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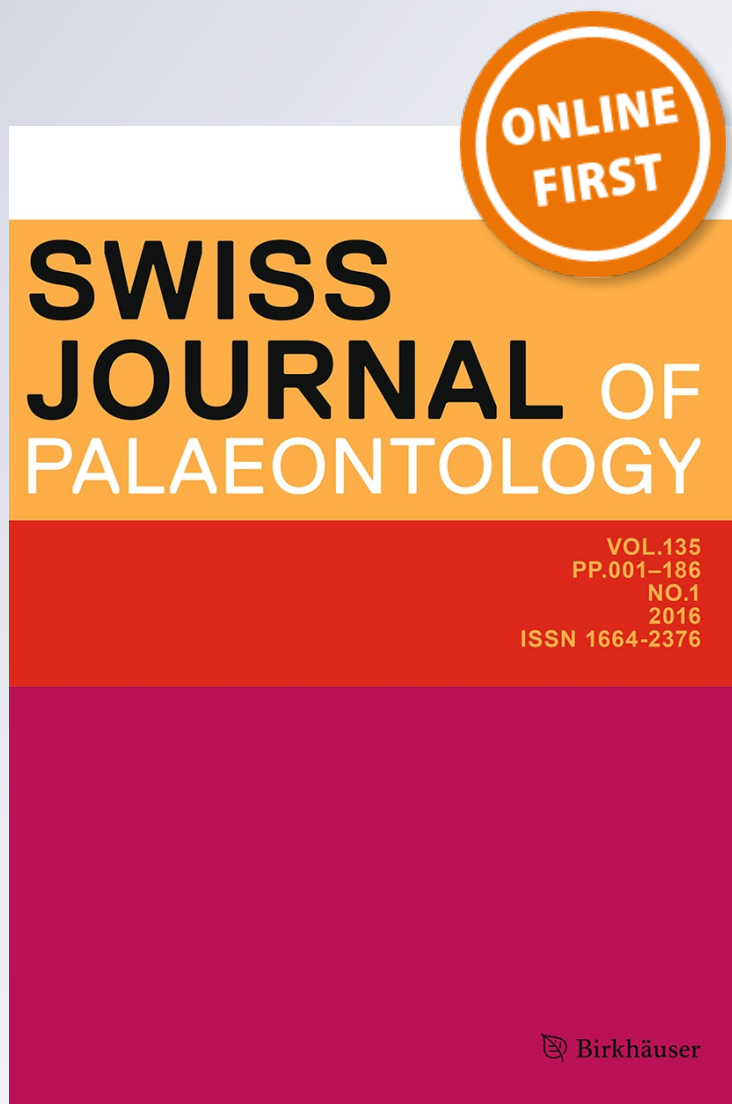
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**Swiss Journal of Palaeontology**

ISSN 1664-2376

Swiss J Palaeontol

DOI 10.1007/s13358-016-0114-5



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# Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part II: Gadidae and Lotidae

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Received: 9 January 2016 / Accepted: 1 March 2016  
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**Abstract** Gadid otoliths are among the most common otoliths in the Neogene of Europe. To date, these have been recorded in situ and therefore correlated with the skeletal record only in two cases, *Paratrisopterus avus* and *Palimphemus anceps*. Here, we describe otoliths in situ from three gadiform taxa from the Sarmatian of the Central Paratethys—*Palimphemus macropterygius*, *Paratrisopterus caspius* and *Enchelyopus susedanus*. A number of specimens previously described by Kramberger (Paläontol. Österr.-Ungar. und des Orients 3:65–85, 1883) and Andjelković (Glas. Prir. Muz. A 24:127–154, 1969) are revised. Kramberger's *Morrhua macropterygia* is reassigned to the extinct gadid genus *Palimphemus*; moreover, *Morrhua lanceolata* is considered a junior synonym of *P. anceps* Kner 1862. All the *Palimphemus* specimens studied from the Sarmatian of the Central Paratethys belong to *P.*

*macropterygius*, while *P. anceps* does not seem to be present in the Paratethys after the late Badenian/Konkian. The otolith-based species *Palimphemus minusculoides* (Schubert 1912) is considered as a junior synonym of *P. macropterygius*. *Paratrisopterus caspius* is regarded as a senior synonym of *P. avus* Fedotov 1971, whose otoliths in situ were previously described by Fedotov (1976). The new data allow further synonymization of otolith-based species, such as *P. insectus* (Weiler 1943) and possibly also *P. irregularis* (Gaemers 1973). Moreover, *Properca sabbai* Pauca 1929 is removed from the faunal list of Sarmatian fishes in the Paratethys. Kner's *Brosmius susedanus* is reassigned to the extant lotid genus *Enchelyopus*, with *Brosmius elongatus* Kramberger 1883 representing a junior synonym. There is no record of isolated otoliths correlating with *E. susedanus* in the literature; however, a number of previously undescribed specimens of *E. susedanus* have been identified from the middle Sarmatian s.l. of Jurkino, Crimea.

Editorial handling: L. Cavin & D. Marty.

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**Keywords** Gadidae · Lotidae · *Palimphemus* · *Paratrisopterus* · *Enchelyopus* · Otoliths in situ

## Introduction

This is the third study dealing with the otoliths in situ from Sarmatian fishes of the Paratethys. The first of these was devoted to the Atherinidae (Schwarzhans et al. 2016), and the second one to clupeid fishes (Baykina and Schwarzhans 2016).

Skeletal remains and otoliths of the families Gadidae and, to a lesser extent, of the Lotidae are among the most common teleosts in the Middle Miocene of the Central and Eastern Paratethys. During the early Badenian, most of the gadid otoliths of the Central Paratethys also occurred in the

North Sea Basin (*Palimphemus anceps*, *Gadiculus argenteus*, *Paratrisopterus labiatus*) (Schwarzahns 2010; Nolf 2013), where they are the dominant teleosts. In the Central and Eastern Paratethys, gadid and lotid fishes become really abundant only during the Sarmatian, as clearly testified by articulated skeletons and otoliths. *Paratrisopterus avus* and *P. anceps* were the first cases of Neogene fossil gadids for which articulated skeletons with otoliths in situ became known (Fedotov 1976; Schwarzahns 2014).

Several nominal skeleton- and otolith-based gadid and lotid species have been described from the Sarmatian s.s. of the Central Paratethys and the Sarmatian s.l. to Pontian of the Eastern Paratethys (see below). A thorough revision of both skeletal and otolith data, when possible, would likely reduce the large number of established taxa in this group, even if this is beyond the scope of this study. Our aim is to provide link between skeletal and otolith finds as much as possible, and for this reason we restrict our efforts to review the taxa with otoliths in situ. Nevertheless, below we list the key data for all relevant taxa from the Sarmatian and younger strata of the Central and Eastern Paratethys in order to provide a general overview, and add short comments on their current status. The list follows the sequence of description of the individual species, first skeletons, then otoliths, with their original designation.

### Annotated list of skeleton-based Gadidae

*Palimphemus anceps* Kner 1862: Middle Miocene, late Badenian of St. Margarethen, Austria. Recently reviewed and re-described by Carnevale et al. (2012); otoliths in situ described in a specimen from the middle Badenian of Poland by Schwarzahns (2014), including synonymization of several otolith-based species, notably *Colliolus sculptus* (Koken 1891).

*Morrhua aeglefinoides* Kner & Steindachner 1863: Middle Miocene (late Badenian or Sarmatian s.s.) of Podsused, Croatia. In need of revision; based on the meristic data provided in the original description, it appears to be a species of the genus *Trisopterus*.

*Morrhua szagadatensis* Steindachner 1863: Middle Miocene, Sarmatian s.s. of Zagorje ob Savi (Szakadát, Sagor), Slovenia. In need of revision; based on the short description by Steindachner, it appears to be a problematic taxon based on an incomplete specimen.

*Morrhua lanceolata* Kramberger 1883: Middle Miocene (late Badenian or Sarmatian s.s.) of Podsused, Croatia. Holotype reviewed in this study and considered as a junior synonym of *Palimphemus anceps*.

*Morrhua macropterygia* Kramberger 1883: Middle Miocene, Sarmatian s.s. of Dolje, Croatia. Holotype and syntypes reviewed in this study and considered as a valid species of the genus *Palimphemus*.

*Morrhua extensa* Kramberger 1885: Sarmatian s.s. of Zagorje ob Savi (Szakadát, Sagor), Slovenia. In need of revision.

*Morrhua minima* Kramberger 1885: Middle Miocene (late Badenian or Sarmatian s.s.) of Podsused, Croatia. Kramberger mentioned about 16 specimens, none of which could be located at CNHM. Based on the meristic data provided in the original description, this is probably a species of the extinct genus *Paratrisopterus*.

*Gadus caspius* Bogatshov 1929: Late Miocene, middle to late Sarmatian s.l. of Azerbaijan. The two type specimens are probably lost. Based on the original description by Bogatshov, the species is considered herein as *Paratrisopterus caspius*.

*Gadus kiplingi* Bogatshov 1929: Middle to late Miocene, middle to late Sarmatian s.l. of Azerbaijan. The type specimens are probably lost. Based on the original description by Bogatshov, the species can be considered as a species of the extinct genus *Paratrisopterus*.

*Gadus kwitkae* Bogatshov 1933: Middle to late Miocene, Pontian of Azerbaijan. The type specimen is probably lost. Based on the original description by Bogatshov, it probably represents a species of the genus *Gadiculus*.

*Paratrisopterus avus* Fedotov 1971: Middle Miocene, Sarmatian s.l. of Moldavia. Reviewed by Prokofiev (2004) and considered valid as *Gadiculus avus*. Fedotov (1976) provided a figure of an otolith found in situ in the holotype, but Prokofiev (2004) could not locate the otolith. In this study, the genus *Paratrisopterus* is considered valid and the species is considered as a junior synonym of the otolith-based species *Paratrisopterus insectus* (Weiler 1943) and also of the skeletal-based species *P. caspius* (Bogatshov 1929).

### Annotated list of otolith-based Gadidae

*Otolithus (Gadidarum) minusculus* Schubert 1906: Middle Miocene, late Burdigalian and Sarmatian s.s. of localities in Slovakia and Hungary. Reviewed by Nolf (1981) who selected a lectotype and rejected the species because of inadequate preservation and non-diagnostic juvenile status of the specimens. Bratishko et al. (2015) considered the lectotype as a juvenile of *Palimphemus anceps*.

*Otolithus (Gadidarum) minusculoides* Schubert 1912: Middle Miocene, Sarmatian s.s. of Hungary. Reviewed by Nolf



(1981) and rejected because of inadequate preservation of the type specimen. Re-established and re-described by Bratishko et al. (2015) as *Palimphemus minusculoides*; considered herein as a junior synonym of *Palimphemus macropterygius*.

*Otolithus (Gadidarum) insectus* Weiler 1943: Middle Miocene, late Badenian of Melicesti, Romania. Reviewed by Nolf (1985), Schwarzahns (2010) and in this study, and considered as a junior synonym of *Paratrisopterus caspius*.

*Macrurus rumanus* Weiler 1943: Middle Miocene, late Badenian of Melicesti and Sciaosi, Romania. Reviewed by Nolf (1985) who considered it as a doubtful taxon; Schwarzahns (2010) considered it valid as *Paratrisopterus rumanus*.

*Macrurus dorsolobatus* Weiler 1943: Middle Miocene, late Badenian of Melicesti, Romania. Reviewed by Nolf (1985) who considered it as a doubtful species based on a not interpretable juvenile holotype; considered as a synonym of *Paratrisopterus rumanus* by Schwarzahns (2010).

*Macrurus altus* Weiler 1943: Middle Miocene, late Badenian of Sciaosi, Romania. Reviewed by Nolf (1985) who considered it as a doubtful species based on not interpretable juvenile specimens.

*Macrurus rhombicus* Weiler 1943: Middle Miocene, late Badenian of Melicesti, Romania. Reviewed by Nolf (1985) who considered it as a doubtful species based on not interpretable juvenile specimens; it has been considered as a synonym of *Paratrisopterus rumanus* by Schwarzahns (2010).

*Macrurus rotundus* Weiler 1943: Middle Miocene, late Badenian of Melicesti, Romania. Reviewed by Nolf (1985) who considered it as a doubtful species because of the juvenile nature of the specimens; considered as a synonym of *Paratrisopterus rumanus* by Schwarzahns (2010).

*Otolithus (Macruridarum) acuminatus* Weiler 1943: Middle Miocene, late Badenian of Sciaosi, Romania. Reviewed by Nolf (1985) who considered it as a doubtful species based on not interpretable juvenile specimens; reviewed in this study and considered as a synonym of *Paratrisopterus caspius*.

*Otolithus (Macruridarum) ovalis* Weiler 1943: Middle Miocene, late Badenian of Sciaosi, Romania. Reviewed by Nolf (1985) who considered it as a doubtful species based on not interpretable juvenile specimens; reviewed in this study and considered as a synonym of *Paratrisopterus caspius*.

*Macrurus obliquus* Weiler 1950: Middle Miocene, late Badenian of Sciaosi, Romania. Reviewed by Nolf (1985) who considered it as a doubtful species based on not interpretable juvenile specimens; considered as a synonym of *Paratrisopterus rumanus* by Schwarzahns (2010).

*Macrurus simplex* Smigielska 1966: Middle Miocene, late Badenian of Gliwice, Poland. Considered as a doubtful species based on not interpretable juvenile specimens by Nolf (1985); considered as a synonym of *Paratrisopterus rumanus* by Schwarzahns (2010).

*Macrurus planus* Smigielska 1966: Middle Miocene, late Badenian of Gliwice, Poland. Considered as a doubtful species based on not interpretable juvenile specimens by Nolf (1985); considered as a junior synonym of *Paratrisopterus rumanus* by Schwarzahns (2010).

*Macrurus dorsoconcavus* Smigielska 1966: Middle Miocene, late Badenian of Gliwice, Poland. Considered as a doubtful species based on not interpretable juvenile specimens by Nolf (1985); considered as a junior synonym of *Paratrisopterus rumanus* by Schwarzahns (2010).

*Otolithus (Gadidarum) angustus*; Suzin 1968 (in Zhizhchenko): Middle Miocene, middle Sarmatian s.l. of Crimea and northern Caucasus. Name not available according to ICZN article 13.1.1.; considered as a synonym of *Palimphemus minusculoides* by Bratishko et al. (2015).

*Otolithus (Gadidarum) labiatiformis* Suzin 1968 (in Zhizhchenko): Middle Miocene, middle Sarmatian s.l. of Crimea and northern Caucasus. Name not available according to ICZN article 13.1.1.; likely a synonym of *Paratrisopterus caspius*.

### Annotated list of skeleton-based Lotidae

*Brosmius susedanus* Kner 1863: Middle Miocene (late Badenian or Sarmatian s.s.) of Podsused, Croatia. Non-type specimens reviewed in this study; species considered valid as *Enchelyopus susedanus*.

*Brotula longipinnata* Kramberger 1880: Middle Miocene, Sarmatian s.s. of Moravia. Considered as a species of the genus *Brosmius* by Andjelković (1989). Taxon in need of revision.

*Brosmius elongatus* Kramberger 1883: Middle Miocene, Sarmatian s.s., Dolje, Croatia. Reviewed in this study and considered as a junior synonym of *E. susedanus*.

*Brosmius fuchsianus* Kramberger 1883: Middle Miocene (late Badenian or Sarmatian s.s.) of Podsused, Croatia. Type specimen not located at CNHM; Problematic taxon in need of revision.

*Brosmius strossmayeri* Kramberger 1883: Late Miocene, Pannonian of Fruska Gora (Beocin), Serbia. A very large and incomplete holotype analyzed in this study and considered problematic.

*Gaidropsarus pilleri* Carnevale and Harzhauser, 2013: Middle Miocene, late Badenian of St. Margarethen, Austria.

### Annotated list of otolith-based Lotidae

*Otolithus (Crenilabrus) simplicissimus* Schubert 1906: Middle Miocene, late Burdigalian and Sarmatian s.s. of Slovakia. Reviewed by Nolf (1981) who selected a lectotype and rejected the species because of inadequate preservation and non-diagnostic juvenile status of the specimens. Bratishko et al. (2015) re-validated and re-described the species as *Onogadus simplicissimus*.

*Bodianus josephinae* Strashimirov 1984: Middle Miocene, Sarmatian s.l. of Tolbuhin, Bulgaria. Considered as a junior synonym of *Onogadus simplicissimus* by Bratishko et al. (2015).

