the configuration of the supraoccipital are typical for *Arnoglossus* (Amaoka 1969; Bruno Chanut, personal communication August 26–29, 2016). The morphology of the otoliths generally fits well with that of extant species of the genus *Arnoglossus* (Schwarzhan 1999), from which they differ, however, by having a rather shallow sulcus, rounded outline and reduced ostial opening. In their discussion of the taxonomic allocation of *Arnoglossus? tenuis* (Schubert 1906), which is now considered a junior synonym of *A. bassanianus*, Bratishko et al. (2015) hypothesized that these differences may point to the presence of a separate, extinct genus. According to Bruno Chanut (personal communication August 29, 2016) the genus *Arnoglossus* as it is currently defined is almost certainly polyphyletic. Therefore, although we have assigned the Sarmatian fossils documented herein to the genus *Arnoglossus*, we are aware of the preliminary nature of such attribution that would not be conclusively demonstrated until a proper review of the extant species of the genus will be performed.

A number of potentially related bothid flatfishes have been described from the Miocene of Europe. The first to mention is *Rhombus heckeli* Kner 1861 presumably from the upper Badenian Leitha Limestone cropping out in the surroundings of St. Margarethen, Austria. Following Chanut and Schultz (1994), the number of vertebrae (35 or 36) is identical to that of *A. bassanianus*, even if the number of abdominal vertebrae is different (8 vs 9). The number of dorsal-fin rays is slightly higher than in *A. bassanianus* (70+ vs 65) while the number of anal-fin rays is comparable (48 vs 48–55). The dorsal fin extends over the skull with eight fin pterygiophores contacting the supraoccipital crest, just like in *A. bassanianus*. The shape of the first neural spines is straight like in *A. bassanianus*. Other important diagnostic characters (e.g., the urohyal) are not preserved in the only available specimen of *Rhombus heckeli*. Chanut and Schultz (1994) suggested that the specimen might belong to a pleuronectoid family but not the Bothidae due to the apparent absence of the myorhabdoi. Moreover, it appears that the first vertebra bears a short neural spine which would also exclude the possibility of an attribution to the Bothidae (Amaoka 1969), even if the nature of such a vertebral complement is still uncertain. The taxonomic status of this Middle Miocene Paratethyan taxon was extensively discussed by Chanut and Schultz (1994) who concluded that the unique holotype does not provide enough diagnostic characters, thereby implying that its name should be regarded as *nomen dubium*. The synonymization of the otolith-based species *Arnoglossus? tenuis* proposed herein clearly indicates that *A. bassanianus* has a stratigraphic range comprising at least the late Badenian (Konkian) and the Sarmatian s.s., implying that this species was in existence in the same time and same region of the dubious

Rhombus heckeli. Therefore, we cannot exclude that future finds of articulated skeletons of *Arnoglossus* from late Badenian deposits would reveal that *Rhombus heckeli* and *Arnoglossus bassanianus* are indeed synonyms.

Chanut and Schultz (1994) also described *Miobothus weissi* Chanut & Schultz 1994 from the late Badenian of St. Margarethen. *Arnoglossus bassanianus* differs from *Miobothus weissi* in having a larger number of vertebrae (35–36 vs 33), straight (vs curved) anterior neural spines, less dorsal- and anal-fin rays (65 and 48–55 vs 73 and 57, respectively), and the urohyal with the upper branch being slightly to distinctly longer than the lower branch (vs of equal length) and a plate-like bone stretching across the full length of the upper branch just above the inner ridge (vs absent). A number of *Arnoglossus* species have been described from Early and Middle Miocene (Tshokrakian to Karaganian) of the Eastern Paratethys, i.e., *A. distinctus* Switchenska 1981, *A. ovalis* Switchenska 1981 and *A. sumgaiticus* Switchenska 1981. They all differ from *Arnoglossus bassanianus* in having a higher number of dorsal- and anal-fin rays (76–86 and 58–62 vs 65 and 48–55, respectively) and a higher number of precaudal vertebrae (10–11 vs 9). *Arnoglossus distinctus* also differs from *A. bassanianus* in having a higher number of vertebrae (37 vs 35–36), whereas *A. ovalis* has a lower number of caudal-fin rays (15 vs 17 in *A. bassanianus*) and *A. sumgaiticus* exhibits curved anterior neural spines (vs straight in *A. bassanianus*). *Arnoglossus sauvagei* (D’Erasmus 1930) from the Messinian of Italy differs from *A. bassanianus* in the number of vertebrae (10–11 + 27–28 vs 9 + 26–27), number of dorsal-fin rays (70–76 vs 65), number of dorsal-fin rays articulating with the neurocranium (11 vs 8), and by having the head higher than long (vs longer than high), and anterior neural spines curved (vs straight) (see Landini 1981). It is interesting to note, however, that Gaudant et al. (2010) reported 9 + 27 or 28 vertebrae in a single specimen from the Tortonian of Pecetto di Valenza (Italy) which they identified as *Arnoglossus sauvagei*.

After the synonymization the otolith-based species *Arnoglossus? tenuis*, *Arnoglossus bassanianus* appears to be restricted to the Central and Eastern Paratethys during the Konkian (=late Badenian) and Sarmatian s.s. times, i.e., after the Karaganian Crisis. In our assessment, it is not related to the supposed *Arnoglossus* species recorded from Karaganian and earlier times in the Eastern Paratethys or from the Upper Miocene strata of the Mediterranean region. As a final note, it is reasonable to expect that after a comprehensive review of the extant species, the genus *Arnoglossus* would become split-up and that *A. bassanianus* would be placed in a different genus or in a new extinct genus.

Genus *Bothus* Rafinesque 1810

Bothus parvulus (Kramberger 1883)
(Figure 3a–i)

1883 *Rhombus parvulus* Kramberger.—Kramberger: pl. 8, fig. 3

?1962 *Rhombus parvulus* Kramberger 1883.—Anđelković: pl. 1, fig. 8 (not verified)

?1970 *Rhombus parvulus* Kramberger 1883.—Anđelković: pl. 25, fig. 1 (not verified)

?1989 *Rhombus parvulus* Kramberger 1883.—Anđelković: pl. 20, fig. 2 (not verified)

Material: Two small articulated skeletons from Dolje, Croatia, Sarmatian s.s. (Volhynian); CNHM 163, holotype, 17 mm SL (Fig. 3a–c), CNHM 275, 25 mm SL (Fig. 3d–i); CMHN 275 contains an otolith in situ (Fig. 3i) with the outer surface exposed. An attempt to retrieve the otolith resulted in a badly damaged inner face.

Description: The body is moderately slender to moderately compressed, with a compressed head. The depth of the head is larger than its length. The mouth is oblique, small, forming an angle ranging between 45° and 60° and with a short mouth gape measuring between 3.3 and 5.0% SL. Counts and measurements are summarized in Table 2.

Scales. Body scales are not clearly recognizable, but there is a distinct line of large scales along the bases of the dorsal and anal fins. This scales are peripherally ctenoid measuring about 0.3–0.4 mm; they are not homologous to the bony plates observed in fishes of the pleuronectid genus *Platichthys* (see Norman 1934).

Neurocranium. The neurocranium is only partially preserved in both the specimens lacking most of its anterior parts including the orbits. Individual bones cannot be recognized. The supraoccipital crest is rounded, much higher in the holotype. The anterior dorsal-fin pterygiophores are incompletely preserved and in some instances appear to be hourglass shaped (Fig. 3f). The number of dorsal-fin pterygiophores overlying the neurocranium cannot be conclusively assessed, but appears to exceed 8–10. In CNHM 275 there is a distinct indication of the anterior extension of the anterior dorsal-fin rays up to the ethmoid region. The dorsal margin of the neurocranium is very steep, particularly in CNHM 163. This feature might be related to sexual dimorphism or, alternatively to the very small, probably juvenile size of CNHM 163, or to a combination of both.