### Materials and methods

Nine gadid and lotid specimens with otoliths in situ were found in the collection of the Croatian Natural History Museum, Zagreb (CNHM), belonging to the species *Palimphemus macropterygius* and *Enchelyopus susedanus*; three specimens with otoliths in situ belonging to *Paratrisopterus caspius* were found in the collection of the Chair of Historical Geology, Department of Regional Geology, Faculty of Mining and Geology, University of Belgrade (RGF) under the collection registration AJ (referring to the collection of Jelena Andjelković). The specimens were originally identified as *Morrhua macropterygia* and *M. lanceolata* by Gorjanović-Kramberger, *Brosmius susedanus* by Kner (holotype) and Gorjanović-Kramberger (non-types) according to the files of CNHM and *Gadus lanceolatus* and *Properca sabbai* by Andjelković (1969, 1989). Other species reviewed in the course of this study are the skeletal-based taxa *Morrhua lanceolata*, *Brosmius elongatus* and *B. strossmayeri*, and the otolith-based taxa *Palimphemus minusculoides*, *Paratrisopterus insectus*, *P. acuminatus* and *P. ovalis*. Another gadid fish specimen with otolith in situ was revisited from the Sarmatian s.l. of Tsurevsky, southern Russia, formerly described as *Micromesistius* sp. by Carnevale et al. (2006) and considered herein as a species of the fossil genus *Palimphemus* as also reported by Bannikov and Kotlyar (2015).

All the specimens with otoliths in situ housed at the CNHM are from the Sarmatian s. s. (Vohlynian) deposits cropping out near Dolje, north of Zagreb. They are preserved in a finely laminated diatomite. The bones of the individual specimens are relatively well preserved, even if preparation is extremely difficult due to the brittle nature of

the matrix. The delicate otoliths are difficult to extract from the matrix due to their weak mineralization. As a consequence, the otoliths were left in their in situ position as much as possible, particularly when their inner surface is exposed, and were carefully extracted when necessary. The RGF specimens with otoliths in situ were collected from temporary excavations in 1961–1962 during the renovation of the football stadium 'Red Star' in Belgrade. The fishes are embedded in a relatively hard grey mudstone and the preparation of the bones again is very difficult. In contrast, otoliths are well preserved and relatively easy to extract, but extracted otoliths are difficult to clean from the attached sediment or skeletal material. In any case, otoliths are left in situ as much as possible and the extraction was attempted only, when the inner surface was not exposed.

The morphological terminology of otoliths was established by Koken (1891) modified by Weiler (1942) and Schwarzzhans (1978). Abbreviations: general: vs = versus, HT = holotype; skeletons: SL = standard length, TL = total length, HL = head length, VE = vertebrae, D = dorsal fin rays (including D1, D2 and D3 as the case may be), A = anal fin rays (including A1 and A2 as the case may be), P = pectoral fin rays, V = pelvic fin rays, C = principal caudal fin rays; Roman numbers indicate fin spines, Arabic numbers indicate branched soft rays; otoliths: OL = otolith length, OH = otolith height, OT = otolith thickness, SuL = sulcus length, SuH = sulcus height, OsL = ostium length, OCL = ostial colliculum length, CoL = collum length, CaL = cauda length, CCL = caudal colliculum length.

### Systematic paleontology

Order Gadiformes Goodrich 1909

Family Gadidae Rafinesque 1810

Genus †*Palimphemus* Kner 1862

The fossil genus *Palimphemus* was redefined by Carnevale et al. (2012) and considered to contain the type species *P. anceps* only. The observation of otoliths in situ in a specimen of *P. anceps* allowed Schwarzzhans (2014) to include otolith characters to the diagnosis, and to re-assign a number of otolith-based species to the genus *Palimphemus*. Bannikov and Kotlyar (2015) referred specimens identified as *Micromesistius* sp. by Carnevale et al. (2006) from the Sarmatian s.l. of Tsurevsky (northern Caucasus) to the genus *Palimphemus* as well. In the following review, species hitherto recorded as assigned to *Morrhua* or *Gadus* like *Gadus lanceolatus* and *G. macropterygius* are assigned to the genus *Palimphemus*. *Palimphemus lanceolatus* is considered as a junior synonym of *P. anceps*.

As a result, we recognize two, possibly three skeleton-based species within the genus *Palimphemus*, which

consequently require a modification of the diagnosis presented by Carnevale et al. (2012).

**Diagnosis** [modified from Carnevale et al. (2012)] Gadine fish with elongate body; head length about one-third of SL; gape of the mouth wide, extending posteriorly to the mid-length of the orbit; anal-fin insertion well behind the first dorsal-fin origin; preanal distance  $>40\%$  SL, exceeding the base length of the first anal fin; length of the first anal fin base reduced, measuring about  $21\text{--}28\%$  SL;  $41\text{--}46$  ( $12\text{--}18 + 27\text{--}30$ ) vertebrae; first dorsal fin with  $7\text{--}12$  rays; second dorsal fin with  $10\text{--}14$  rays; third dorsal fin with  $14\text{--}21$  rays; first anal fin with  $18\text{--}21$  rays; second anal fin with  $14\text{--}20$  rays; caudal fin with  $38\text{--}43$  rays, possibly as low as 32 in some specimens of *P. macropterygius*; pectoral fin with  $14\text{--}18$  rays; large massive neurocranium, its maximum width measured in the postorbital sector contained less than two times in its length; outer margins of the frontals thickened and ornamented by longitudinal pits and ridges along the ventral surface; premaxilla with short narrow, and anteriorly inclined ascending process, and wide backward inclined articular process of equal height separated from each other by a broad interprocess notch; hyomandibula with a relatively large ventrally directed preopercular process; opercle with a thick horizontal rib arising from the articular condyle; otolith elongate with rounded anterior tip and pointed, tapering posterior tip; its sulcus with moderately wide to wide collum and pseudocolliculum.

**Discussion** Carnevale et al. (2012) extensively discussed the status and different point of views of gadid interrelationships, as well as the possible affinities of the extinct genus *Palimphemus*, suggesting that the general appearance of *Palimphemus* is in many ways reminiscent of that of *Micromesistius* to which it appears to be related. The morphological evidence supporting this relationship consists of a number of shared features, such as lower jaw projecting beyond the upper one, broad separation between the first and second and the second and third dorsal fins, absence of the posterior process of the basiptyrgium, absence of the lower process of the hyomandibula, possession of a moderately elongate postcleithrum, and absence of the lateral flop of the posttemporal. Based on the observations on the specimens of *P. macropterygius* some characters can be added to the list of features shared by *Micromesistius* and *Palimphemus*, including premaxilla with a short, forward bent ascending process not longer than the articular process, and the stout dorsal and ventral prezygapophyses of the caudal vertebrae (see, e.g., Watt et al. 1997).

The characters that clearly separate these two genera remain valid despite the expansion of the diagnosis necessary for the inclusion of *P. macropterygius*. The most

important of these is the longer head ( $28\text{--}33\%$  SL vs  $22\text{--}24\%$  SL), anal-fin insertion located well behind the first dorsal fin associated with a shorter first anal-fin base of  $21\text{--}28\%$  SL (vs  $32\text{--}38\%$  SL) and a longer preanal length ( $43\text{--}47\%$  SL vs  $30\text{--}33\%$  SL), longer predorsal distance ( $35\text{--}39\%$  SL vs  $29\text{--}31\%$  SL), lower number of vertebrae ( $41\text{--}46$  vs  $55\text{--}58$ ), and lower number of first and second anal-fin rays ( $17\text{--}20$  vs  $33\text{--}39$  and  $14\text{--}20$  vs  $24\text{--}27$ , respectively). The distinction between *Palimphemus* and *Trisopterus* remains stable, mainly related to the lower number of vertebrae ( $41\text{--}46$  vs  $47\text{--}52$ ), much shorter second dorsal fin base ( $10\text{--}15\%$  SL vs  $22\text{--}28\%$  SL) with reduced number of fin rays ( $10\text{--}12$  vs  $20\text{--}28$ ), similar differences in head proportions, predorsal and preanal lengths and anal-fin ray counts, and the morphology of the premaxilla with its short forward bent ascending process (vs more upright ascending process being distinctly longer than articular process). Otoliths of *Palimphemus* can be distinguished from those of *Trisopterus* and *Micromesistius* for the presence of a widened collum underpinned by a moderately developed pseudocolliculum (vs no pseudocolliculum). They also differ from those of *Trisopterus* by having a rounded anterior rim (vs dorsally inclined) and the ridge on the outer face being located along the central axis of the otolith (vs close to the ventral rim of the otolith). All of these three genera (plus *Gadiculus* and *Paratrisopterus*) represent distinct and separate lineages since Oligocene times.

*Palimphemus macropterygius* (Kramberger 1883)  
(Figures 1b–k, 2a–d)

1883 *Morrhua macropterygia* Kramberger. Kramberger: pl. 13, Fig. 6.

1906 *Otolithus (Gadidarum) minusculus* Schubert. Schubert (part): pl. 19, Figs. 48, 49, ?50 (non 51, 52) [otolith-based species].

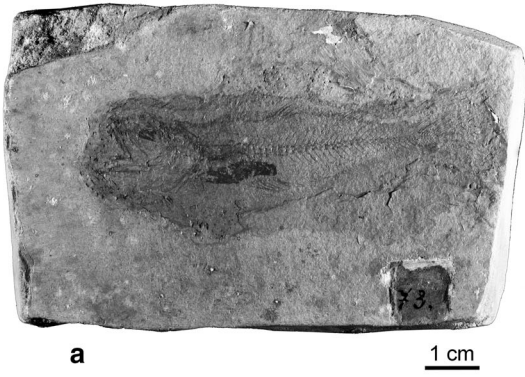
1912 *Otolithus (Gadus) minusculoides* Schubert. Schubert: Fig. 16 [otolith-based species].

non 1933 *Gadus macropterygius* (Kramberger 1883). Bogatshov: pl. 8, Figs. 1–4 (*Palimphemus* sp.).

non 1962 *Gadus macropterygius* (Kramberger 1883). Jerzmanska: Fig. 2 (*P. anceps*).

2015 *Palimphemus minusculoides* (Schubert 1912). Bratishko, Schwarzahns & Reichenbacher: Figs. 4–14 to 4–21 (see also for a comprehensive synonymy listing of otolith-based data).

**Material** Seven specimens from Dolje, Croatia, Sarmatian s.s. (Volhynian): holotype, CNHM 180 (SL 94 mm) (Fig. 1b), plus six referred specimens collected by Kramberger and identified as *M. lanceolata* Kramberger 1883: CNHM 178 (SL 50 mm), CNHM 215 (SL 118 mm), CNHM 218 (SL 54.5 mm), CNHM 219 (60.5 mm), CNHM 270 (incomplete); or *Morrhua* cf. *lanceolata*:



a

1 cm



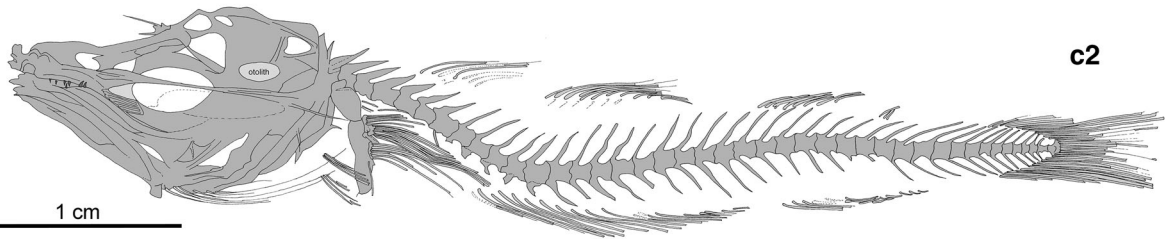
b

1 cm



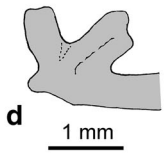
c1

1 cm



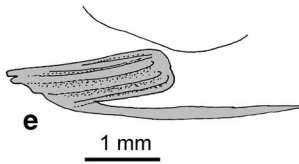
c2

1 cm



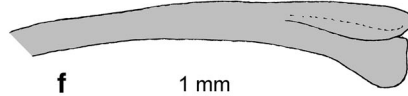
d

1 mm



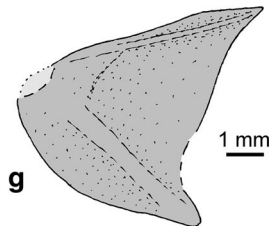
e

1 mm



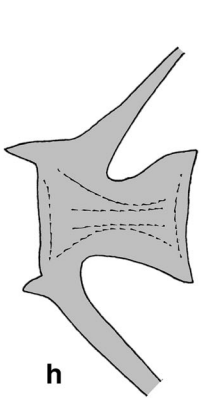
f

1 mm

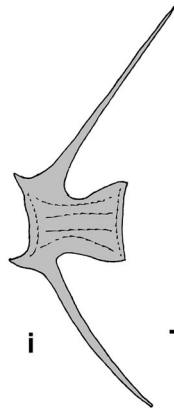


g

1 mm

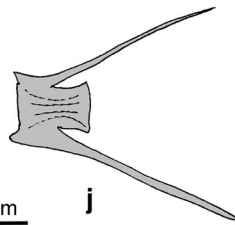


h

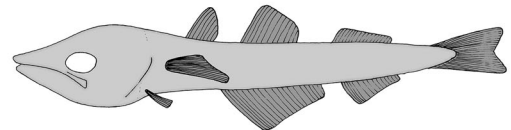


i

1 mm



j



k



**Fig. 1** *Palimphemus anceps* and *Palimphemus macropterygius*. **a** *Palimphemus anceps* Kner 1862, holotype of *M. lanceolata* Kramberger 1883, CNHM 73, late Badenian or early Sarmatian of Podsused, Croatia. **b** Holotype of *Palimphemus macropterygius* (Kramberger 1883), CNHM 180, early Sarmatian of Dolje, Croatia. **c–k** *Palimphemus macropterygius* (Kramberger 1883), early Sarmatian of Dolje, Croatia. **c** CNHM 219 (reversed); **c2** reconstruction of the skeleton. **d** CNHM 219 (reversed), anterior part of premaxilla. **e** CNHM 219 (reversed), lachrymal. **f** CNHM 215, Posterior end of maxilla. **g** CNHM 215, opercle. **h** CNHM 215, anterior caudal vertebra. **i** CNHM 178, mid-caudal vertebra; **j** CNHM 178, posterior caudal vertebra. **k** life reconstruction

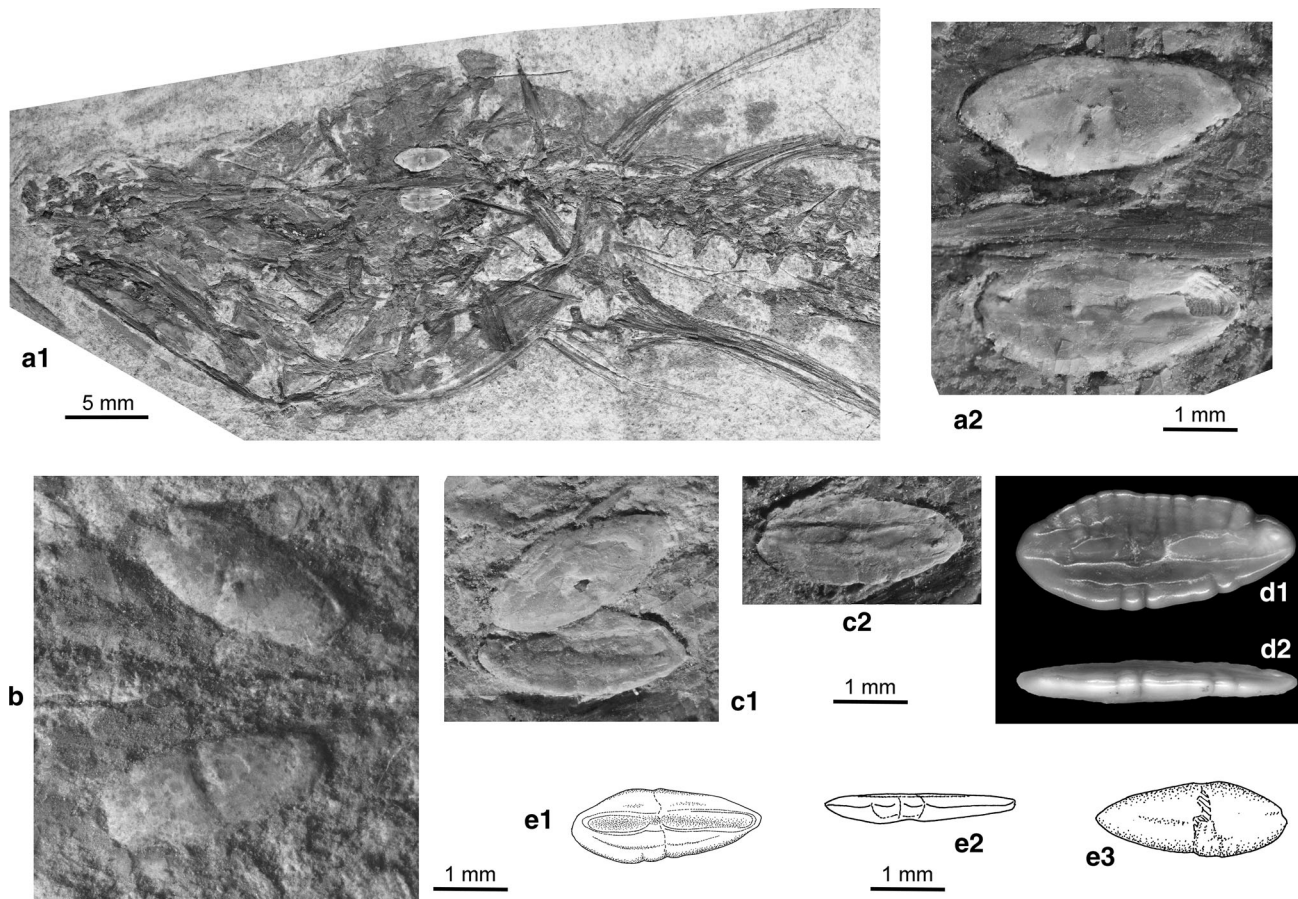
CNHM 172 (SL 56 mm); five of these specimens (including the holotype) contain otoliths in situ.

**Diagnosis** Vertebral column with 41–44 vertebrae of which 12 or 13 abdominal; first dorsal fin with 7 to 8 rays; second anal fin with 14–17 rays; first dorsal-fin base 5 to 6 % SL; pelvic fin very short containing five rays; pectoral fin

reaching the anterior end of the second anal fin; premaxilla and dentary bearing few curved conical teeth; upper jaw projecting slightly anterior than lower jaw; otoliths thin, elongate, and flat; sulcus with broad collum, and ventrally expanded and elongate pseudocolliculum.

**Description** (based primarily on CNHM 219, Figs. 1c–e, k): body elongate and moderately compressed laterally judging from the variable orientation of the fish imprints. Counts and measurements are reported in Table 1.

**Neurocranium** The head bones are extremely crushed in all the examined specimens so that the morphology of the individual bones is usually difficult to recognize. CNHM 219 exhibits a well preserved straight parasphenoid (Fig. 1c) and a lachrymal characterized by several longitudinal ridges along its outer surface (Fig. 1e). A post-temporal is partially preserved in CNHM 215, showing a forked shape with an acute angle measuring about 40°.



**Fig. 2** *Palimphemus macropterygius* and *Palimphemus* sp. otoliths. **a–c** *Palimphemus macropterygius*, early Sarmatian of Dolje, Croatia. **a** CNHM 215; **a1** head with otolith in situ; **a2** close-up of otoliths. **b** close-up of otoliths in situ in the holotype of *P. macropterygius*, CNHM 180. **c** CNHM 270; **c1** close-up of otoliths in situ; **c2** extracted right otolith. **d** isolated otolith from the Konkian of Mangyshlak,

Kazakhstan refigured from Bratishko et al. 2015 [as *Palimphemus minusculoides* (Schubert 1912)]; **d1** inner face; **d2** ventral view. **e** otolith found in situ in *Palimphemus* sp. from the Early Sarmatian of Tsurevsky, southern Russia; **e1** inner face; **e2** ventral view; **e3** outer face

**Table 1** Counts and measurements of *Palimphemus macropterygius* and selected related species

	<i>Palimphemus anceps</i>		<i>Palimphemus macropterygius</i>			' <i>Gadus macropterygius</i> ' from Azerbaijan
	After Carnevale et al. (2012)	Holotype of <i>Morrhua lanceolata</i> CNHM 73	Holotype of <i>Morrhua macropterygia</i> CNHM 180	Identified as <i>Morrhua lanceolata</i>		
	NHMW* specimen 1975/1752/248			CNHM 219	CNHM range	After Bogatshov (1933)
SL (mm)	115*	59	94	60.5	54.4–118.0	83
<i>Meristics</i>						
Precaudal vertebrae	18	16+	12	12	12–13	10
Total vertebrae	45–46	46+	42	42	41–44	35
D1	10–12	10	8	7	(5?) 7–8	8 (10?)
D2	10–12	12	10	11	10–12	>14
D3	17–21	16	14	16	14–17	20
A1	18–21	20	–	19	17–19	24 (22?)
A2	18–19	20	–	14	14–17	20 (16?)
Pectoral	15–18	18	17	15	14–18	20 (>18)
Pelvic	6	7	–	5	5	
Caudal	41–43	34+	–	32	32–38	
D1/VE	7	6	5	5	5	5
D2/VE	14	11	11	11	10–11	9 or 10
D3/VE	26	20	20	22	20–23	22
VE/A1	12	nm	–	9	9–10	6 or 7
VE/A2	27	nm	–	23	22–25	22 or 23
<i>Morphometrics (% of SL)</i>						
Head length	29.3*	31.8	33.0	33.1	28.6–33.1	37.3
Pectoral length	14.1			13.2	16.0–17.5 (21.2**)	24.1
Predorsal 1	37.5*	36.7	38.8	38.3	34.7–38.8	40***
Predorsal 2	52.1*	49.8	51.6	50.6	48.0–51.6	53***
Predorsal 3	71.7*	69.3	68.1	71.4	68.1–73.0	77***
Preanal 1	46.0*	46.1	–	45.1	43.2–46.5	55***
Preanal 2	74.1*	72.1	–	74.8	70.0–75.0	
Base D1	7.5*			5.8	5.0–6.0	
Base D2	10.3*			11.1	11.1–12.5 (15.3**)	
Base D3	14.2*			12.5	12.5–15.8	
Base A1	23.7*			26.0	21.0–28.0	
Base A2	14.2*			13.1	(13.1) 16.0–17.8	
Distance D1—D	7.5*			6.6	5.4–7.7	
Distance D2—D3	9.0*			9.6	8.0–9.6	
Distance A1—A2	5.4*			4.1	4.1–6.3	

\* Specimen NHMW 1975/1752/248, \*\* Increasing with size, \*\*\* Measured and calculated from photographs in Bogatshov (1933)

**Jaws** The tip of the premaxilla (CNHM 219, Fig. 1d) is bent forward, with a short ascending process and an equally elongate, broader articular process separated from each other by a wide notch. The rear end of the maxilla (CNHM 215, Fig. 1f) is slightly widened ventrally. A small, ovoid supramaxilla is also present. The mandible is preserved in CNHM 219 and does not project forward as much as the

premaxilla. The dentary and premaxilla bear at least three to four slightly curved lateral canines in CNHM 219 (Fig. 1c). No further teeth are visible in any of the specimens.

**Suspensorium** The bones of the suspensorium are badly damaged and difficult to recognize, except for the fan-shaped quadrate.

**Opercular series** The opercle is preserved in CNHM 215 (Fig. 1g) and shows a subtriangular outline with a nearly straight dorsal margin characterized by a bony ridge terminating into a short spine, a convex ventral margin supported by a rather indistinct straight ridge culminating into a very short and broad spine, and a broadly concave posterior margin. The other bones of the opercular series are inadequately preserved and their morphology cannot be described.

**Visceral arches** Six or seven elongate branchiostegal rays are preserved in CNHM 219 (Fig. 1b). Remains of large pharyngobranchials (possibly the second and third elements) and their associated toothplates are exposed in CNHM 215.

**Axial skeleton** The vertebral column is well preserved in CNHM 215 (Fig. 1h) and CNHM 178 (Fig. 1i, j). The anterior three abdominal vertebrae are slightly shorter than the following and the first is often hidden under the overlying fragments of the head bones. The neural spines of the first seven abdominal vertebrae are large and anteroposteriorly expanded. Stout and broad parapophyses emerge ventrolaterally in the vertebrae eight or nine to 12. The caudal vertebrae show long neural and haemal spines that become gradually inclined backward. The centra are subrectangular, slightly longer than high. Stout and moderately strong developed dorsal and ventral prezygapophyses insert at the bases of the neural and haemal spines. The caudal skeleton is not clearly exposed and inadequately preserved in all the examined specimens.

**Median fins** (Fig. 1c). There are three dorsal fins. The first dorsal fin contains 7–8 rays inserts above the fifth vertebra, the second dorsal fin contains 10–12 rays and inserts above the 10th or 11th vertebra, and the third dorsal fin contains 14–17 rays and originates above the vertebrae 20–23. The dorsal-fin pterygiophores appear to be generally small and thin. The dorsal fins are separated from each other by large gaps. The base of the first dorsal fin is very short (5–6 % SL), slightly shorter than the gap between the first and the second dorsal fin (5.5–8 % SL). The base of third dorsal fin is slightly longer than that of the second dorsal fin. The dorsal-fin rays are rarely preserved in their full length; these are usually rather short, being about equally long in the first and second dorsal fins and nearly two times as long as those of the third one. There are two anal fins. The first anal fin contains 17–19 rays and inserts below the ninth or tenth vertebra, i.e. just one vertebra in front of the second dorsal fin. The second anal fin is opposite to the third dorsal fin below the vertebrae 22–25 and contains 14–17 rays. The base of the first anal fin is longer than that of the second anal fin; the rays of the first anal fin are rather elongate, longer than those of the second anal fin. The rays of the

second anal fin are slightly longer than those of the third dorsal fin.

**Paired fins and girdles** (Fig. 1c) The pectoral fin and girdle are always incomplete with negative implications for counts and measurements. The specimen CNHM 219 shows a pectoral fin with the lower half considerably longer than the upper half. The longest rays of the pectoral fin reach the tip of the first anal fin. The pelvic fins are short, with the tips of their rays reaching the of the pectoral-fin insertion.

**Otolith** (Fig. 2a–d) The description of the otolith in situ is based on the specimen CNHM 270 with additional comparative information derived from the descriptive analysis of *P. minusculoides* by Bratishko et al. (2015), which is based on abundant and well preserved material. The otoliths are elongate and thin, reaching about 8 mm in length in isolated specimens. The largest in situ specimen (CNHM 215, Fig. 2a) is 3.5 mm long. OL:OH = 2.2–2.35 (up to 2.7 in the largest isolated otoliths), increasing with size; OL:OT = 6–8 (observed in isolated otoliths only). Dorsal rim anteriorly and posteriorly inclined, its median part nearly flat, pre- and postdorsal angles broadly rounded; ventral rim gently curved, not very deep, deepest slightly before its midlength, smooth or with small notch at its middle. The anterior tip is slightly pointed or rounded; the posterior tip somewhat tapering. The inner face is nearly flat along the horizontal axis. The sulcus is long, moderately wide, with its deepest point at the level of the collum. CaL:OsL = 1.2 (1.1–1.6 in isolated otoliths). The ostial colliculum terminates rather distant from anterior tip of the otolith; the caudal colliculum almost reaches the posterior tip of the otolith. CCL:OCL = 1.6 (1.3–2.2 in isolated otoliths). The collum is rather wide, with a convex lower margin and a weak pseudocolliculum; the dorsal field has a narrow and indistinct depression; the ventral furrow is distinct, running at some distance from the ventral rim of the otolith, particularly at its middle section. The outer face (CNHM 215) is rather smooth, slightly concave, with few short vertical furrows at mid-section.

**Discussion** *Palimphemus macropterygius* can be easily distinguished from *P. anceps* by the lower number of total (41–44 vs 45–46) and abdominal (12–13 vs 16–18) vertebrae, lower number of rays in the first dorsal (7–8 vs 10–12), second anal (14–17 vs 18–20) and pelvic (5 vs 6–7) fins, as well as for the otolith with its thin, flat appearance and the wide collum. It is assigned to the genus *Palimphemus* based on the overall morphological and meristic similarity (see refined generic diagnosis above) and otolith morphology. The specimens assigned to *Gadus macropterygius* by Jerzmańska (1962) from the Late Badenian of Poland have been referred to *P. anceps* by



Schwarzzhans (2014). Specimens formerly referred by Bogatshov (1929) to *Gadus lanceolatus* and later assigned to *Gadus macropterygius* by Bogatshov (1933) from the Middle to Late Sarmatian s.l. of Azerbaijan differ significantly from *P. macropterygius* in several meristic values, such as the lower number of vertebrae (10 abdominal and 35 total vs 12–13 and 41–44, respectively), higher number of fin rays in the third dorsal (20 vs 14–17), first anal (22–24 vs 17–19), second anal (>18–20 vs 14–18) fins, and the more anterior insertion of the first anal fin located below the sixth or seventh vertebra (vs 9–10). These specimens likely represent an undescribed species of *Palimphemus*. According to personal information by Artem Prokofiev (Aug. 2015) it is doubtful whether the specimens have been preserved and therefore unfortunately may not be available for review.

The collection of fishes from Dolje in the Croatian Natural History Museum in Zagreb contains a number of fishes that were originally identified by Kramberger as *Morrhua lanceolata*, a species originally described from the unique holotype from Podsused. The latter is embedded in a hard calcareous rock quite different from the soft diatomite of Dolje (Fig. 1a). The holotype of *M. lanceolata* significantly differs from *P. macropterygius* in several meristic features, including the number of vertebrae (16+ abdominal and 46+ total vs 12–13 and 41–44, respectively), number of rays in the first dorsal (9 or 10 vs 7–8), anal (20 or 21 in the first and 20 [18 counted by Kramberger] in the second vs 17–19 and 14–17, respectively) and pelvic (7 vs 5) fins. All of these meristic differences are consistent with those of *P. anceps*, and we therefore consider *M. lanceolata* as a junior synonym of *P. anceps*. There are no confirmed records of *P. anceps* in the Sarmatian based on both skeletal remains or otoliths. All gadid fishes examined from Dolje belong to *P. macropterygius*.

Another species described from Podsused is *Morrhua aeglefinoides*. The type specimen of this taxon has not been subject to any revisionary study and, based on the original description by Kner and Steindachner (1863), it resembles *P. macropterygius* by having a similar number of abdominal and total vertebrae and pelvic-fin rays, but differs in the higher number of rays in the first dorsal (11–12 vs 7–8), second dorsal (19 vs 10–12), first anal (24 vs 17–19) and second anal (18–20 vs 14–18) fins. The higher number of rays in the second dorsal fin contrasts with the definition of the genus *Palimphemus*, and is more consistent with the complement of the genus *Trisopterus*—number of second dorsal-fin rays of *Trisopterus* is 20–28 versus 12–14 in *Micromesistius* and 10–14 in *Palimphemus*. We therefore tentatively refer to the species as *Trisopterus? aeglefinoides*, pending a detailed review of the type specimen.

Carnevale et al. (2006) reported 39 specimens of a small gadid fish from the early Sarmatian s.l. of Tsurevsky,

southern Russia, as *Micromesistius* sp. In agreement with Bannikov and Kotlyar (2015), we regard this indeterminate species as belonging to the genus *Palimphemus*. An otolith found in situ in one of the specimens and refigured herein (Fig. 2e) differs from those of *P. macropterygius* in the more regularly tapering, slender posterior tip, ostial colliculum not reduced and a narrow collum, all three traits resembling specimens of *P. anceps*, but they differ in the thinner and more elongate appearance and the narrowed anterior tip. To date, there are no isolated gadid otoliths in the Sarmatian of the Central or Eastern Paratethys that would relate to this find.

Schubert (1906) mentioned the otoliths in situ of the holotype of *M. macropterygia* and regarded them as similar to those of the species described as *Otolithus (Gadidarum) minusculus* in the same article. Based on the otoliths found in situ in the specimens CNHM 215 and CNHM 270, the otolith-based species *P. minusculoides* is now synonymized with *P. macropterygius*, including all revised otolith-based synonymies as listed and discussed in Bratishko et al. (2015). The size ranges of the isolated otoliths exceed much those found in situ. The largest isolated otolith is about 8 mm long, while the largest otolith in situ found in specimen CNHM 215 of 118 mm SL is about 3.5 mm long. This indicates that *P. macropterygius* may have reached 250–300 mm SL.