Jaws and suspensorium. Premaxilla, maxilla, dentary and angulo-articular are moderately well preserved (Fig. 3b, f). The premaxilla has a very thin and sharp ascending process and a broad and slightly shorter articular process. No teeth are discernible on the premaxilla and the dentary.

Urohyal and branchiostegal rays. The urohyal is preserved in CNHM 275 (Fig. 3g), but it is partially obscured by the

overlying branchiostegal rays. It is fishhook-shaped with the two branches forming an angle of less than 40°. The upper branch is broad, with a bony lamina stretching across its full length leading to a long cardiac apophysis; the sciatic part is also broad, but appears to be incomplete ventrally. Six branchiostegal rays can be recognized.

Opercular series. The opercle and subopercle are not properly distinguishable in both the specimens but they appear to be large, albeit incomplete; the interopercle is exclusively visible in CNHM 163. The preopercle is slender, boomerang-shaped with a distinct median sharp bend. **Axial skeleton.** The vertebral column contains 35 (10 + 25) vertebrae. The first vertebra is obscured by head bones in both the specimens, but vaguely discernible in CNHM 275 (Fig. 3g) and bears no neural spine. The vertebral centra are subrectangular higher than long, becoming subquadrangular posteriorly. The neural spines are long. The first three or four neural spines show a conspicuous kink-bend near the base, where the spines are bent forward. The neural spines of the abdominal vertebrae five to ten are the longest and nearly vertically oriented. Short parapophyses are visible on the posterior six abdominal vertebrae, slightly increasing in length backward. The caudal vertebrae bear long neural and haemal spines that are increasingly more inclined backward. The first haemal spine is broad and very elongate. Myorhabdoi are visible along the entire dorsal and ventral margins of the trunk and are particularly well visible in its posterior part (Fig. 3h).

Caudal skeleton. The caudal skeleton is not clearly preserved in both the specimens. There are 17 principal caudal-fin rays.

Median fins. The dorsal fin seems to originate well in front of the eye, possibly above the ethmoid region of the cranium with at least two rays, and contains at least 70 rays (73+ in CNHM 275). There are at least eight or ten dorsal-fin pterygiophores overlying the neurocranium, some of which are hour-glass shaped and located in front of the eyes. A few pterygiophores inserted behind the eyes on the expanded supraoccipital crest appear to be extended downwards into the crest, possibly in cavities, in CNHM 163 (Fig. 3c). There are one or two pterygiophores positioned between the posterior wall of the neurocranium and the first neural spine. The anterior dorsal pterygiophore formula is 2 + – 10 + – 1 or 2. The anal fin contains about 50 rays. The first anal-fin pterygiophore is greatly elongate and curved and articulates with the first anal-fin spine. Seven or eight subsequent pterygiophores insert in the space between the enlarged first anal-fin pterygiophore and the first haemal spine, and one or two occupy the first interhaemal space, resulting in an anterior anal pterygiophore formula of 1 – 7 or 8 – 1 or 2. The dorsal- and anal-

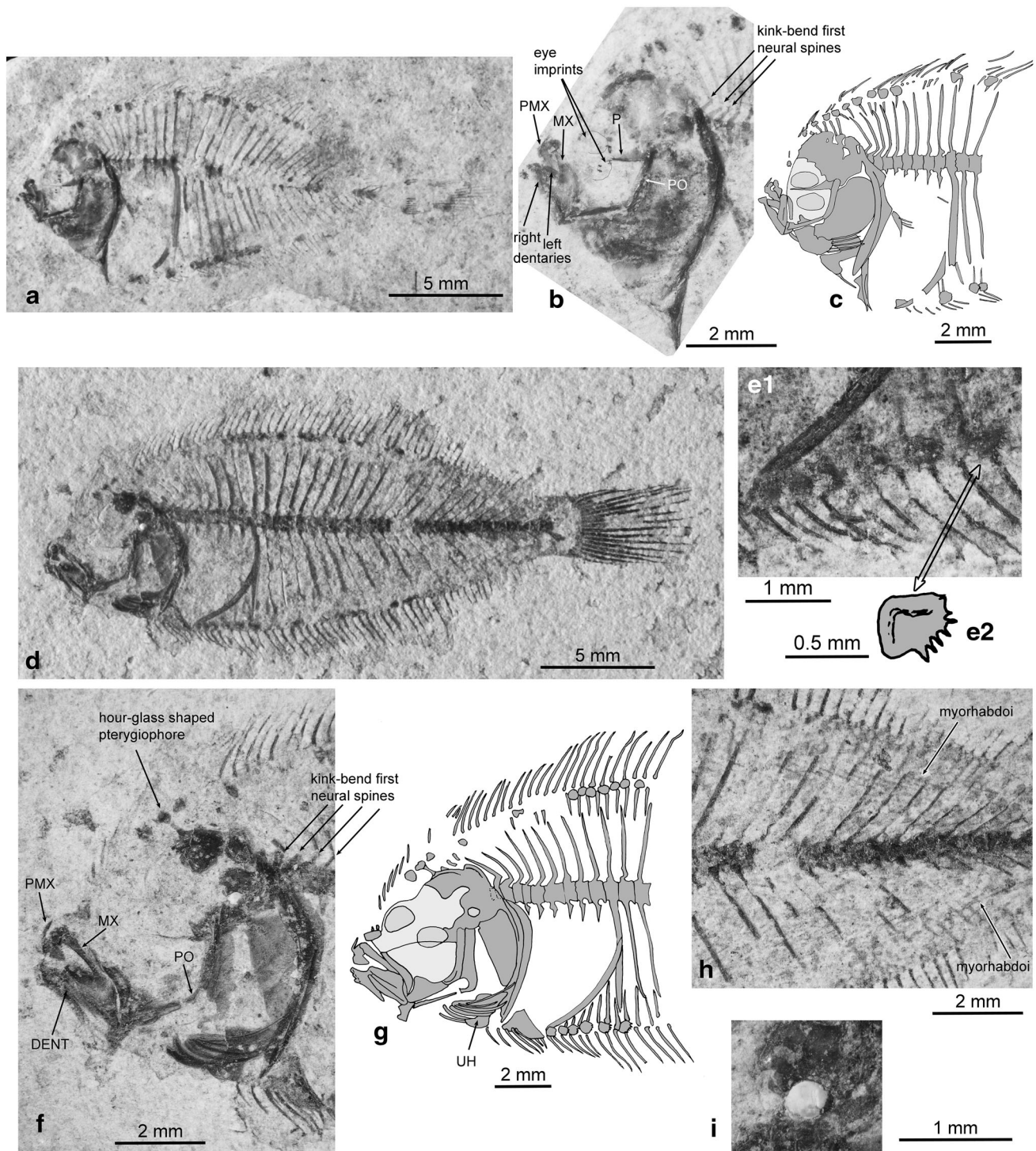


Fig. 3 *Bothus parvulus* (Kramberger 1883). **a–c** CNHM 163, holotype; **a** articulated skeleton; **b** photograph of the head; **c** reconstruction of the head and abdominal region; **d–i** CNHM 275; **d** articulated skeleton; **e1–2** photograph of the anterior part of anal fin with

showing row of large scales along the fin base and interpretative drawing of a single scale; **f** photograph of the head; **g** reconstruction of the head and abdominal region; **h** photograph of the rear part of trunk showing the myorhabdoi; **i** photograph of the otolith in situ

fin rays are uniformly elongate along the trunk becoming shorter posteriorly in the series, with a maximum length of about 10.0% SL.