**Distribution** As evidenced by skeletal and otolith finds, *P. macropterygius* is widely distributed in the Central and Eastern Paratethys through late Badenian to Sarmatian s.s. and Konkian to early Sarmatian s.l. (Volhynian), respectively. It is not recorded from other European basins and from older strata in the Paratethys, i.e. early Badenian or Chokrakian, whereas *P. anceps* was a long ranging species from Late Oligocene to Early Pliocene times in the North Sea Basin, while it apparently disappeared in the Central Paratethys after the late Badenian/Konkian. The coexistence of *P. anceps* and *P. macropterygius* during the late Badenian in the Central Paratethys is explained by in situ survival of *P. anceps* meddling with invading *P. macropterygius* from the Eastern Paratethys (Bratishko et al. 2015), where no specimens of *P. anceps* have been recorded. The origin of the sudden occurrence of *P. macropterygius* in the Paratethys remains unresolved. Records of *Palimphemus* in the Eastern Paratethys during middle to late Sarmatian s.l. (Bessarabian) probably represents a different, undescribed species apparently related to *P. macropterygius*.

Genus †*Paratrisopterus* Fedotov 1971

The fossil genus *Paratrisopterus* was established by Fedotov (1971) based on two specimens from the early Sarmatian of Moldavia and Abkhazia. Recently,



Schwarzahns (2010) synonymized the following otolith-based fossil genera with *Paratrisopterus*: *Archaegadiculus* Schwarzahns 1978, *Microgadiculus* Schwarzahns 1978, *Conferencea* Gaemers 1983 and *Ovigadiculus* Gaemers 1990. Prokofiev (2004) synonymized *Paratrisopterus* with *Gadiculus*, potentially in subgeneric ranking, after a critical review of the type specimens of *P. avus*, but Schwarzahns (2010) found arguments to maintain generic ranking of *Paratrisopterus*.

Fedotov (1976) included the following species within the genus *Paratrisopterus*, *P. avus* Fedotov 1971, *P. caspius* (Bogatshov 1929), *P. kiplingi* (Bogatshov 1929), *P. kwitkae* (Bogatshov 1933) and *P. macropterygius* (Kramberger 1883); however, he apparently did not review the specimens previously documented by Bogatshov (1929, 1933) and Kramberger (1883). We consider *P. avus* as a junior synonym of *P. caspius*, *Paratrisopterus macropterygius* as a representative of *Palimphemus* (see above), and, finally *Paratrisopterus kwitkae* is assigned to *Gadiculus*. *Paratrisopterus labiatus* (Schubert 1905) was described with otoliths in situ by Landini and Sorbini (1999) as *Gadiculus labiatus*. Moreover, *Morrhua minima* Kramberger 1885 might also pertain to the genus *Paratrisopterus*; however, a careful review of the specimens originally described by Kramberger (1885) would be necessary to demonstrate its affinities with *Paratrisopterus* and for this reason it is not considered in the diagnosis presented below. For otolith-based species we refer to Schwarzahns (1994a) for Late Oligocene species formerly included within *Archaegadiculus*, and Schwarzahns (2010) for the Neogene taxa.

Therefore, a new revised diagnosis of *Paratrisopterus* that included newly recognized morphological features and otolith data appears to be necessary to improve the critical review by Prokofiev (2004) and is provided herein.

**Diagnosis** Small gadid fish, apparently not exceeding 60 mm SL characterized by an elongate and laterally compressed body; maximum body height ranging from 10 to 15 % SL; head length about one-third of SL; gape of the mouth wide, extending backward to about midlength of orbit, inclined at about 15°–30°; anal-fin insertion well behind the first dorsal-fin origin; preanal distance >40 % SL, nearly twice the base length of the first anal fin (21–27 % SL); 38–45 (9–12 + 29–35) vertebrae; first dorsal fin with 7–10 rays; second dorsal fin with 10–15 rays; third dorsal fin with 15–18 rays; first anal fin with 18–25 rays; second anal fin with 16–20 rays; caudal fin with 28–36 rays; pectoral fin with 14–20 rays; pelvic fin with eight rays (five in *P. labiatus*); gap between first and second dorsal fins 4–5 % SL; gap between second and third dorsal fins 8–16 % SL; gap between first and second anal fins 4–5 % SL; mesethmoid columnar, with a notch along

the anterior margin; infraorbitals narrow; parasphenoid straight; ascending process of the premaxilla at right angle to the ascending process; otolith compressed, anteriorly and posteriorly rounded in small specimens and pointed in larger ones; its sulcus with small, widely separated colliculi terminating at considerable distance from anterior and posterior otoliths rims respectively and with pseudocolliculum.

**Discussion** Fedotov (1976) considered *P. avus* to be closely related to *P. macropterygius* (Kramberger 1883), which he also placed in *Paratrisopterus*; however, as discussed above, we assign this species to the genus *Palimphemus*. Prokofiev (2004) reviewed the type specimens of *P. avus* and discussed its taxonomic position. He considered the diagnostic characters used by Fedotov (1976) to distinguish *Paratrisopterus* from *Trisopterus* (larger head and snout length, shorter lower jaw, shorter caudal peduncle, smaller number of vertebrae and rays in the dorsal and anal fins and absence of chin barbel) not fully adequate, and identified a number of other characters that appear more useful to distinguish both genera. However, he concluded that *Paratrisopterus* exhibits a high degree of similarity with *Gadiculus*. According to his interpretation the most significant differences between *Gadiculus argenteus* and *P. avus* can be recognized in the shape of the mesethmoid, narrow infraorbitals, apparent smaller size of the seis-mosensory system canals on the head and significantly less oblique mouth in *P. avus*. He considered these differences as not relevant to recognize *Paratrisopterus* as a separate genus and consequently synonymized it with *Gadiculus*. In a subsequent paper, Schwarzahns (2010) argued that additional characters, i.e. differences in eye size and in first and second dorsal and first anal fin counts, provide support to the separate status of these two genera; moreover, Schwarzahns (2010) also mentioned that the long separation of the *Gadiculus* and *Paratrisopterus* lineages as evidenced by fossil otoliths can warrant recognition of two separate genera.

Our investigations support the conclusions of both Prokofiev (2004) and Schwarzahns (2010) that *Paratrisopterus* and *Gadiculus* are closely related to each other. The new data presented herein show that the different dorsal fin ray counts and eye size may not be stable, but further traits were identified to support the validity of both genera. These are: body height <15 % SL (vs >20 % SL in *Gadiculus*), mouth cleft inclined at 15°–30° (vs 45°–60° in *Gadiculus*), parasphenoid straight (vs curved posteriorly in *Gadiculus*), mesethmoid columnar with a nearly straight vertical margin [(with an obliquely oriented and irregular anterior margin in *Gadiculus*, see e.g., Svetovidov (1948)], caudal vertebrae 29–35 (vs 27–30 in *Gadiculus*, possibly 36 in *G. kwitkae*), first anal fin with 18–25 ray (vs 11–18 in

*Gadiculus*, possibly 25 in *G. kwitkae*), and gap between first and second anal fins 4–5 % SL (vs 6–9 % SL in *Gadiculus*).

Prokofiev (2004) regarded the type specimens of *P. avus*, as juvenile individuals. However, all known *Paratrisopterus* specimens are rather small and their common and abundant otoliths also indicate that one should not expect specimens significantly larger than 60 mm SL. *Gadiculus* is also a relatively small gadid with extant specimens reaching sizes of about 150 mm SL. The larger size of individuals of *Gadiculus* vs *Paratrisopterus* is also supported by the differences in the maximum size of their otoliths, whereas those of the largest *Paratrisopterus* specimens attain about half of the size of those of the largest *Gadiculus* specimens. Therefore, we conclude that the species of *Paratrisopterus* were characterized by a relatively small size. We assume that the *Paratrisopterus* species were adapted to an epipelagic lifestyle possibly similar to that of the codlets of the family Bregmaceroiidae; *Gadiculus* species primarily occupy the mesopelagic zone.

Schwarzzhans (1994a) noted the parallel occurrence of pairs of *Paratrisopterus* otolith-based species (then *Archaeogadiculus*) in many of the Late Oligocene deposits of the North Sea Basin and speculated that such “species-pairs” could represent sexual dimorphism in otoliths. This has not been observed in any extant gadid species, and, more generally, has been rarely observed in teleost fishes (see Schwarzzhans, 1994b); however, this may be a possible explanation for the co-occurrence of such pairs of fossil otolith-based taxa. The uncommon articulated skeletons are certainly not fully adequate to further investigate on this hypothesis for which additional comparative information would be necessary.

#### *Paratrisopterus caspius* (Bogatshov 1929)

(Figures 3a–i, 4a–j)

1929 *Gadus caspius* Bogatshov. Bogatshov: pl. B, Figs. 7–8.

1933 *Gadus caspius* Bogatshov 1929. Bogatshov: pl. 8, Figs. 5 and 6.

1943 *Otolithus (Gadidarum) insectus* Weiler. Weiler: pl. 1, Fig. 38 [otolith-based species].

1943 *Otolithus (Macruridarum) ovalis* Weiler. Weiler: pl. 1, Figs. 60–62 [otolith-based species].

1943 *Otolithus (Macruridarum) acuminatus* Weiler. Weiler: pl. 1, Figs. 50–51 [otolith-based species].

1949 *Otolithus (Gadidarum) insectus* Weiler 1943. Weiler: pl. 5, Fig. 38.

1949 *Otolithus (Macruridarum) ovalis* Weiler 1943. Weiler: pl. 7, Figs. 60–62.

1949 *Otolithus (Macruridarum) acuminatus* Weiler 1943. Weiler: pl. 6. Figs. 50–51.

**Fig. 3** *Paratrisopterus caspius*, from the excavations of the 'Red Star' football stadium in Belgrade 1961–1962, early Sarmatian. **a** RGFAJ 25 (reversed); **a2** reconstruction of the skeleton. **b** RGFAJ 25, anterior tip of snout with tip of premaxilla and dentition on vomer. **c** RGFAJ 24. **d** RGFAJ 25, left and right dentary. **e** RGFAJ 26 (reversed), identified as *Properca sabbai* by Andjelković (1969). **f**, **g** Caudal vertebrae, anterior caudal vertebra (**f**), middle caudal vertebra (**g**), posterior caudal vertebra (**h**). **i** Life reconstruction

1950 *Otolithus (Gadidarum)* sp. 1 Weiler: pl. 10, Fig. 77.

1950 *Otolithus (Gadidarum)* sp. 2 Weiler: pl. 10, Fig. 76, pl. 11, Fig. 78.

1950 *Otolithus (Gadidarum)* sp. 3 Weiler: pl. 8, Figs. 55–56.

1950 *Otolithus (Gadidarum) insectus* Weiler 1943. Weiler: pl. 10, Figs. 73–75

1950 *Gadus? minusculoides* (Schubert 1912). Weiler: pl. 9, Fig. 69, pl. 10, Fig. 72.

1950 *Hymenocephalus? labiatus* Schubert 1905. Weiler: pl. 8, Fig. 57, pl. 11, Fig. 79

1950 *Otolithus (Macruridarum) ovalis* Weiler 1943. Weiler: pl. 8, Fig. 58.

1954 *Otolithus (Gadidarum) minusculus* Schubert 1906. Pobedina: pl. 3, Fig. 2.

1956 *Otolithus (Gadidarum) minusculus* Schubert 1906. Pobedina: pl. 23, Fig. 1.

1968 *Otolithus (Gadidarum) labiatiformis* Suzin 1968 (in Zhizhchenko). Suzin: pl. 18, Fig. 28 [otolith-based species; name not available according to ICZN article 13.1.1.].

1968 *Otolithus (Gadidarum) minusculus* Schubert 1906. Suzin: pl. 18, Figs. 32–33.

1969 *Properca sabbai* Pauca 1929. Andjelković: pl. 4, Fig. 4.

1971 *Paratrisopterus avus* Fedotov. Fedotov: Figs. 1 and 2. ?1973 *Macruridarum irregularis* Gaemers. Gaemers: pl. 2, Fig. 8 [otolith-based species].

1976 *Paratrisopterus avus* Fedotov. Fedotov: pl. 7, Figs. 1 and 2; Figs. 22–23.

1989 *Gadus lanceolatus* (Kramberger 1883). Andjelković: pl. 5, Fig. 4.

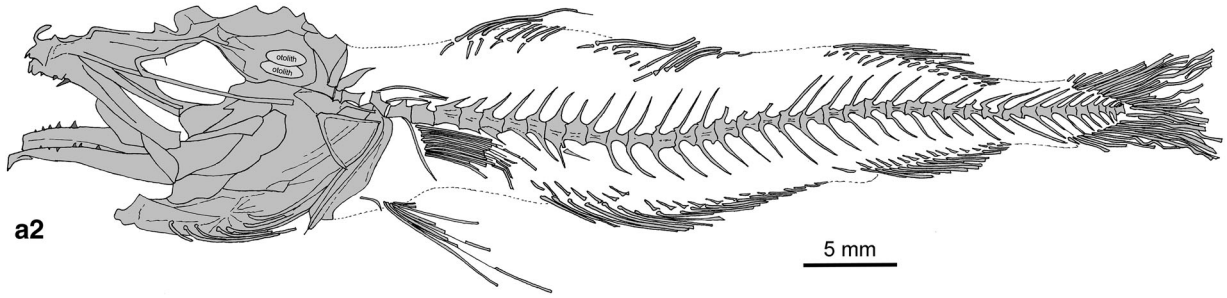
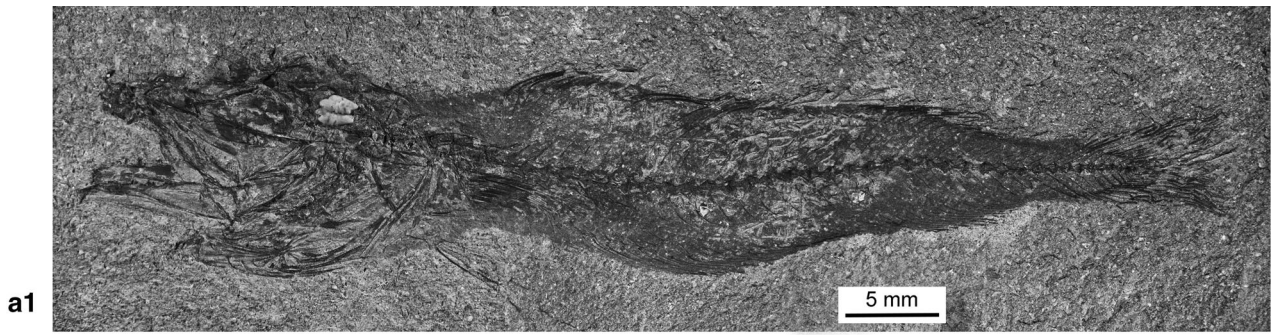
2004 *Gadiculus avus* (Fedotov 1971). Prokofiev: Figs. 1, 2a, b.

2006 *Macrurus* sp. Djafarova: pl. 9, figs, 1, 3, 4, pl. 10, Figs. 1?, 4.