Paired fins and girdles. The pectoral fin and girdle are not preserved at all or only incompletely preserved. A very long cleithrum is preserved in both the specimens. The

Table 2 Counts and measurements of *Bothus parvulus*

Meristics	<i>Bothus parvulus</i>	
	CNHM 163 (HT)	CNHM 275
SL (mm)	17	25
HL (mm)	4.7	6.5
Otolith		Yes
Vertebrae	10 + 25 = 35*	10 + 25 = 35*
Abdominal vertebrae with parapophyses	6	6
D	59+	ca. 73
A	43+	ca. 50
P	?	?
V	?	17
C	17	6
B		2 + - 8 - 2
Dorsal pterygiophore formula**	? - 10 + - 1	1 - 7 - 2
Anal pterygiophore formula***	1 - 7? - 1	
Morphometrics (% of SL)		
Head length (HL)	27.5	26.0
Max head height (HH)	35.5	30.0
HL:HH	HL < HH	HL < HH
Max. body depth	48.0	37.5
Snout length	4.5	5.0
Angle of mouth	60°	45°
Mouth gape	3.3	5.0
Orbit diameter		
Caudal peduncle Depth		10.8
Longest dorsal-fin ray	10.7	10.0
Longest anal-fin ray		10.0
Pectoral length		
Pelvic length		8.7

* First vertebra obscured

** Ethmoidal pterygiophores—neurocranial pterygiophores—additional pterygiophores prior to first neural spine

*** 1st anal pterygiophore—pterygiophores before 1st haemal spine—pterygiophores between 1st and 2nd haemal spines

proximal portions of the basipterygia are broad and bear six or seven short rays.

Otolith (Fig. 3i). CNHM 275 exhibits a very small, circular otolith with a strongly convex outer surface measuring about 0.4 mm length. The morphology of the inner face cannot be observed. No isolated otoliths are known from coeval strata that could be related to this species.

Discussion: The holotype of *Bothus parvulus* is a very small, possibly juvenile individual or at least a young subadult. The second specimen assigned herein to *Bothus parvulus* (CNHM 275) is somewhat larger and slightly differs from the holotype in the shape of the neurocranium and the more slender body. They share, however, a number of features that are highly diagnostic, including the stretch of large peripherally ctenoid

scales along the bases of the dorsal and anal fins, the kink at the base of the anteriormost neural spines and the narrow, sharply bent preopercle. Therefore, it is reasonable to suggest that the apparent differences in the two specimens might be related to intraspecific variability such as sexual dimorphism or allometric ontogeny. Carnevale et al. (2006) figured three very small *Bothus* specimens (12–15 mm SL), which show a similar degree of length to height variation. These are the only other specimens belonging to the genus *Bothus* recorded from the Middle Miocene of the Paratethys and they do not exhibit the conspicuous line of large scales along dorsal- and anal-fin bases nor the kink at the base of the anterior neural spines or the boomerang-shaped preopercle.

Despite its small and immature size, *Bothus parvulus* is clearly attributed to the family Bothidae because of the

presence of myorhabdoi. The presence of hour-glass-shaped anterior dorsal-fin pterygiophores and the apparent insertion of some dorsal-fin pterygiophores into cavities of the supraoccipital crest are diagnostic of *Bothus* and a few related genera including *Crossorhombus*, *Engyproson*, *Parabothus* and *Tosarhombus* (personal communication by Bruno Chanet, September 23, 2016). The osteological differentiation of these genera is rather problematic; the inclusion within the genus *Bothus* for the fossil *B. parvulus* is also justified by biogeographic arguments since extant species of this genus are currently common in the Mediterranean and North-eastern Atlantic. In this context, it is interesting to know that the low number of vertebrae of *Bothus parvulus* is unusual and not observed in any extant species of *Bothus* (38–40; see Norman 1934). The small size of the otoliths is consistent with the observations made in extant *Bothus* species (Schwarzahns 1999). The presence of enlarged peripherally ctenoid scales along the bases of the dorsal and anal fins has not been recorded in any extant pleuronectiform.

Family Soleidae Bonaparte 1835

Genus *Parasolea* n. gen.

Type species: *Rhombus serbicus* Anđelković 1966.

Etymology: The generic name refers to the similarity with the genus *Solea*.

Diagnosis: A genus of the family Soleidae with the following combination of characters: eight abdominal vertebrae; erisma (first enlarged dorsal-fin pterygiophore) short, lying on the anterior part of the neurocranium and nearly straight; anterior dorsal pterygiophore formula 1 (erisma)—1 or 2 pterygiophores lying on the erisma—3 or 4 pterygiophores inserting on the rear part of the neurocranium—1 pterygiophore inserting in front of the neural spine of the second vertebra; first abdominal vertebra with neural spine minute or absent, second vertebra with expanded neural spine bent forward but not curved or bent over the neurocranium; urohyal with long, anteriorly widened dorsal branch and shorter ventral branch, its length being about half the length of the dorsal branch; the angle formed by the two branches of the urohyal at about 90°–100°; otolith with flat inner face except for elevated central region and extremely small sulcus (OL:SuL = 2.2–3.0) terminating anteriorly at some distance from the anterior rim of the otolith.

Discussion: The short and nearly straight erisma and the pterygiophore formula resemble the condition observed in *Solea* (Chapleau 1989) and possibly represents the plesiomorphic condition within the Soleidae. The number of abdominal vertebrae (eight) is lower than in the genus

Solea (nine or ten), as well as of most soleids (Vacheron et al. 2008) and can be considered to represent a derived character of *Parasolea*. The morphology of the first abdominal vertebra and neural spine of the second vertebra are very similar to those of the genus *Solea* (Chapleau & Keast 1988). The urohyal is characterized by a dorsal branch almost two times longer than the ventral one, while in *Solea*, *Pegusa*, *Synapturichthys*, *Microchirus* or *Buglossidium* they are about equal in size or, in some cases, the dorsal branch is slightly longer than the ventral branch (Desoutter 1987, 1994; Vacheron et al. 2008). A similar condition as in *Parasolea* has been observed in *Dicologlossa* and *Vanstraelenia* (Vacheron et al. 2008), but in these two genera the angle formed by the two branches is much wider, exceeding 130° (vs 90°–100°). The shape of the urohyal of *Parasolea* is morphologically intermediate between both groups. The rather flat inner face of the otolith remarkably contrasts with the strongly convex inner face (and concave outer face) observed in the otoliths of *Solea* (Schwarzahns 1999) including the early Miocene *Solea kirchbergeana* (v. Meyer 1848), the only other fossil soleid from which otoliths in situ have been recorded (Weiler 1955, Chanet 1996). A very peculiar specialization of the otolith of *Parasolea* furthermore is the extremely small sulcus, which is much larger in *Solea*. A few species of *Microchirus* show a reduced sulcus size, but similarly small sulci are only observed in *Vanstraelenia* (see Schwarzahns 1999). *Parasolea* exhibits a set of plesiomorphic traits shared with *Solea* combined with certain apomorphic traits that in some ways resemble those characteristic of *Vanstraelenia*.

Chapleau (1989) and Vacheron et al. (2008) hypothesized that the three genera *Solea*, *Dicologlossa* and *Vanstraelenia* form a monophyletic group, primarily supported by the anterior dorsal pterygiophore formula. *Parasolea* shares the same pterygiophore formula and for this reason is interpreted to belong to this group. Within this group, the urohyal and the otoliths closely resemble those of *Vanstraelenia*, but the ventral branch of the urohyal is much more reduced and the aperture angle is larger in the latter genus. The low number of caudal vertebrae, also clearly indicates a placement of *Parasolea* separate from all three other genera. We conclude that *Parasolea* is probably closest related to *Vanstraelenia*, a monotypic genus restricted to the tropical East Atlantic.

Species: The genus *Parasolea* solely includes *P. serbica* known from the early Sarmatian of the Central Paratethys (articulated skeletons) and the middle Sarmatian of the Eastern Paratethys (isolated otoliths). The genus possibly represents a Paratethyan endemism.

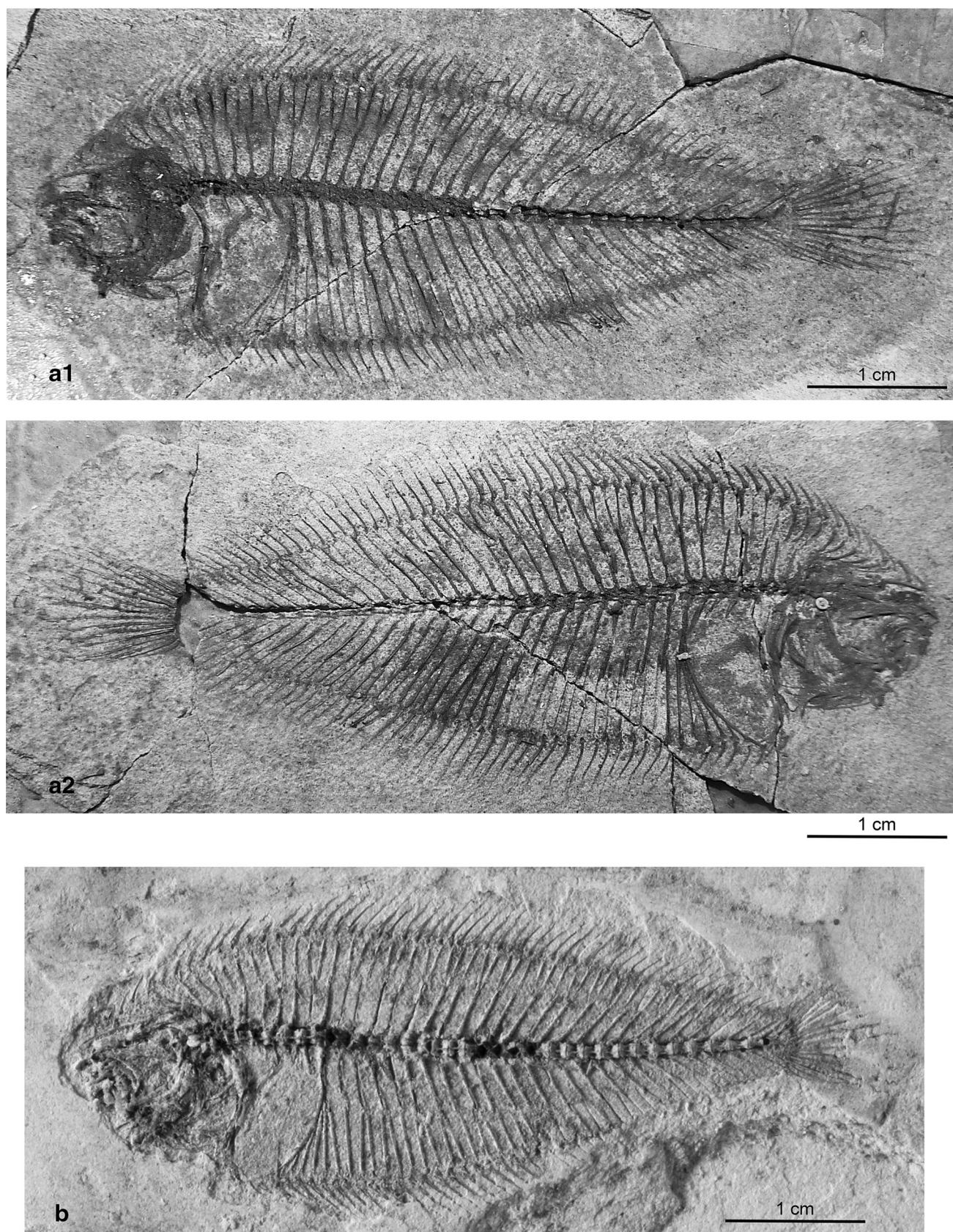


Fig. 4 *Parasolea serbica* (Anđelković 1966), articulated skeletons. **a1–2** CNHM 278; **b** CNHM 158

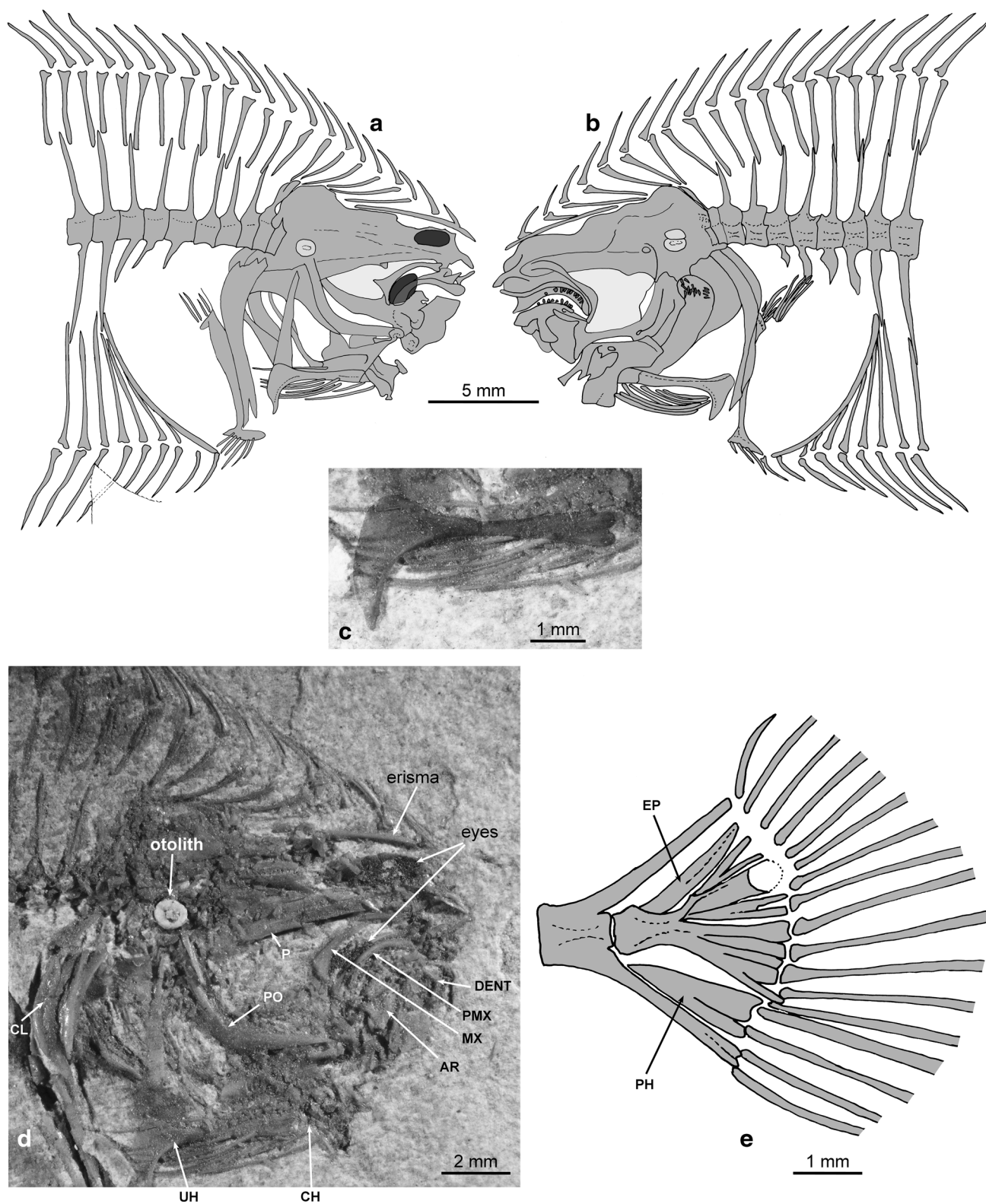


Fig. 5 *Parasolea serbica* (Andelković 1966). **a** CNHM 278, reconstruction of the head and abdominal region; **b** CNHM 158 reconstruction of the head and abdominal region; **c** CNHM 278,