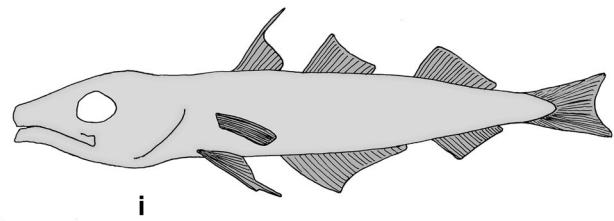
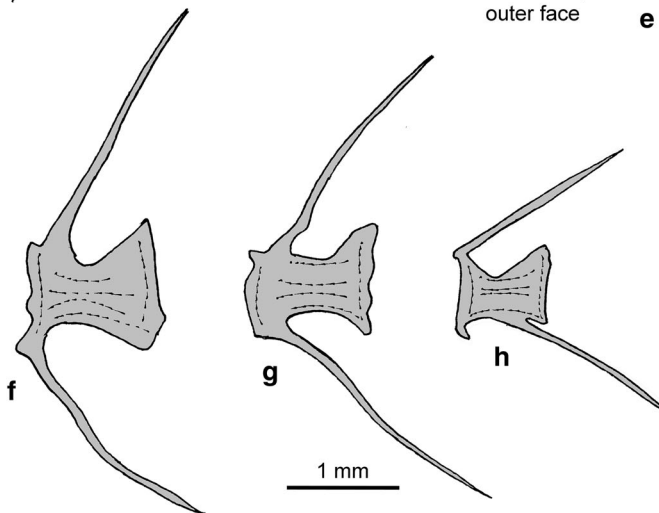
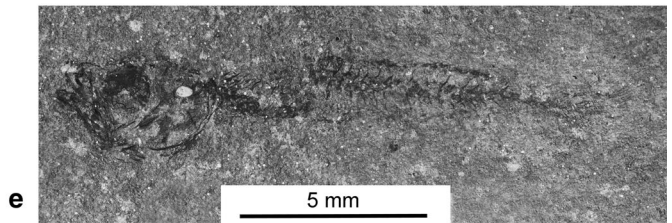
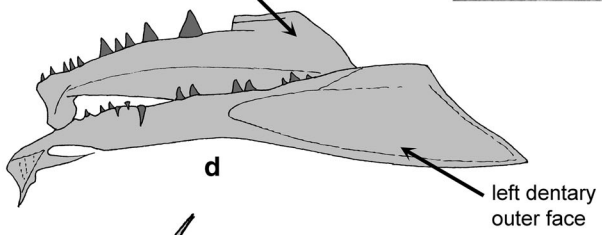
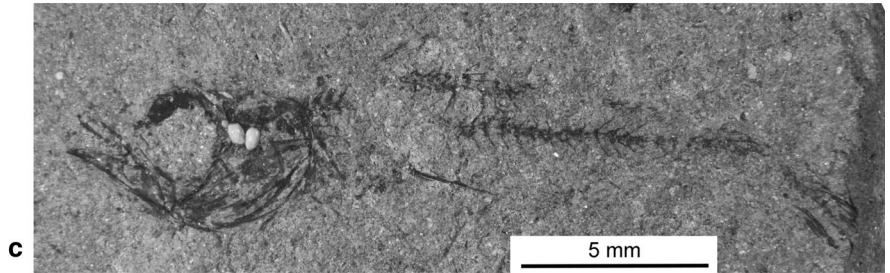
?2010 *Paratrisopterus irregularis* (Gaemers 1973). Schwarzzhans: pl. 33, Fig. 1

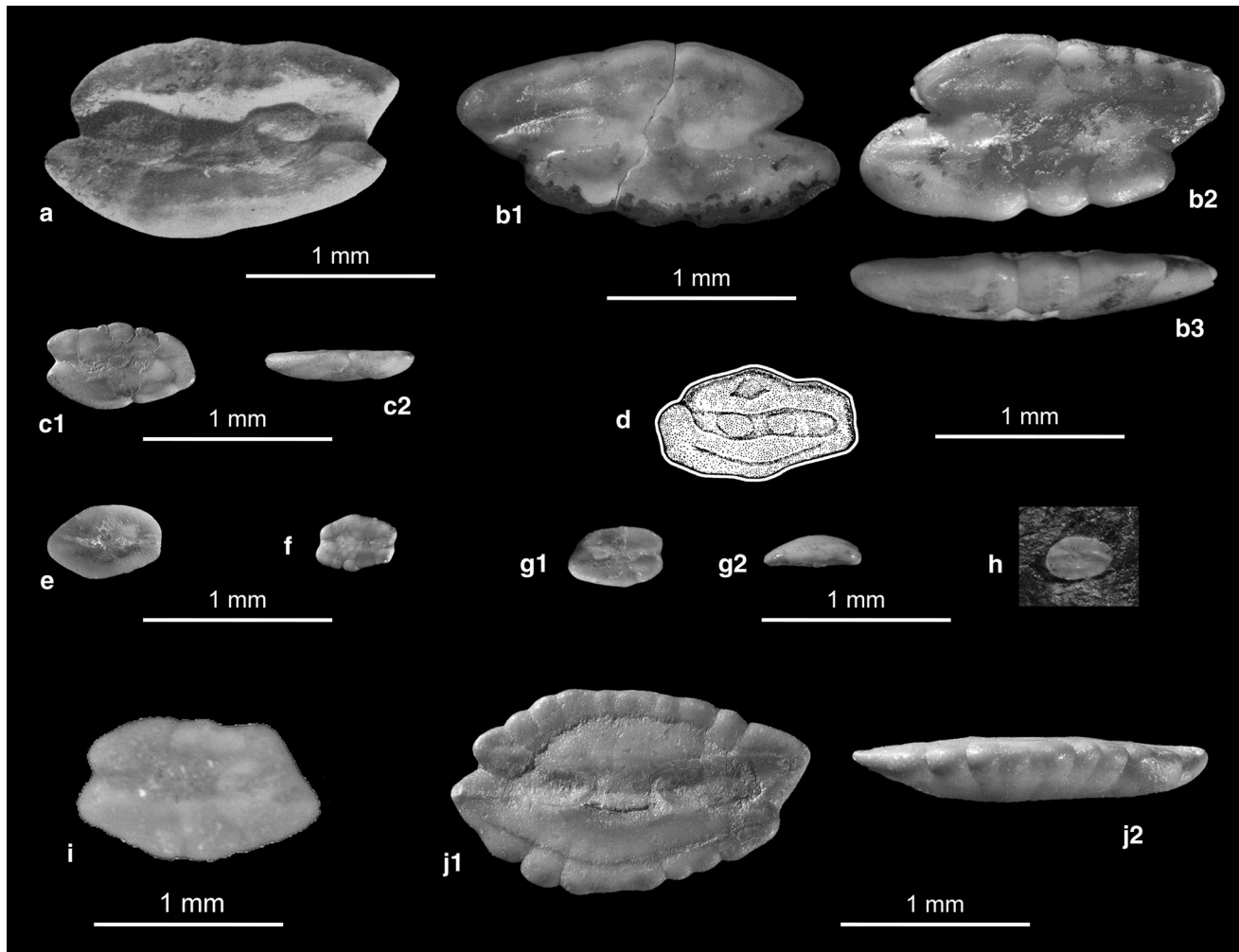
2010 *Paratrisopterus insectus* (Weiler 1943). Schwarzzhans: pl. 33, Figs. 2–4.

**Material** Three specimens collected in 1961–1962 during the renovation of the Red Star Belgrade football stadium, Belgrade, Serbia, Sarmatian s.s. (Volhynian): RGFAJ 24 (SL 21 mm) (identified as *Properca sabbai* in Andjelković 1969), RGFAJ 25 (SL 56 mm) [identified as *Gadus*



right dentary inner face





**Fig. 4** *Paratrisopterus caspius* otoliths. **a** SMF P 2657a, holotype of *Otolithus (Gadidarum) insectus*, refigured from Weiler (1943); **b** RGFAJ 25; **b1** inner face of left otolith; **b2** inner face of right otolith; **b3** ventral view of right otolith. **c** SMF P 2922, paratype of *O. (G.) insectus* refigured from Schwarzzhans (2010); **c1** inner face; **c2** ventral view. **d** PIN 3118/1, otolith found in situ in holotype of *Paratrisopterus avus*, refigured from Fedotov (1976); **e** SMF P 2665a,

holotype of *Otolithus (Macruridarum) acuminatus* Weiler 1943. **f** SMF P 2729, paratype of *O. (G.) insectus* refigured from Schwarzzhans (2010). **g** RGFAJ 24; **g1** inner face; **g2** dorsal view. **h** RGFAJ 26. **i** early Sarmatian of Barajevo, Serbia. **j** SMF PO 64778, Tortonian-Messinian (Sylvian), Goch, northern Germany, refigured from Schwarzzhans (2010) as *Paratrisopterus irregularis* (Gaemers 1973)

*lanceolatus* (Kramberger 1883) in Andjelković (1989)], RGFAJ 26 (SL 14.5 mm).

**Diagnosis** Vertebral column with 42–45 vertebrae, of which 10 or 11 abdominal; first dorsal fin with 8–10 rays; second dorsal fin with 12–14 rays; pectoral fin with 18–20 rays; pelvic fin with 8 rays; first dorsal-fin base 5–6 % SL; body depth 11–15 % SL; first and second rays of pelvic extended, second ray longest reaching 14.5–17 % SL; first ray of first dorsal elongated, reaching 10.5–13.5 % SL; upper and lower jaws nearly equally elongate; ascending process of the premaxilla at an angle of about 90° with respect to the alveolar process; otoliths oval in shape, OL:OH = 1.4–1.8, increasing with size, with flat inner face; sulcus with small,

oval colliculi and broad collum with distinct pseudocolliculum.

**Description** (based primarily on RGFAJ 25, Fig. 3a, b, d, f–i) Body elongate, slender and laterally compressed. Counts and measurements are reported in Table 2.

**Neurocranium** The head bones are badly damaged in all the examined specimens so that the morphology of the individual bones are not clearly recognizable except for the a well preserved, nearly straight parasphenoid. The columnar mesethmoid is well exposed in RGFAJ 25 (Fig. 3a) and is firmly articulated ventrally with the vomer. The orbit is well recognizable in all the examined specimens (Fig. 3a, c, e) and ranges from 8 % SL in the largest specimen to 10.5 % SL in the smallest showing a pronounced inverse ontogenetic allometry.



**Table 2** Counts and measurements of *Paratrisopterus caspius* and selected related species

		<i>Paratrisopterus caspius</i> (Bogatshov 1929)				<i>Paratrisopterus kiplingi</i> (Bogatshov 1929)		<i>Paratrisopterus labiatus</i> (Schubert 1906)		<i>Gadiculus argenteus</i>		<i>Gadiculus jonas</i> (d'Erasmio 1930)		<i>Gadiculus kwitkai</i> (Bogatshov, 1933)	
		As <i>Paratrisopterus avius</i> in Fedotov (1971), after Prkofiev (2004)		As <i>Gadus lanceolatus</i> by Andjelković (1969)		As <i>Properca sabbai</i> by Andjelković (1969)		Range		From Landini and Sorbini (1999)		After d'Erasmio (1930) and Carnevale (2006)		After Bogatshov (1933)	
		HT PIN 3118/1	PT PIN 2181/89	AJ 25	AJ 26	AJ 24	AJ 26	Rounded to nearest 1/2 decimal							
SL (mm)	57	35	60	56	21	14.5	60.6	38.5	195						
<i>Meristics</i>															
Precaudal vertebrae	10	10	10	11	10	10	9–10	9	12–13	10	8				
Total vertebrae	42	45	44	42	42	39+	40–42	38	37–43	37–38	44				
D1	8	8	9	8	10?		8–9	7	8–13	6–7	10–11				
D2	12–14	12	10+	12	7+		14–15	8+	10–16	8–12	12				
D3	16–18	16	15–16	16	6+		17–18	17	11–17	12–17	16–18				
A1	18–22	22	24	19	8+		22–25	18	11–18	13–15	25				
A2	16	18	18	17	2+		20	17	12–17	15–17	18–19				
Pectoral	18	20	20	19			18	14	17	13					
Pelvic	36	8		8			8	5	8	6					
Caudal	36	36		36	24+		36	28	42	50+					
D1/VE	7	7	6	7	6 or 7		6–7	6	4–5	6	4–5				
D2/VE	10	14	13	14	13		10–14	10	12	15–16	11–12				
D3/VE	25	25	23	27	26		23–27	21	23–24	22–23	22–23				
VE/A1	7	11	10	10	8?		(7) 10–11	10	11–12	15–16					
VE/A2	23	25	24	28	24		23–28	21	23–25	22–23	22–23				
<i>Morphometrics (% of SL)</i>															
Head length	35.0	31.3		30.6	31.1	31.3	30.8	27.0	27.0–28.5	29.5	30.4				
Angle of mouth cleft	Low angle	18°		20°			30°	20° <sup>d</sup>	55–60° <sup>e</sup>	45–60° <sup>e</sup>	45°				
Body height	About 15	11.4		13.7	10.8		14.3°	12.0	21.0	19.1	23.0				
Orbit diameter	nm	8.5		7.8	9.9	10.3	5.6	9.0	10.5	8.6	8.7				
Shape of parasphenoid	Straight <sup>a</sup>	± Straight	Straight	± Straight	± Straight	± Straight	Straight <sup>c</sup>	Straight <sup>d</sup>	Curved	Curved <sup>e</sup>	Slightly curved <sup>f</sup>				
1st + 2nd Pelvic fin rays	Long <sup>a</sup>	Short?	nv	Long	nv	nv	Short	Short	Short	Short	nv				

Table 2 continued

Paratrisopterus caspius (Bogatshov 1929)		Paratrisopterus kiplingi (Bogatshov 1929)	Paratrisopterus labiatus (Schubert 1906)	Gadaculus argenteus	Gadaculus jonas (d'Erasmus 1930)	Gadaculus kwiitkae (Bogatshov, 1933)	
Holotype after Bogatshov (1929)	As <i>Paratrisopterus avius</i> in Fedotov (1971), after Prkofiev (2004)	As <i>Gadus lanceolatus</i> by Andjelković (1969)	As <i>Properca sabbai</i> by Andjelković (1969)	Range	From Landini and Sorbini (1999)	From X-rays and literature	After Bogatshov (1933)
HT PIN 3118/1	PT PIN 2181/89	AJ 25	AJ 24 AJ 26	Rounded to nearest 1/2 decimal	After d'Erasmus (1930) and Carnevale (2006)		
Pectoral length		12.8		13.0		12.0	
Predorsal 1	35.7	34.6	37.5	34.5–37.5	36.0	33.5–34.0	38.5
Predorsal 2	48.6	50.0	49.5	48.5–50.0		49.5–51.5	53.8
Predorsal 3	68.6	70.8	70.8	68.5–71.0		73.073.5	74.3
Prenal 1	42.9	43.3	42.9	43.0–43.5	43.0	48.0	42.5
Prenal 2	68.6	72.0	68.9	68.5–72.0		73.0–75.0	74.4
Base D1	12.6	8.3		8.5–12.5	6.0	12.0–12.5	
Base D2	14.6	10.2		10.0–14.5	10.0	15.0	
Base D3	13.8	15.0		14.0–15.0	21.0	15.5	
Base A1	21.3	26.4		21.5–26.5	23.0	19.0–21.0	
Base A2	14.6	15.3		14.5–15.5	18.0	12.5–14.5	
Distance D1—D2		4.6		4.5	4.0	5.0–6.0	3.9
Distance D2—D3		8.0		8.0	16.0	7.5–8.0	10.8
Distance A1—A2		4.0		4.0	5.0	6.0–8.5	8.0

<sup>a</sup> From photo of Bogatshov (1929, 1933)

<sup>b</sup> Decreasing with size

<sup>c</sup> From photo and drawing of Bogatshov (1929)

<sup>d</sup> From photo of Landini and Sorbini

<sup>e</sup> From photos of d'Erasmus and Carnevale

<sup>f</sup> From Photo of Bogatshov (1933)

**Jaws** The tip of the premaxilla is blunt, with a near vertically arising and moderately long ascending process (Fig. 3b). The articular process is not preserved. The rear end of the maxilla is incomplete in specimens RGFAJ 25 and AJ 24 and appears to be only slightly expanded ventrally. The mandible is preserved in all the three specimens and projects forward as much as the premaxilla. In small specimens (AJ 24 and AJ 26) it is pointed anteriorly almost like a beak (Fig. 3c, e). The dentary and maxilla bear a few slightly curved to straight caniniform teeth of different size (Fig. 3b, d).

**Suspensorium** Some bones of the suspensorium are partially recognizable in the specimen RGFAJ 25, including the quadrate, a fragmented hyomandibula, the metapterygoid, ectopterygoid and palatine.

**Opercular series** The opercle is triangular in outline with nearly straight and thickened anterior and dorsal margins, and a slightly convex posterior margin. No other opercular bones are preserved well enough for description.

**Visceral arches** The hyoid bar is stout and rather thick. Six elongate saber-like branchiostegal rays can be recognized in RGFAJ 25.

**Axial skeleton** The vertebral column is well preserved in the specimen RGFAJ 25 and somewhat incomplete in the two other specimens. The anterior five abdominal vertebrae bear short neural spines, those of the sixth and seventh abdominal vertebrae are slightly depressed and slightly expanded anteroposteriorly than the successive ones. Parapophyses are present along the ventrally along the lateral side of the vertebrae seven to nine and not visible on subsequent vertebrae due to inadequate preservation. The caudal vertebrae (Fig. 3f–h) show long neural and haemal spines which become gradually inclined backward. The centra are subrectangular, slightly longer than high, slightly constricted in the middle. Dorsal and ventral prezygapophyses are scarcely developed and difficult to recognize. The caudal skeleton is not clearly exposed in any of the examined specimens.