photograph of the urohyal (*highlighted*); **d** CNHM 278, photograph of the head; **e** CNHM 278, reconstruction of the caudal skeleton

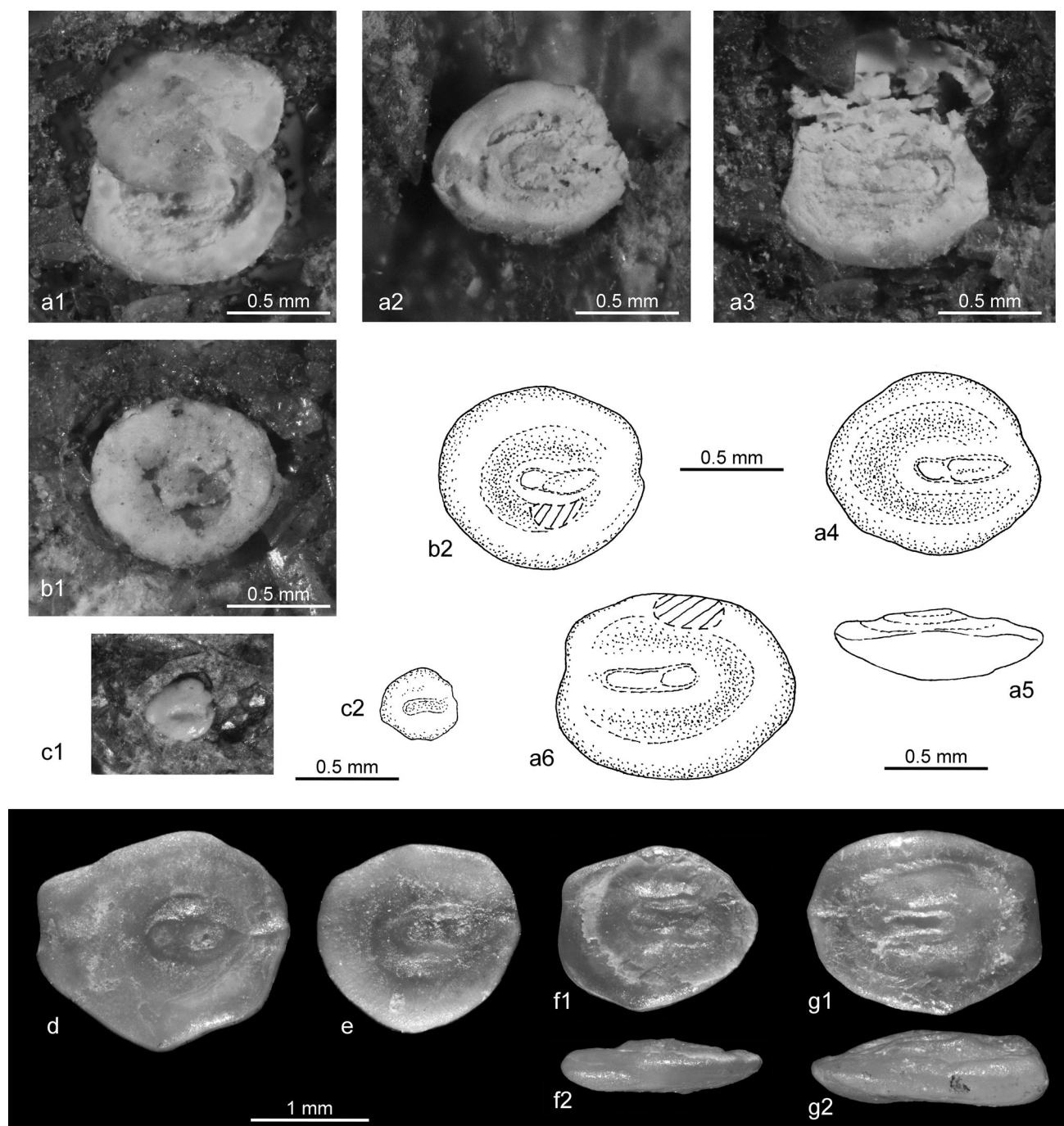


Fig. 6 *Parasolea serbica* (Anđelković 1966), otoliths. **a1–6** CNHM 158; **a1–3** photographs of otoliths in situ; **a1** otoliths in place; **a2** left otolith removed; **a3** right otolith in place; **a4–6** reconstructions of the otoliths; **a4** inner face of the left otolith; **a5** ventral view of the left otolith; **a6** inner face of the right otolith; **b1–2** CNHM 278,

photograph and reconstruction of the otolith in situ; **c1–2** RGF-AJ 32, photograph and reconstruction of the otolith in situ; **d–g** photographs of the isolated otoliths from the Middle Sarmatian s.l. of Jurkino, Crimea (courtesy A. Bratishko); **d, e, f1, g1** inner faces; **f2, g2** ventral views

Parasolea serbica (Anđelković 1966)

(Figures 4a, b, 5a–e, 6a–g)

1966 *Rhombus serbicus* Anđelković.—Anđelković: pl. 1, fig. 1, 1a

1969 *Rhombus stamatini* Pauca 1931.—Anđelković: pl. 5, fig. 3

1970 *Rhombus serbicus* Anđelković 1966.—Anđelković: pl. 25, fig. 3

1970 *Rhombus stamatini* Pauca 1931.—Anđelković: pl. 25, fig. 4

1989 *Rhombus serbicus* Anđelković 1966.—Anđelković: pl. 20, fig. 1 (refigured from 1966)

Table 3 Counts and measurements of *Parasolea serbica*

Meristics	<i>Parasolea serbica</i> n.gen			
	CNHM 158	CNHM 278	RGF-AJ 32	RGF-AJ 241 (HT)
SL (mm)	52	54	16	80
HL (mm)	12.3	12.0	4.1	27
Otolith	Yes	Yes	Yes	
Vertebrae	8 + 27 = 35	8 + 28 = 36	8 + 25 = 33*	8 + 27 = 35
abdominal vertebrae with parapophyses	4	3	3	4
D	57	60	62	60
A		48		45
P	5	5		8 (?)
V	4+	6		
C	17	17	17	15+
B	7	7		
Dorsal pterygiophore formula**	[1] 1 – 3 – 1	[1] 1 – 4 – 1		[1] 1 – 3 – 1
Anal pterygiophore formula***	1 – 5 – 2	1 – 5 – 2		1 – 4 – 2
Morphometrics (% of SL)				
Head length (HL)	23.6	21.5	25.6	23.5
Max head height (HH)	26.9	23.0		26.6
HL:HH	HL < HH	HL < HH		HL << HH
Max. body depth	37.5	41.1		29.6
Snout length			2.0	3.5
Angle of mouth	nm	nm	nm	
Mouth gape	8.0			
Orbit diameter		2.8	4.5	
Caudal peduncle depth	9.4	8.3	7.0	8.9
Longest dorsal-fin ray	9.6	9.3	6.3	11.0
Longest anal-fin ray	10.7	9.4		9.1
Pectoral length	6.3	5.5		6.6
Pelvic length	3.8	3.2		