**Median fins** (Fig. 3a) There are three dorsal fins. The first dorsal fin contains 8–10 rays and inserts above the sixth or seventh vertebra, the second dorsal fin contains 12–14 rays and inserts above the 10th–14th vertebra, and the third dorsal fin contains 15–18 rays and inserts above 23th–27rd vertebra. The dorsal-fin pterygiophores appear to be small and thin. The dorsal fins are separated from each other by large gaps, i.e. about 5 % SL between the first and second dorsal fins and about 8 % SL between the second and third dorsal fins. The base of the first dorsal fin is moderately long (8.5–12.5 % SL), in certain cases almost as long as the base of the second dorsal fin (10–14.5 % SL). The base of the third dorsal fin is slightly longer than the base of the

second dorsal fin (14–15 % SL). Some rays of the dorsal fin appear to be preserved in their full length in specimen RGFAJ 25, and are moderately elongate, becoming gradually shorter posteriorly in the series. The first dorsal fin bears a significantly extended first ray visible in the specimens RGFAJ 24 and AJ 25 of about 10.5–13.5 % SL. There are two anal fins. The first anal fin contains 18–24 rays and inserts below the seventh to eleventh vertebra, i.e. slightly anterior to the second dorsal-fin origin. The second anal fin contains 16–18 rays and is opposite to the third dorsal fin, being developed below the vertebrae 23–28. The base of the first anal fin is distinctly longer than that of the second anal fin. The fin rays of the anterior part of the first anal fin are almost as long as the opposed rays of the second dorsal fin, and become rather short posteriorly in the series. The second anal fin appears to be symmetrical to the third dorsal fin.

**Paired fins and girdles** (Fig. 3a) The pectoral fin and girdle are only partially preserved in RGFAJ 25, in which a slender postcleithrum is preserved. The same specimen shows a pectoral fin with 19 incompletely preserved rays. The pelvic fin contains eight rays and is well preserved in the specimen RGFAJ 25 and partially preserved in the specimen RGFAJ 24. In both the specimens the anterior two pelvic-fin rays are much elongated, particularly the second, which is nearly twice as long as the third and about 30 % longer than the first. The length of the second pelvic fin ray is about 14.5–17 % SL.

**Otolith** (Fig. 4) Otoliths are preserved in all three specimens. The following description is based on the largest otolith from RGFAJ 25 (Fig. 4b). The otolith is oval, moderately elongate and thin, and about 2 mm long. [The largest otoliths known from any species of *Paratrisopterus* is about 3.5 mm long, while otoliths of *Gadiculus* reach sizes of 8 mm (Schwarzahns, 2010)]. OL:OH = 1.8; OL:OT = 5.5. The dorsal and ventral rims are shallow, irregularly and rather strongly and coarsely undulating anteriorly. The dorsal rim is shifted backwards and the ventral rim forwards which results in a parallelogram-like shape of the otolith. The anterior rim is ventrally projecting, similar to a rostrum, and the posterior rim is dorsally projecting. Both anterior and posterior rims show incisions at the level of the sulcus. The inner face is completely flat with a narrow, central sulcus which indistinctly opens anteriorly and posteriorly. Ostium and cauda are about equal in length and width (homosulcoid pattern) and show much reduced, small colliculi which terminate far from the anterior and posterior rims of the otolith, respectively, and are widely separated at the collum which bears a sometimes indistinct pseudocolliculum. The dorsal field does not show a dorsal depression. The ventral furrow is usually distinct, running at some distance from the ventral rim of

the otolith. The outer face is slightly convex, smooth at the center and with variable amounts of short radial furrows towards the otolith rims.

The known otoliths in situ show a remarkable variability as well as a notable ontogenetic allometry. The two large otoliths extracted from RGFAJ 25 (Fig. 4b1, 4b2) and the holotype of *P. avus* figured in Fedotov (1976) (Fig. 4d) differ in several details of the outline of the otolith, particularly in the anterior and posterior tips of the otolith, which are more blunt in the specimen figured by Fedotov (1976), as well as in the depth of the ventral rim. This may indicate that other *Paratrisopterus* species currently known only from otoliths may have a wider range of variability than often assumed, which could also result in fewer valid species than previously recognized in literature. The ontogenetic changes are mostly expressed in a more rounded outline of smaller specimens and a more compressed proportion. The ratio OL:OH is only 1.4 in the smallest specimen from RGFAJ 26 (Fig. 4h) as compared to 1.8 in the largest specimen of RGFAJ 25 (Fig. 4b).

**Discussion** The specimens from RGF fit well with the types of *P. avus* described by Fedotov (1976) and Prokofiev (2004), as well as with the description of *Gadus caspius* provided by Bogatchov (1929). Minor differences in the number of total vertebrae (*P. avus* type specimens) and in the insertion of the second dorsal and first anal fins relative to the vertebrae (*G. caspius*) are within the expected variation of the species. The photographs of *G. caspius* also seem to show the presence of elongated rays in the pelvic fin just like RGFAJ 25 and AJ 24. However, neither Fedotov (1976) nor Prokofiev (2004) reported the presence of elongated pelvic-fin rays in the drawings of the holotype of *P. avus*. We assume that this apparent discrepancy is due to the partial preservation of the fins, even if the role of sexual dimorphism cannot be ruled out. Despite of the difference of the pelvic fin all other characters suggest that *Gadus caspius* and *P. avus* belong to the same species, of which *P. caspius* (Bogatshov 1929) represents the senior synonym. Several otolith-based species are also considered as synonyms of *P. caspius*, most notably *P. insectus* (Weiler 1943) (refigured holotype in Fig. 4a). Considering the now observed broad variability of the otoliths we also tentatively synonymize *P. irregularis* (Gaemers 1973) (Fig. 4j) from the Late Miocene (Tortonian/Messinian) of the North Sea Basin with *P. caspius*. The tentative nature of this assignment is due to the fact that these specimens are younger than any records from the Paratethys; there are no intermittent geographical occurrences between the Central and Eastern Paratethys, and the North Sea Basin, which were effectively separated during this period.

**Fig. 5** *Enchelyopus susedanus* from the early Sarmatian of Dolje, Croatia. **a** CNHM 168/239; **a1** CNHM 168; **a2** CNHM 239 (reversed); **a3** photographs of CNHM 168 and 239 merged; **a4** interpretative reconstruction of the skeleton based on CNHM 168 and 239. **b** CNHM 240

The separated status from the other two confirmed skeleton-based *Paratrisopterus* species, *P. kiplingi* and *P. labiatus* relies mostly on differences in meristics and, to a lesser extent, morphometrics. *Paratrisopterus kiplingi* differs in the higher number of rays in the second dorsal fin (14–15 vs 12, and 14 in a single case), the higher number of rays in the second anal fin (20 vs 16–18), the more anterior insertion of the second anal fin located below vertebrae 21–22 (vs 23–28), and the small orbital diameter (5.5 % SL vs 8–10.5 % SL). *Paratrisopterus labiatus* differs primarily in the lower number of total vertebrae (38 vs 42–45), lower number of pectoral-fin rays (14 vs 18–20) and pelvic-fin rays (5 vs 8), and the long bases of the third dorsal (21 % SL vs 14–15 % SL) and the second anal (18 % SL vs 14.5–15.5 % SL) fins.

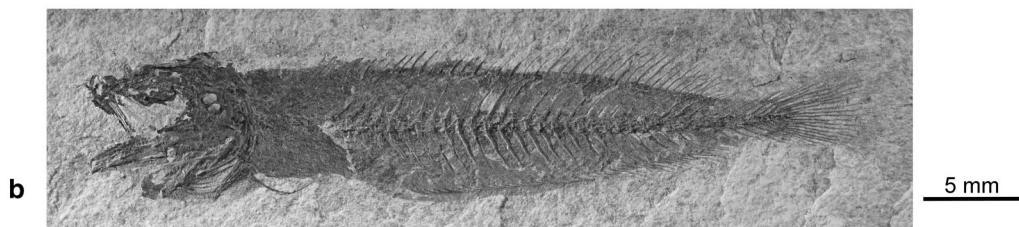
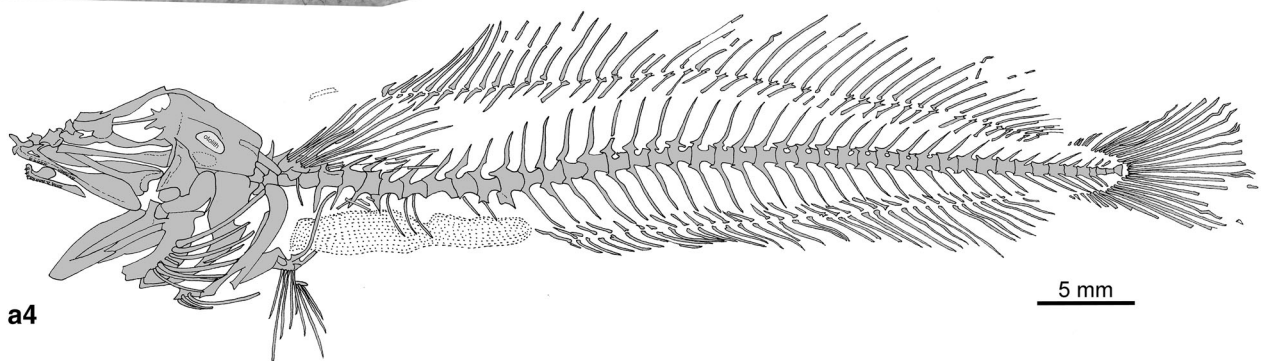
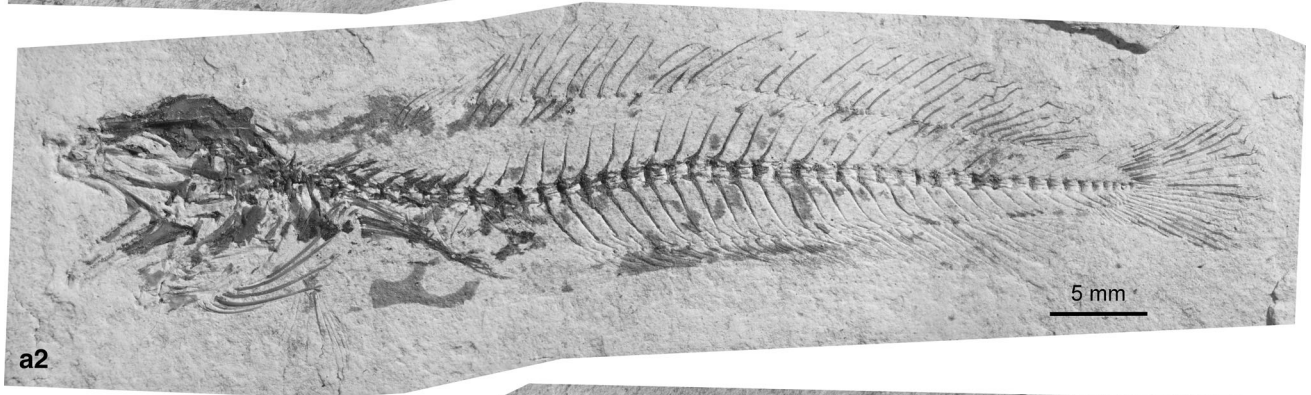
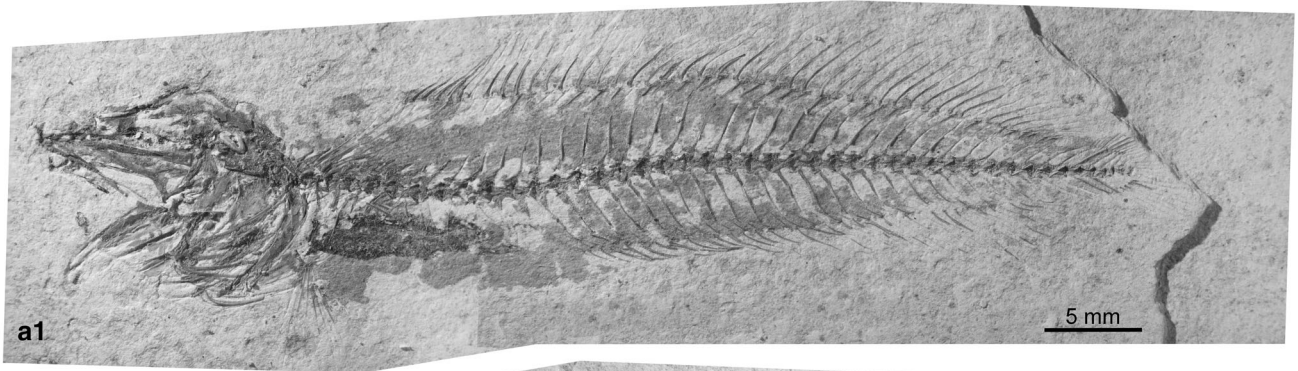
The record of *Properca sabbai* from the Sarmatian of the Paratethys is clearly erroneous and the specimen recorded by Andjelković (1969) represents a juvenile individual of *Paratrisopterus caspius*.

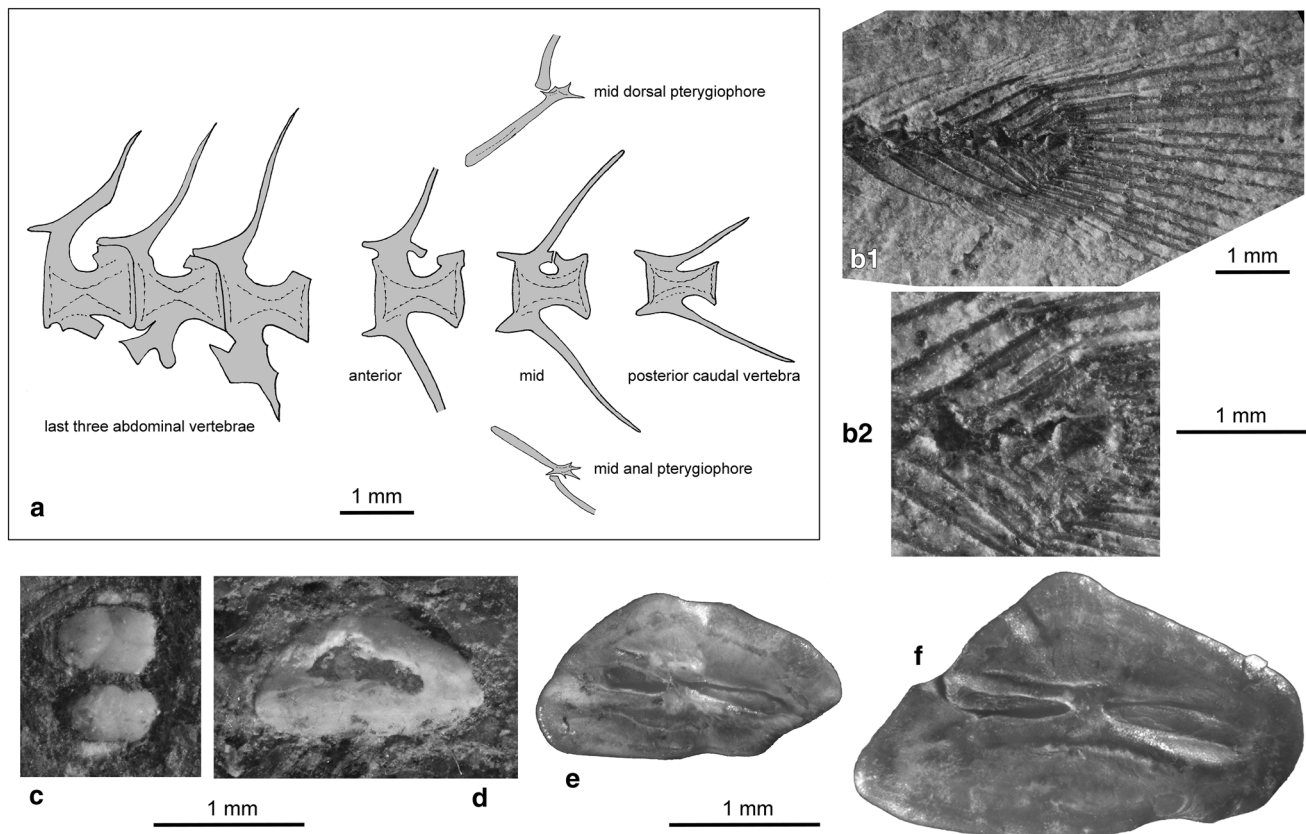
**Distribution** *Paratrisopterus caspius* is a common species in the Middle and Late Miocene of the Paratethys. The earliest records of the species are from Djafarova (2006) from the Chokrakian of Azerbaijan (as *Macrurus* sp.). Other records are from the late Badenian of Romania, the Sarmatian s.s. of the Central Paratethys, and the early to middle Sarmatian s.l. of the Eastern Paratethys (Weiler 1943; Pobedina 1954, 1956; Djafarova 2006). A second species of the genus is known from the same time interval in the Central and Eastern Paratethys by otoliths [*P. rumanus* (Weiler 1943)], and a species from the Eastern Paratethys by skeletons [*P. kiplingi* (Bogatshov 1929)]. A number of *Paratrisopterus* species are known outside of the Paratethys in the Mediterranean and the North Sea Basin from Late Oligocene to Early Pliocene, but none of them occur in the Paratethys after the early Badenian. Vice versa, the two otolith-based species from the Paratethys have been rarely found outside: *P. caspius* in the Late Miocene of the North Sea Basin (assuming *P. irregularis* to represent a junior synonym) and *P. rumanus* in the Messinian of Greece (unpublished data).

#### Family Lotidae Bonaparte 1835

We follow Markle (1989) and Howes (1989) in recognizing the Lotidae as a separate family mainly because of the high degree of dissimilarity in otolith pattern that has been shown to be separate at least since Paleocene times.







**Fig. 6** *Enchelyopus susedanus*. **a–d** early Sarmatian of Dolje, Croatia. **a** CNHM 168, posteriormost abdominal vertebrae, anterior, middle and posterior caudal vertebrae, mid-dorsal and mid-anal pterygiophores. **b** CNHM 240, caudal skeleton; **b2** detail of median

hypural fan. **c** CNHM 240, close-up of otoliths in situ. **d** CNHM 168, close-up of right otolith in situ. **e, f** Isolated otoliths, middle Sarmatian, Jurkino, Crimea

#### Subfamily Gaidropsarinae Rafinesque, 1810

#### Genus *Enchelyopus* Bleeker 1862

#### *Enchelyopus susedanus* (Kner 1863)

(Figs. 5a, b, 6a–d)

1863 *Brosmius susedanus* Kner. Kner: pl. 3, Fig. 3.

1883 *Brosmius elongatus* Kramberger. Kramberger: pl. 15, Fig. 2.

**Material** Seven specimens from Dolje, Croatia, Sarmatian s.s. (Volhynian): CNHM 168 and its counter-plate CNHM 239 (SL 56.5 mm) (Fig. 5a); CNHM 169 (SL 44.5 mm); CNHM 240 plate and counter-plate (SL 35.5 mm) (Fig. 5b); CNHM 252 (SL 27 mm); CNHM 294 (SL 45.5 mm); plus the holotype of *B. elongatus*, CNHM 121 (SL 41 mm). Two of these specimens contain otoliths in situ (CNHM 168 and 240).

**Diagnosis** Vertebral column with 44–46 vertebrae, of which 12 or 13 abdominal; second dorsal fin with 44–48 rays; anal fin with 32–37 rays; pectoral fin with 14–17 rays; pelvic fin with 5 rays; second dorsal fin inserts above vertebrae 6–8; anal fin inserts below vertebrae 13–15;

second dorsal-fin base 56–59 % SL; anal-fin base 38–41.5 % SL; head profile blunt; head depths 16 to 17 % SL; slender parapophyses on the last three to six abdominal vertebrae; otoliths triangular with flat ventral rim and compressed (OL:OH = 1.7–1.85); sulcus narrow throughout.

**Description** (based primarily on CNHM 168/239 and 240, Figs. 5a, b, 6a, b): body elongate and laterally compressed. Counts and measurements are reported in Table 3.

**Neurocranium** The neurocranium appears compact and stout, but the head bones are too much crushed in all the examined specimens so that the individual bones and their morphology are difficult to recognize except for the straight parasphenoid (Fig. 5a).

**Jaws** The tip of the premaxilla shows a slightly forward inclined, slender and moderately long ascending process (Fig. 5a). The articular process is not preserved. The posterior end of the maxilla appears to be widened. The upper jaw bears a set of small teeth anteriorly in CNHM 168 (Fig. 5a1). The mandible is preserved in the specimens CNHM 239 and 240

**Table 3** Counts and measurements of *Enchelyopus susedanus*

Details as measured	Holotype of <i>Brosmius elongatus</i>	<i>Enchelyopus susedanus</i>					Range
		Identified as <i>Brosmius susedanus</i> by Kramberger					
		CNHM 121	CNHM 168/239	CNHM 240	CNHM 169	CNHM 252	
SL (mm)	40.8	56.5	36	44.6	26.8	45.5	
<i>Meristics</i>							
Precaudal vertebrae	13	13	12	12	13	7+	12–13
Total vertebrae	44–45	45	44	45	44	38+	44–45
Depressed haemal spines	v2–5 (6)		V3–5	v3–8			v2–8
Parapophyses (broad)	v8–13 (8–11)		v8–11 (9–11)				v8–13 (8–11)
D1	nv	nv	nv	nv	nv	nv	nv
D2	44–46	46–47	45	48	45?	44	44–48
A	33–34	36–37	36–37	33	33?	32	32–37
Pectoral	13 or 14	14	16–17	nv	nv	16	13–17
Pelvic	nv	5	4+	nv	nv	nv	5
Caudal	31	32–33	30	28+	nv	31	30–33
D2/VE	5	7	8	6	nv		5–8
VE/A	12	14–15	13	13	nv		12–15
<i>Morphometrics (% of SL)</i>							
Head length	25.7	23.0	23.2	27.1	23.5	22.6	23.0–27.1
Head height		16.7	16.2				16.2–16.7
Pectoral length		15.5	18.2				15.5–18.2
Predorsal 2	36.3	33.5	34.5	34.8	35.4	35.2	33.5–36.3
Preanal	47.5	47.3	47.6	50.2	43.3		43.3–50.2
Base D2		59.0	56.0				56.0–59.0
Base A		41.4	37.8				37.8–41.1

(Fig. 5a2, b) and projects forward as much as the premaxilla. The dentary bears numerous small teeth.

*Suspensorium* The structure of the suspensorium is not clearly recognizable in any of the examined specimens. However, some bones (i.e., quadrate, pterygoids) are partially preserved in CNHM 168/239 (Fig. 3) and their morphology is consistent with that of other gaidropsarines (see, e.g., Stainier et al. 1986; Endo 2002; Carnevale and Harzhauser 2013).

*Opercular series* Opercular bones are not well enough preserved to warrant detailed description. Specimen CNHM 240 shows a partially preserved opercle with a thickened upper margin.

*Visceral arches* A robust hyoid bar bearing six elongate branchiostegal rays is preserved in CNHM 239 (Fig. 5a2); an additional ray appears to be present in its counterpart (CNHM 168).

*Axial skeleton* The vertebral column is well preserved in CNHM 168/239 and, except for the anterior four to five vertebrae, also in CNHM 240. The first two abdominal

vertebrae are compressed usually hidden under the overlying head bones; the subsequent abdominal vertebrae have short neural spines, which appear to be depressed up to about the eighth vertebra and more upright and slender in the following ones. Parapophyses are visible only in the last three abdominal vertebrae in both figured specimens, even if other specimens showed parapophyses in the last five to six abdominal vertebrae. The parapophyses are mostly short and slender except for the posterior one emerging on the last abdominal vertebra, which is more massive and thickened (Fig. 6a). The caudal vertebrae (Fig. 6a) show long neural and haemal spines which become gradually inclined backward. The centra are subrectangular, about as long as high, with a notably concave dorsal profile. Dorsal and ventral prezygapophyses are broad and moderately elongate. The postzygapophyses are usually poorly developed. The central part of the neural arch of the central caudal vertebrae is characterized by a sort of incomplete foramen, which appears to be a unique within gadids and lotids according to Watt et al. (1997). The small hypural fan (hypurals 3–5) is well preserved in

CNHM 240 (Fig. 6b); however, the lower hypaxial hypural, parhypural and the epurals are difficult to identify.

**Median fins** (Fig. 5) A single elongate dorsal fin is clearly preserved; however, there are vague indications of the presence of the anterior dorsal fin (Fig. 5a1, a4), which is synapomorphic of gaidropsarine fishes and, due to their very delicate nature, uncommonly preserved in fossils (see Carnevale, 2007; Carnevale and Harzhauser 2013). The (second) dorsal fin inserts above the fifth to eighth vertebrae and contains 44–48 rays. The anterior rays are short and increase in length up to the fifth ray, which is the first fully developed. The dorsal-fin ray length remains homogenous and gradually decrease posteriorly in the series. The dorsal fin base is rather large, reaching almost 60 % SL. There is a single elongate anal fin containing 32–37 rays, which inserts below vertebrae 12–15; the anal-fin base represents 38–41.5 % SL. The anal fin rays of the anterior half of the fin are about half as long as most of the dorsal-fin rays; the posterior rays are considerably longer, the longest being the eighth counted from the back, which is equally long as the longest dorsal-fin ray. The dorsal- and anal-fin pterygiophores are well developed and delicate as shown in Fig. 6a. The caudal fin is rounded with 28–35 rays, six of which are procurent both dorsally and ventrally.

**Paired fins and girdles** (Fig. 5) The pectoral fin is moderately long. It contains 14–17 rays and in the case of the holotype of '*Brosmius elongatus*' the first and second rays are notably elongate. The pelvic fin is well preserved in the specimen CNHM 168/239 and shows five rays with the second apparently being the longest.

**Scales and soft tissue** The body is densely covered with many small cycloid scales up to 0.5 mm in diameter and show up as a dark film marking the body contours in the two figured specimens. No scales are visible on the head. Specimen CNHM 168 shows an elongate patch of dark organic tissue below the abdominal vertebrae representing remnants of the gut. No details are preserved that would allow identification of the fish diet.

**Otolith** (Fig. 6c, d) Otoliths are preserved in two specimens (CNHM 168 and 240). Specimen CNHM 168 shows a right otolith from the inner face, but unfortunately part of it is damaged carrying a major portion of the sulcus. The smaller specimen CNHM 240 shows two otoliths from the outer face. Extracting them unfortunately did not reveal much features on the inner face. However, the outline of the otolith of specimen CNHM 168 and the few features still visible on the inner face are very characteristic for a gaidropsarine otolith. We found many isolated otoliths in the middle Sarmatian s.l. of Jurkino, Crimea (unpublished data), which fit well and are interpreted to represent the

same species (Fig. 6e–f), and these are used here for the description.

The otoliths are roughly triangular in outline with a nearly flat ventral rim and a distinct mediadorsal angle, which in small specimens is less pronounced and more rounded. Isolated otoliths reach a size of about 3.5 mm length. OL:OH = 1.7–1.85; OL:OT = 4–5. The dorsal rim shows a prominent angle slightly anterior of the middle, which is variably expressed and usually more rounded and less prominent in juveniles smaller than 1.5 mm length. The predorsal part is usually straight, inclined upwards, the postdorsal part less steeply inclined and often slightly convex. The ventral rim is nearly flat and horizontal, but occasionally shows a broad, slightly upwards inclined posterior portion close to the posterior tip of the otolith. The anterior and posterior tips of the otolith show are much ventrally shifted and moderately pointed, the anterior tip usually sharper than the posterior tip. All rims are smooth or show a broad, irregular undulation. The inner face is slightly bent with a narrow, slightly posterior-ventrally inclined sulcus, which indistinctly opens anteriorly and posteriorly. Ostium and cauda are about equal in length or the cauda is slightly longer. Both are also about equally high or ostium slightly higher. The colliculi are narrow, somewhat deepened, and terminate at some distance from the anterior and posterior rims of the otolith, respectively. The collum is narrow and without a pseudocolliculum. The dorsal field shows a small dorsal depression above the collum. The ventral furrow is distinct, its posterior part running closer to the ventral rim of the sulcus than to the ventral rim of the otolith. The outer face is slightly convex, smooth or with few vertical furrows.

The otoliths show considerable variability, particularly in the expression of the mid-dorsal angle as well the anterior and posterior tips. Ontogenetic changes are related to the outline, which is much more rounded in small specimens and the generally thicker appearance of juvenile otoliths.

**Discussion** Kramberger (1883) established *B. elongatus* solely based on the unique holotype and distinguished it from *E. susedanus* for the more slender shape and lower number of fin rays in the dorsal and anal fins. A review of the holotype by one of us (WS) revealed that the number of vertebrae and dorsal- and anal-fin rays may in fact be slightly higher than noted by Kramberger and would be well within an expected variation of *E. susedanus*, although probably close to its lower limit of range. We therefore consider *B. elongatus* as a junior synonym of *E. susedanus*.

*Enchelyopus susedanus* is notable for its low number of fin rays and is readily distinguished from all extant gaidropsarines for the low number of anal-fin rays (32–37 vs 38–51), short anal-fin base (38–41.5 % SL, which is



only matched by *Onogadus argentatus*), and the forward position of the dorsal fin inserting above vertebrae 6–8 (vs 9–12). Other distinguishing characters are the stout, high profile of the head (16–17 % SL), and the peculiar shape of certain caudal vertebrae with a sort of incomplete foramen in the central part of the neural arch, representing a feature unique within gadids and lotids (see Watt et al. 1997); moreover, *E. susedanus* exhibits compressed, triangular otoliths with a narrow sulcus.

In his monographic analysis of gadiform fishes, Svetovidov (1948) distinguished three gaidropsarine genera (*Onogadus* considered as a synonym of *Gaidropsarus*) based on the number of barbels on the snout, skull shape, vomerine tooth patch shape, and number and distribution of supratemporal pores. All these characters are not prone to the fossilization processes (barbels and pores) or are rarely exposed (see also Carnevale and Harzhauser 2013). According to Cohen and Russo (1979) of the traits used by Svetovidov only the number of barbels ‘unequivocally divides their material according to Svetovidov’s classification’. Svetovidov (1948) also noted that *Gaidropsarus* has short and broad parapophyses, thereby suggesting that the morphology of the parapophyses may represent a useful feature to distinguish fossil gaidropsarines (Carnevale and Harzhauser 2013). However, the data used by Svetovidov (1948) were based exclusively on *G. mediterraneus*. In a subsequent review of the genus *Gaidropsarus* Svetovidov (1986) did not recognize the taxonomic relevance of this character, and also indicated that meristic features, particularly number of vertebrae, are not useful for the separation of the gaidropsarine genera. The analysis of a number of X-rays of fishes from various species of *Gaidropsarus*, *Ciliata*, *Enchelyopus* and *Onogadus* of different sizes from the collection of the Zoological Museum of the University of Copenhagen (ZMUC), led to the conclusion that the shape of the parapophyses is not a stable trait to distinguish *Gaidropsarus* from the other three genera, particularly not with small specimens like the fossils studied here. On the other hand, meristics and head morphology and proportions may be still valuable in fossils in the absence of soft tissue characters. Another useful character to recognize *Gaidropsarus* from the other gaidropsarine genera are otoliths as recently assessed by Bratishko et al. (2015). Two types of otoliths were defined within gaidropsarines: “one with thin otoliths with convex inner and concave outer faces, an elongate outline, a low and rounded mediodorsal rim, a wide cauda and a notable twist along the horizontal axis, found in the genus *Gaidropsarus* and in *Ciliata mustela*; the other with thick otoliths with a flat or slightly convex inner and a flat or slightly convex outer face, a moderately elongate to compressed outline with a

distinct mediodorsal angle, a rather narrow cauda and no or only a slight twist along the horizontal axis found in *Ciliata septentrionalis*, *Enchelyopus* and *Onogadus*”.