* First vertebra obscured

** [Erisma]—on erisma—neurocranial pterygiophores—additional pterygiophores prior to first neural spine

*** 1st anal pterygiophore—pterygiophores before 1st haemal spine—pterygiophores between 1st and 2nd haemal spines

1989 *Rhombus stamati* Pauca 1931.—Anđelković: pl. 20, fig. 5 (refigured from 1969)

Material: Three articulated skeletons containing otoliths in situ characterized by different degrees of preservation; two medium-sized and relatively well-preserved specimens from Dolje, Croatia, Sarmatian s.s. (Volhynian); CNHM 158, 52 mm SL (Figs. 4b, 5b, 6a), CNHM 278, in plate and counterplate, 54 mm SL (Figs. 4a, 5a, c–e, 6b); a single small and incomplete specimen (RGFAJ 32) from Belgrade, Serbia, originally described by Anđelković (1969) as *Rhombus stamati* Pauca 1931 (Fig. 6c). In addition, four isolated otoliths from the Middle Sarmatian s.l. of Jurkino, Crimea from the collection of A. Bratishko.

Description: The body is relatively slender, with regularly curved dorsal and ventral margins and a protruding snout with rounded tip (Fig. 4a, b). The depth of the head is slightly larger than its length. The mouth shows the typical curved shape of soleids, with a mouth gape measuring about 8.0% SL. The scales are not preserved. Counts and measurements are summarized in Table 3.

Neurocranium. The outline of the neurocranium is clearly exposed, but only a few individual bones can be tentatively recognized (Fig. 5a, b, d). The dorsal margin of the neurocranium is depressed behind the upper eye. The dorsal-fin origin is located just above the upper eye or slightly in front of it. The parasphenoid is long and straight.

Jaws and suspensorium. Premaxilla, maxilla, dentary and angulo-articular are recognizable on both the eyed and blind sides (CNHM 278; Fig. 5a, d). The premaxilla shows a very short and thin ascending process; the articular process is not exposed. The premaxilla curves downward below the lower eye on the eyed side; the alveolar process bears a dense cluster of moderately large conical teeth with rounded tips apparently arranged in several rows, which can be seen on the blind side (CNHM 158, Fig. 5b). The maxilla is well exposed on the eyed side of CNHM 278 (Fig. 5a, d); it follows the curved outline of the premaxilla but shifted above the lower eye and exhibits a slight distal expansion. Dentary and angulo-articular are largely incomplete; the angulo-articular is well exposed on the eyed side of CNHM 278 (Fig. 5d), while the dentary is clearly recognizable on the blind side of CNHM 158 (Fig. 5b), where it bears numerous moderately long, conical teeth similar to those of the premaxilla.

Urohyal and branchiostegal rays. The urohyal is well exposed in the eyed side of the specimen CNHM 278 (Fig. 5a, c, d), as well as in the blind side of CNHM 158 (Fig. 5b) in a position slightly inclined downwards anteriorly (Amaoka 1969). It is fishhook-shaped with a long, horizontally oriented dorsal branch and a short ventral branch, forming an angle of about 90°–100°. The upper branch is nearly twice as long as the lower branch and anteriorly widened with a club-shaped tip; it bears a dorsal bony lamina from the beginning of the cardiac apophysis that stretches across the full length of the lower branch until its tapering tip (Fig. 5c). The hyoid bar is mostly obscured, hidden under cranial bones, and supports seven branchiostegal rays.

Opercular series. The opercular series is not preserved in any of the specimens except for the large, boomerang-shaped preopercle. Some pharyngobranchial teeth are observable in CNHM 158.

Axial skeleton. The vertebral column consists of 35 or 36 (8 + 27 or 28) vertebrae. The first vertebra is recognizable in CNHM 278 (Fig. 5a) and mostly obscured by underlying head bones in CNHM 158 (Fig. 5b); it apparently bears a very short neural spine. The vertebral centra are subrectangular, higher than long and dorsally expanded in the abdominal region, becoming more regularly rectangular in the caudal region. The neural spine on the second abdominal vertebra is moderately long and distally broadened, bent forward along the rear margin of the neurocranium (Fig. 5a). The subsequent neural spines are straight, almost vertical, becoming increasingly inclined posteriorly in the caudal vertebrae. Relatively large parapophyses are present only on the posterior three or four abdominal vertebrae, slightly increasing in length posteriorly in the series. The caudal vertebrae bear long neural and haemal

spines. The first haemal spine is slightly shorter than the successive ones.

Caudal skeleton. The caudal skeleton is reasonably well preserved in CNHM 158 (Fig. 5e). The hypural fan is multifurcated and consists of coalesced hypurals 1–4 that are joined at the base. The parhypural is broad and bifurcated distally. The epural is massive. There are 17 caudal-fin rays. Anđelković (1966) reported 15 caudal-fin rays in the description, but 17 are reported in the accompanying table. In our assessment, the caudal fin may be incomplete along its dorsal margin.

Median fins. The dorsal fin originates just above the anterior margin of the upper eye and contains 57–62 rays. The anterior configuration of the dorsal fin is characterized by a relatively short and nearly straight erisma reaching the posterior third of the dorsal margin of the neurocranium, one or two pterygiophores lying on the erisma, three or four pterygiophores inserting on the neurocranium and a single pterygiophore associated to the neural spine of the second abdominal vertebra. Therefore, the resulting anterior dorsal pterygiophore formula ranges from 1 – 3 – 1 to 2 – 4 – 1. The anal fin contains 45–48 rays. The first anal-fin pterygiophore is elongate and curved and articulates with the haemal spine of the first caudal vertebra. Five subsequent pterygiophores insert in the space between the first anal-fin pterygiophore and the first haemal spine, and one or two occupy the first interhaemal space, resulting in an anterior anal pterygiophore formula of 1 – 5 – 1 or 2. The dorsal- and anal-fin rays are relatively short and uniformly developed reaching a length of about 8.0 to 10.7% SL.

Paired fins and girdles. The pectoral fin and girdle are incompletely preserved. The pectoral fin contains five preserved short rays measuring about 5.5–6.3% SL. However, Anđelković (1966) reported the presence of eight pectoral-fin rays, which we cannot verify. The long and slender cleithrum and the coracoid are well preserved in the two specimens from Dolje. The basipterygia are long and slender distally and slightly expanded proximally. There are six short pelvic-fin rays, reaching about 3.2–3.8% SL.

Otolith (Fig. 6a–g). The right and left otolith are preserved in situ in CNHM 158 (Fig. 6a) and the left otoliths is exposed in both CNHM 278 (Fig. 6b) and RGFAJ 32 (Fig. 6c). The otoliths of the Dolje specimens are very fragile and the area which bears the sulcus is often somewhat damaged because it is slightly elevated above the remainder of the inner face. The otolith outline is circular to subcircular with a ratio OL:OH ranging from 1.05 to 1.25. The otoliths of the right side are more elongate than those of the left side. The largest specimen found in situ is 1.15 mm long (CNHM 158 at 52 mm SL, fig. 6a3, 6a6); the largest isolated otolith is 2.1 mm long (Fig. 6d). The index OH:OT ranges from 2.5 to 3.0. The rounded outline is quite irregular, sometimes with variably

spaced rounded postdorsal and postventral angles. The inner face is almost flat in left otoliths, with an elevated area around the sulcus (figs. 6a5, 6f2), and slightly convex towards the margins in right otoliths (fig. 6g2). The sulcus is extremely small and narrow, terminating far from the anterior rim of the otolith and towards the rear extending only slightly across the middle of the otolith. The index OL:SuL ranges from 2.2 to 3.0. The ostium is slightly longer than the cauda, but the distinction of these parts is often problematic, depending entirely on the margin existing between the slightly deepened colliculi. A very broad circumsulcal depression runs closely around the entire sulcus except for its anterior margin; its outer margin is gradual. The outer surface is more convex than the inner face in left otoliths and nearly flat in right otoliths.

Isolated otoliths with this very characteristic morphology have been found but not yet published in the middle Sarmatian sediments of Jurkino, Crimea. A publication about this rich otolith assemblage is in progress by Bratishko & Schwarzhans. The size of the isolated otoliths indicates that *Parasolea serbica* would have reached sizes of at least 100 mm SL. Extant specimens of related genera may reach lengths of about 200–300 mm SL.

Discussion: For differential diagnosis and comparison with extant soleids see the discussion about *Parasolea* above (monotypic genus). The holotype of *Parasolea serbica* is a well-preserved specimen (RGFAJ 241) with the anterior dorsal-fin pterygiophore formula and erisma morphology identical to those of the specimens described herein. It also shows a close similarity in vertebrae and dorsal- and anal-fin ray counts. The urohyal unfortunately is not recognizable. *Buglossodium apsheronkiense* Bannikov 2001 from the Early Miocene of the southern Russia is a slender fish with 43 vertebrae (9 + 34), at least 76 dorsal-, 63 anal- and 20 caudal-fin rays. The anal fin originates anteriorly to the first anal-fin pterygiophore. The anterior dorsal pterygiophore formula is 2 – 4 – 1 and shows a nearly straight and short erisma (see Bannikov 2010). *Solea proocellata* Arambourg 1927 from the Messinian of the Mediterranean has 34 vertebrae (9 + 25) according to D'Erasmus (1930) and the coeval *Microchirus abropteryx* (Sauvage 1870) 36 vertebrae (10 + 26) and 68–72 dorsal-fin rays. A number of extant soleid taxa have also been described from the Messinian of the Mediterranean area by Landini (1981), including *Solea* cf. *solea* (Linnaeus 1758) (as *Solea* cf. *vulgaris*), *Buglossidium luteum* (Risso 1810) (as *Solea lutea*) and *Monochirus hispidus*.

Conclusions

This represents the final section of our series of studies on Sarmatian fishes from the Paratethys with otoliths in situ, in this case dealing with pleuronectiform fishes. Two of the

three species described herein can be linked to isolated otoliths and one of them, the otolith-based species *Arnoglossus? tenuis* (Schubert 1906), is synonymized with a skeleton-based species *Arnoglossus bassanianus* (Kramberger 1883). The generic allocation of this species remains provisional until a much detailed morphological revision of the extant species of the genus has been performed. Its otoliths indicate that it could even represent an extinct endemic Paratethyan genus (Bratishko et al. 2015). The second bothid species, *Bothus parvulus* (Kramberger 1883), exhibits certain unusual characters which are not shared with any of the extant and fossil bothid fishes, such as the series of large peripherally ctenoid scales along the bases of the dorsal and anal fins and a kink at the bases of the anteriormost neural spines. However, both available specimens are very small and probably juveniles or sub-adults and hence the phylogenetic relevance of these characters is uncertain. *Parasolea serbica* (Anđelković 1966) finally, a species originally assigned to the Bothidae, represents an extinct endemic Paratethyan soleid taxon. This find expands the number of the known endemic taxa that flourished during the Miocene in the Paratethyan realm (see Baykina and Schwarzhans 2016a, b; Schwarzhans et al. 2016a, b) providing evidence of the dynamic evolution that took place shortly after the separation of the Paratethys from the world oceans. Integration of skeleton-based and otolith-based data again were found to be very helpful in the recognition of these endemic taxa.

Another aspect observed here as well as in previous studies concerns the fact that most articulated fish skeletons found in Sarmatian deposits document small fishes or even juvenile individuals. In the case of the pleuronectiforms investigated here, isolated otoliths indicate that most species involved must have reached sizes of at least twice that of the largest articulated skeletons available. However, otolith assemblages in many instances are also dominated by small specimens deriving from small-sized fishes and those of large specimens can be very rare (Schwarzhans et al. 2015, 2016b; Weiler 1943). As far as the otoliths are concerned, the predominance of small specimens is not uncommon and is probably related to the abundance of juvenile and small fishes representing the prey of larger predators. In any case, the abundance of small articulated fish skeletons might have a different explanation and is not fully understood. Carnevale et al. (2006) hypothesized about the possibility of a dwarfed early Sarmatian fish fauna. Even though isolated otoliths point to fish sizes that is at least twice the observed sizes of articulated skeletons, the resulting maximum sizes would often still be significantly less than those of the majority of the related extant fish species (see discussion to *Arnoglossus bassanianus*, Bratishko et al. 2015 and Schwarzhans et al. 2016b, 2017).

Acknowledgements We wish to thank B. Chanet (Paris) most cordially for his many contributions to this article during its early phase and the many advices and insights without which this manuscript would have been impossible to generate. Unfortunately, it was impossible for Bruno to participate as co-author. New photographs of the holotype of *Parasolea serbica* were kindly provided by Lj. Rundić (Belgrade). We are thankful for support in respect to comparative Recent material to J. Nielsen and P. Møller (Copenhagen) and A. Allen and S. Morrison (Perth), and A. Bratishko (Tallahassee) for making photographs of comparative fossil otoliths available. The research of GC was supported by grants (ex-60% 2015 and 2016) from the Università degli Studi di Torino. We thank A. Bannikov (Moscow) and an anonymous reviewer for their recommendations during the reviewing process.