The meristics and morphometrics of *E. susedanus* are close to those of extant species of the genera *Ciliata*, *Enchelyopus* and *Onogadus*. It shares a low number of vertebrae with *Ciliata*, the stout head profile and the short anal-fin base with *Onogadus*, and the low number of dorsal-, pelvic- and caudal-fin rays with *Enchelyopus*. *Enchelyopus cimbrius*, the only extant species of the genus, shows a similar low number of dorsal-fin rays (47–48 vs 44–48), as well as the anterior position of the dorsal fin inserting above vertebrae 9–11 (vs 6–8). Watt et al. (1997) figured caudal vertebrae of *Ciliata*, *Enchelyopus* and *Gaidropsarus vulgaris*. Only the vertebrae of *Enchelyopus* show a wide and deep dorsal concavity in the central part of their neural arches, which is even more developed in *E. susedanus*, forming an incomplete foramen-like structure. Finally, the compressed, triangular otolith with the narrow sulcus, particularly narrow cauda and little curvature of the inner face matches with the second pattern defined by Bratishko et al. (2015), more particularly with the otoliths of *Enchelyopus cimbrius* (see also Lombarte et al. 2006). Based on the combination of these characters, we tentatively consider ‘*Brosmius*’ *susedanus* as a representative of the genus *Enchelyopus*. However, additional osteological comparative information about extant gaidropsarine genera would be necessary to conclusively demonstrate the actual affinities of this Sarmatian fossil taxon.

A second fossil otolith-based species—*Enchelyopus gae-mersi* (Schwarzahans 2010)—has been described from the Reinbekian (Langhian equivalent) of the North Sea Basin. This species can be distinguished from *E. susedanus* by having a more elongate shape (OL:OH = 1.85–2.1 vs 1.7–1.85) and the projecting posterior tip, which is more sharply pointed than the anterior tip (vice versa in *E. susedanus*).

*Distribution* *Enchelyopus susedanus* appears to be confined to the early and middle Sarmatian s.l. of the Central and Eastern Paratethys. It is absent in the rich Konkian/late Badenian otolith assemblages of Kazakhstan, which yielded *Onogadus simplicissimus* (Schubert 1906) as the only representative of the Gaidropsarinae. Isolated otoliths of *E. susedanus* are fairly common in the middle Sarmatian s.l. of Jurkino, Crimea, where it occurs associated with *O. simplicissimus* (unpublished data).

## Conclusions

The new finds of otoliths in situ in gadiform fishes from the Neogene of Europe has brought up the correlation of skeleton and otolith data to a total of four taxa. This is still a small part

when compared to the total number of the known otolith-based gadid species. However, it improves our knowledge of the actual taxonomic affinities of many of the isolated otolith finds. In the case of *Palimphemus macropterygius* it helped not only to synonymize with another well known otolith-based species [*P. minusculoides* (Schubert 1912)]; which was recently reviewed and redefined by Bratishko et al. 2015], but also confirms and corroborates the definition of the extinct genus *Palimphemus*. In the case of *Paratrisopterus caspius* several otolith-based species can be synonymized—*P. insectus* (Weiler 1943) and possibly also *P. irregularis* (Gaemers 1973). It also shows that *Paratrisopterus* otoliths may show a larger variability and ontogenetic change than sometimes assumed based on isolated otoliths alone. Isolated otolith data on the other hand did confirm that *Paratrisopterus* indeed was an unusually small gadid probably characterized by an epipelagic lifestyle in shallow seas. Finally, in the case of *Enchelyopus susedanus* we have demonstrated the relevant value of otoliths in situ for the taxonomic assignment at the genus level.

We believe that further studies dealing with otoliths in situ will contribute to a better calibration of isolated otolith finds and, vice versa, that the use of otoliths and their abundance in the fossil record will contribute to a better definition of skeleton-based records and a better understanding of the distribution and evolution of fossil fishes.

**Acknowledgments** We are very thankful to J. Nielsen and P. Møller (Copenhagen) for making available for study extant gadid and lotid specimens from the collection of ZMUC. We thank A. Prokofiev (Moscow) for information concerning material from Bogatshov and Fedotov. We further wish to thank associate editor Lionel Cavin and the two anonymous reviewers for their positive evaluation of the manuscript. The research of GC was supported by Grants (ex-60 % 2014 and 2015) from the Università degli Studi di Torino. The field work of AB in the Crimea was supported by the Institute of Geological Sciences of the National Academy of Sciences of Ukraine and Sepkoski Grant 998X-14-60753-1.

## References

- Andjelković, J. (1969). Fosilne ribe iz donjeg sarmata teritorije Beograda. *Glasnik Prirodnjačkog Muzeja (in Serbian) A*, 24, 127–154.
- Andjelković, J. (1989). Tertiary fishes of Yugoslavia. Stratigraphic-paleontologic-paleoecological study. *Palaeontologia Yugoslavica*, 38, 1–121.
- Bannikov, A. F., & Kotlyar, A. N. (2015). A new genus and species of early Sarmatian porgies (Perciformes, Sparidae) from the Krasnodar Region. *Paleontological Journal*, 49, 627–635.
- Baykina, J., & Schwarzahns, W. (2016, in press). Description of *Karaganops* n.gen. *perrata* (Daniltschenko, 1970) with otoliths in situ, an endemic Karaganian (Middle Miocene) herring (Clupeidae) in the Eastern Paratethys. *Swiss Journal of Palaeontology*.
- Bogatshov, V. V. (1929). Whale and fish remains in diatom deposits of Apsheronki Peninsula. *Azerbaidjanski neftyanoe khozyaistvo (in Russian)*, 77, 33–39.
- Bogatshov, V.V. (1933). Materials on the study of Tertiary ichthyofauna of Caucasus. *Trudi Azerbaidjanski Neftyanoe Issledovaniye in-ta (AzNII), Geologicheskii Otdel (in Russian)*, 15, 1–62.
- Bratishko, A., Schwarzahns, W., Reichenbacher, B., Vernihorova, Y., & Čorić, 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. (2007). New gadiform fishes (Teleostei, Gadiformes) from the Miocene of Algeria. *Journal of African Earth Sciences*, 47, 95–111.
- Carnevale, G., Bannikov, A. F., Landini, W., & Sorbini, C. (2006). Volhynian (Early Sarmatian s.l.) fishes from Tsurevsky, North Caucasus (Russia). *Journal of Paleontology*, 80, 684–699.
- Carnevale, G., & Harzhauser, M. (2013). Middle Miocene rockling (Teleostei, Gadidae) from the Paratethys (St. Margarethen in Burgenland, Austria). *Bulletin of Geosciences*, 88, 609–620.
- Carnevale, G., Harzhauser, M., & Schultz, O. (2012). The Miocene gadid fish *Palimphemus anceps* Kner, 1862: a reappraisal. *Geodiversitas*, 34, 625–643.
- Cohen, D. M., & Russo, J. L. (1979). Variation in the fourbeard rockling, *Enchelyopus cimbrius*, a North Atlantic gadid fish, with comments on the genera of rocklings. *Fishery Bulletin*, 77, 91–104.
- d'Erasmus, G. (1930). Studi sui pesci neogenici d'Italia. Parte III. L'ittiofauna fossile del Gabbro. *Atti dell'Accademia delle Scienze fisiche e matematiche*, 18, 1–87.
- Djafarova, J. D. (2006). *Otolity neogena Azerbaidjana (Neogene otoliths of Azerbaijan)*. Baku: Nafta. (in Russian).
- Endo, H. (2002). Phylogeny of the Order Gadiformes (Teleostei, Paracanthopterygii). *Memoirs of the graduate school of fisheries sciences, Hokkaido University*, 49, 75–149.
- Fedotov, V. F. (1971). Novyi iskopaemyi rod semeistva treskovykh. *Paleontologicheskii Zhurnal (in Russian)*, 3, 121–124.
- Fedotov, V.F (1976). Gadidae of the Palaeogene-Neogene from the USSR. *Trudy Paleontologicheskogo Instituta*, 157, 1–84. [Official English translation of the original Russian version, marked Translation No. 75, by Walter Ivantsoff].
- Gaemers, P. A. M. (1973). New otoliths from the Tertiary of the North Sea Basin. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, 10, 58–75.
- Gaemers, P. A. M. (1983). The otoliths from the Syltian (Late Miocene) of the Morsum Cliff, island of Sylt (Federal Republic of Germany), and the palaeogeography of the North Sea Basin during and after the Syltian. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, 20, 67–91.
- Gaemers, P. A. M. (1990). The definition of the classical Paleogene-Neogene boundary in the North Sea Basin by means of Gadidae otoliths (Pisces). *Tertiary Research*, 11, 97–144.
- Howes, G. J. (1989). Phylogenetic relationships of macrouroid and gadoid fishes based on cranial myology and arthrology. In: Cohen, D. M. (Ed.), *Papers on the systematics of gadiform fishes. Science series, Natural History Museum of Los Angeles County*, 32, 113–128.
- Jerzmańska, A. (1962). Szcetki ryb kostnoszkieletowych z Miocenu Górnego Śląska. *Acta Palaeontologica Polonica (in Polish)*, 7, 235–247.
- Kner, R. (1862). Kleinere Beiträge zur Kenntnis der fossilen Fische Österreichs. *Sitzungsberichte der kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe, Abt. I*, 45, 485–498.

- Kner, R. (1863). Über einige fossile Fische aus den Kreide- und Tertiärschichten von Comen und Podused. *Sitzungsberichte der kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe, Abt. I*, 48, 126–148.
- Kner, R., & Steindachner, F. (1863). Neue Beiträge zur Kenntnis der fossilen Fische Österreichs. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe*, 21, 17–36.
- Koken, E. (1891). Neue Untersuchungen an tertiären Fisch-Otolithen II. *Zeitschrift der deutschen geologischen Gesellschaft*, 43, 77–170.
- Kramberger (Gorjanović-Kramberger), D. (1880). Die fossilen Fische von Würzenegg bei Prassberg in Steiermark. *Jahrbuch der Geologischen Reichsanstalt*, 30, 565–572.
- Kramberger (Gorjanović-Kramberger), D. (1883). Die jungtertiäre Fischfauna Croatiens II. *Beiträge zur Paläontologie Österreich-Ungarns und des Orients*, 3, 65–85.
- Kramberger (Gorjanović-Kramberger), D. (1885). Palaeoichtyološki prilozi. *Rad JAZU (in Croatian)*, 72, 10–65.
- Landini, W., & Sorbini, C. (1999). Systematic and palaeobiogeographical observations on the gadid fish *Gadiculus labiatus* (Schubert 1905). *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 8, 43–58.
- Lombarte, A., Chic, O., Parisi-Baradad, V., Olivella, R., Piera, J., & Garcia-Ladona, E. (2006). A web-based environment for shape analysis of fish otoliths. The AFORO database. *Scientia Marina*, 70, 147–152.
- Markle, D.F. (1989). Aspects of character homology and phylogeny of Gadiformes. In: Cohen, D. M. (Ed.), Papers on the systematics of gadiform fishes. *Science series, Natural History Museum of Los Angeles County*, 32, 59–88.
- Nolf, D. (1981). Révision des types d'otolithes de poissons fossiles décrits par R. Schubert. *Verhandlungen der Geologischen Bundesanstalt*, 2, 133–183.
- Nolf, D. (1985). Handbook of paleoichthyology, Volume 10, Otolithi piscium. Munich: Dr. Friedrich Pfeil, 1–145.
- Nolf, D. (2013). The diversity of fish otoliths, past and present. Brussels: Royal Belgian Institute of Natural Sciences, 1–222.
- Pauca, M. (1929). Vorläufige Mitteilungen über eine fossile Fischfauna aus dem Oligozänschiefern von Suslănești (Muscel). *Bulletin de l'Académie Roumaine, Secteur Scientifique*, 12, 26–34.
- Pobedina, V. M. (1954). Iskopaemye otolity ryb miocenovykh otlozheniy Azerbaidzhan i ih stratigraficheskoe znachenie (Fossil fish otoliths from the Miocene deposits of Azerbaijan and their stratigraphical significance). *Izvestia Akademii Nauk Azerbaidzhanoy SSR (in Russian)*, 10, 23–37.
- Pobedina, V. M., Voroshilova, A. G., Rybina O. I., & Kuznetsova, Z. V. (1956). Spravochnik po mikrofaune sredne—i verkhnemio-cenovykh otlozhenii Azerbaidzhan (Handbook about microfauna of Middle and Upper Miocene deposits of Azerbaijan). Baku: Azerbaidzhanoskoe gosudarstvennoe izdatelstvo neftyanoi nauchno-tekhnicheskoy literatury (in Russian)
- Prokofiev, A. M. (2004). On the attribution of *Paratrisopterus avus* to the genus *Gadiculus* (Gadiformes: Gadidae). *Journal of Ichthyology*, 44, 412–417.
- Schubert, R. J. (1906). Die Fischotolithen des österreichisch-ungarischen Tertiärs. III. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt*, 56, 623–706.
- Schubert, R. J. (1912). Die Fischotolithen der ungarischen Tertiärlagerungen. *Mitteilungen aus dem Jahrbuch der Königlichen Ungarischen Geologischen Reichsanstalt*, 20, 115–139.
- Schwarzhan, 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.
- Schwarzhan, W. (1994a). Die Fisch-Otolithen aus dem Oberoligozän der Niederrheinischen Bucht. Systematik, Palökologie, Paläobiogeographie, Biostratigraphie und Otolithen-Zonierung. *Geologisches Jahrbuch (A)*, 140, 1–248.
- Schwarzhan, W. (1994b). Sexual and ontogenetic dimorphism in otoliths of the family Ophidiidae. *Cybium*, 18, 71–98.
- Schwarzhan, W. (2010). *The otoliths from the Miocene of the North Sea Basin* (pp. 1–352). Weikersheim/Leiden: Backhuys/Margraf.
- Schwarzhan, W. (2014). Synonymisation of the skeleton-based *Palimphemus anceps* Kner 1862 and the otolith-based *Colliolus sculptus* (Koken 1891) (Pisces, Teleostei, Gadidae). *Cainozoic Research*, 14, 9–16.
- Schwarzhan, W., Carnevale, G., Bannikov, A. F., Japundžić, S., & Bradić, K. (2016). Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part I: *Atherina suchovi* Switchenska 1973. *Swiss Journal of Palaeontology*
- Smigielska, T. (1966). Otolity Ryb z Tortonu Południowej Polski. *Rocznik Polskiego Towarzystwa Geologicznego—Annales de la Société géologique de Pologne (in Polish)*, 36, 205–275.
- Stainier, F., Chardon, M., & Vandewalle, P. (1986). Os, muscles et ligaments de la région céphalique de *Ciliata mustela* (Linné 1758) (Pisces, Gadidae). *Cybium*, 10, 327–349.
- Steindachner, F. (1863). Beiträge zur Kenntnis der fossilen Fische Österreichs. *Sitzungsberichte der kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe, Abt. I*, 47, 128–142.
- Strashimirov, B. (1984). Otolity ot dolnia sarmat na Severnaia Bulgaria. *Palaentology, Stratigraphy and Lithology (in Bulgarian)*, 20, 15–41.
- Suzin, A. V. (1968). Otoliths. In B. Zhizhchenko (Ed.), *Micropaleontologicheskii metody stratigraficheskikh postroyeniy v neftegazonosnykh oblastyah (Micropaleontological methods of stratigraphical research in the oil-and-gas bearing region)* (pp. 74–77). Moscow: Nedra. (in Russian).
- Svetovidov, A. N. (1948). Treskoobraznye (Gadiformes). *Fauna SSSR, Zoologicheskii Institut Akademii Nauk SSSR* 34, Ryby (Fishes), new Series, 34, 1–222 (in Russian; English translation, 1962, Jerusalem: Israel Program for Scientific Translation, 304 p.).
- Svetovidov, A. N. (1986). Review of rocklings of the genus *Gaidropsarus* Rafinesque, 1810 (Gadidae), with a description of a new species. *Journal of Ichthyology*, 26, 114–135.
- Watt, J., Pierce, G. J., & Boyle, P. R. (1997). Guide to the identification of North Sea fish using premaxillae and vertebrae. *ICES Cooperative Research Report*, 220, 1–231.
- Weiler, W. (1942). Die Otolithen des rheinischen und nordwestdeutschen 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. (1949). Die Otolithen aus dem Jung-Tertiär Süd-Rumäniens; 1b. Ergänzende Tafeln zu den Otolithen des Buglow und Sarmat. *Senckenbergiana Lethaea*, 30, 291–293.
- Weiler, W. (1950). Die Otolithen aus dem Jung-Tertiär Süd-Rumäniens; 2. Mittel-Miozän, Torton, Buglow und Sarmat. *Senckenbergiana lethaea*, 31, 209–258.