References

- Amaoka, K. (1969). Studies on the sinistral flounders found in the waters around Japan—taxonomy, anatomy and phylogeny. *Journal of the Shimonoseki University of Fisheries*, 18, 58–340.
- Andelković, J. (1962). Beitrag zur Kenntnis von untersarmatischen Fischen des Gebietes von Beograd. *Annales Géologiques de la Péninsule Balkanique*, 29, 115–127. (in Serbian, German Resume).
- Andelković, J. (1966). *Rhombus serbicus* n. sp. from the lower Sarmatian of Serbia. *Annales Géologiques de la Péninsule Balkanique*, 32, 179–184.
- Andelković, J. (1969). Fosilne ribe iz donjeg sarmata teritorije Beograda. *Glasnik Prirodjačkog Muzeja, A*, 24, 127–154. (in Serbian).
- Andelković, J. (1970). Tertiary fishes of Serbia. *Annales Géologiques de la Péninsule Balkanique*, 35, 281–365. (in Serbian, English Resume).
- Andelković, J. (1989). Tertiary fishes of Yugoslavia. Stratigraphic-Paleontologic-Paleoecological study. *Palaeontologia Yugoslavica*, 38, 1–121.
- Arambourg, C. (1927). Les poissons fossiles d'Oran. *Materiaux pour la Carte géologique de l'Algérie, 1er Série—Paleontologie*, 6, 1–218.
- Bannikov, A. (2010). *Fossil vertebrates of Russia and adjacent countries. Fossil Acanthopterygian fishes (Teleostei, Acanthopterygii)* (pp. 1–244). Moscow: Russian Academy of Sciences, Borissiak Paleontological Institute, Geos (in Russian).
- Baykina, E.M. & Schwarzhans, W. (2016a). Description of *Karaganops* n. gen. *perrata* (Daniltschenko, 1970) with otoliths in situ, an endemic Karaganian (Middle Miocene) hering (Clupeidae) in the Eastern Paratethys. *Swiss Journal of Palaeontology*. doi:10.1007/s13358-016-0115-4
- Baykina, E.M. & Schwarzhans, W. (2016b). Review of “*Clupea humilis*” from the Sarmatian of Moldova and description of *Moldavichthys switshenskiae* gen. et sp. nov. *Swiss Journal of Palaeontology*. doi:10.1007/s13358-016-0121-6
- Bratishko, A., Schwarzhans, W., Reichenbacher, B., Vemihorova, Y., & Ćorić, S. (2015). Fish otoliths from the Konkian (Miocene, early Serravallian) of Mangyshlak (Kazakhstan)- testimony of an early endemic evolution in the Eastern Paratethys. *Paläontologische Zeitschrift*, 89, 839–889.
- Carnevale, G., Bannikov, A. F., Landini, W., & Sorbini, C. (2006). Volhynian (early Sarmatian sensu lato) fishes from Tsurevsky, North Caucasus, Russia. *The Paleontological Society*, 80, 684–699.
- Chanet, B. (1996). Osteology of *Solea kirchbergeana* (von Meyer 1848): a soleid fossil fish from the Lower Miocene of Germany and Switzerland. Phylogenetical implications. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 201, 133–144.
- Chanet, B., Chapleau, F., & Desoutter, M. (2004). Os et ligaments intermusculaires chez les poissons plats [Teleostei: Pleuronectiformes]: interprétations phylogénétiques. *Cybium*, 28, 5–8.
- Chanet, B., & Schultz, O. (1994). Pleuronectiform fishes from the Upper Badenian (Middle Miocene) of St. Margarethen (Austria). *Annalen des naturhistorischen Museums in Wien*, 96A, 95–115.
- Chapleau, F. (1989). Étude de la portion supracrânienne de la nageoire dorsale chez les Soleidae (Téléostéens, Pleuronectiformes). *Cybium*, 13, 271–279.
- Chapleau, F., & Keast, A. (1988). A phylogenetic reassessment of the monophyletic status of the family Soleidae, with comments on the suborder Soleioidei (Pisces; Pleuronectiformes). *Canadian Journal of Zoology*, 66, 2797–2810.
- D'Erasmo, G. (1930). Studi sui pesci Neogenici d'Italia; III. L'ittiofauna fossile del Gabbro. *Atti della R. Accademia delle Scienze fisiche e matematiche di Napoli, Memoria*, 18 (Serie 2, n. 6), 1–116.
- Desoutter, M. (1987). Statut de *Microchirus boscanion* Chabanaud, 1926 et de *Buglossidium luteum* (Risso, 1810) (Pisces, Pleuronectiformes, Soleidae). *Cybium*, 11, 427–439.
- Desoutter, M. (1994). Révision des genres *Microchirus*, *Dicologlossa* et *Vanstraelenia* (Pleuronectiformes, Soleidae). *Cybium*, 18, 215–249.
- Djafarova, J.D. (2006). *Otolity neogena Azerbaidjana (Neogene otoliths of Azerbaijan)*. Baku, Nafta press, 168 pp. (in Russian).
- Gaudant, J., Courme-Rault, M.-D., Fornaciari, E., & Fourtanier, E. (2010). The Upper Miocene fossil fish locality of Pecetto di Valenza (Piedmont, Italy): a multidisciplinary approach. *Bollettino della Società Paleontologica Italiana*, 49, 203–225.
- Koken, E. (1891). Neue Untersuchungen an tertiären Fisch-Otolithen II. *Zeitschrift der Deutschen geologischen Gesellschaft*, 43, 77–170.
- Kramberger, D. (1883). Die jungtertiäre Fischfauna Croatiens II. *Beiträge zur Paläontologie Österreich-Ungarns und des Orients*, 3, 65–85.
- Landini, W. (1981). I Pleuronectiformi (Pisces Teleostea) fossili del Neogene Italiano. *Atti Società Toscana di Scienze Naturale, Memoria, Serie A*, 88, 1–41.
- Norman, J.R. (1934). *A systematic monograph of the flatfishes (Heterosomata); Vol. I: Psettodidae, Bothidae, Pleuronectidae*. The Trustees of the British Museum, London, 459 pp.
- Patterson, C., & Johnson, G. D. (1995). The intermuscular bones and ligaments of teleostean fishes. *Smithsonian Contributions to Zoology*, 559, 1–83.
- Pobedina, V. M. (1954). Iskopaemye otolithy ryb miocenovykh otlozheniy Azerbaidjana i ih stratigraficheskoe znachenie (Fossil fish otoliths from the Miocene deposits of Azerbaijan and their stratigraphical significance). *Izvestia Akademii Nauk Azerbaidjanskoy SSR*, 10, 23–37. (in Russian).
- Schubert, R. J. (1906). Die Fischotolithen des österr.-ungar. Tertiärs. III. *Jahrbuch der kaiserlich-königlichen Geologischen Reichsanstalt*, 56, 623–706.
- Schwarzhans, W. (1978). Otolith-morphology and its usage for higher systematical units, with special reference to the Myctophiformes s.l. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, 15, 167–185.
- Schwarzhans, W. (1999). A comparative morphological treatise of recent and fossil otoliths of the order Pleuronectiformes. *Piscium Catalogus, Otolithi Piscium*, 2, 1–391.
- Schwarzhans, W., Ahnelt, H., Carnevale, G., Japundžić, S., Bradić, K., & Bratishko, A. (2016b). 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*. doi:10.1007/s13358-016-0120-7.
- Schwarzhans, W., Bradić, K., & Lj. Rundić. (2015). Fish-otoliths from the marine-brackish water transition from the Middle

- Miocene of the Belgrade area, Serbia. *Palaontologische Zeitschrift*, 89(4), 815–837.
- Schwarzahns, W., Carnevale, G., Bratishko, A., Japundžić, S. & Bradić, K. (2016a). Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part II: Gadidae and Lotidae. *Swiss Journal of Palaeontology*. doi:[10.1007/s13358-016-0114-5](https://doi.org/10.1007/s13358-016-0114-5).
- Schwarzahns, W., Carnevale, G., Japundžić, S. & Bradić, K. (2017). Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part IV: Scorpaenidae, Labridae and Gobiesocidae. *Swiss Journal of Palaeontology*. doi:[10.1007/s13358-017-0124-y](https://doi.org/10.1007/s13358-017-0124-y).
- Vacheron, J., Chapleau, F., & Desoutter-Meniger, M. (2008). Révision taxinomique du genre *Solea* et réhabilitation du genre *Barnardichthys* (Soleidae; Pleuronectiformes). *Cybium*, 32, 9–26.
- Weiler, W. (1942). Die Otolithen des rheinischen und nordwest-deutschen Tertiärs. *Abhandlungen des Reichsamts für Bodenforschung, Neue Folge*, 206, 5–140.
- Weiler, W. (1943). Die Otolithen aus dem Jungtertiär Süd-Rumäniens; 1. Buglow und Sarmat. *Senckenbergiana lethaea*, 26, 87–115.
- Weiler, W. (1955). Untersuchungen an der Fischfauna von Unter- und Ober-Kirchberg bei Ulm, vornehmlich an Hand von Otolith in situ. *Paläontologische Zeitschrift*, 29, 88–102.