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# Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part I: *Atherina suchovi* Switchenska, 1973

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**Abstract** Several well-preserved otoliths were extracted from four slabs containing fish specimens of *Atherina suchovi*. *Atherina suchovi* is one of the five *Atherina* species recorded from the Middle Miocene of the Central and Eastern Paratethys established on articulated skeletal remains. This corresponds to two otolith-based species so far identified from the same time interval in the Paratethys—*Atherina austriaca* and *Atherina gidjakensis*. Our correlation of isolated otoliths and otolith in situ documents in this case that *A. suchovi* is not synonymous to any of the otolith-based species, although it appears to be closely related to *A. gidjakensis*. A list is presented and briefly discussed showing Sarmatian skeleton-based fish records from the Central and Eastern Paratethys with an overview of known and currently studied fishes with otoliths in situ.

**Keywords** Ichthyology · Teleost · Atherinidae · Paleontology · Moldavia

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## Introduction

About 60 fossil fish specimens with otoliths in situ have been studied from Sarmatian strata of the collections of the Croatian Natural History Museum, Zagreb (CNHM), Serbian Natural History Museum, Belgrad (NHMB), the Faculty of Mining and Geology of the University of Belgrade (IGOT) and the Borisyak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN) representing 20 nominal fish species and bringing the total number of Paratethyan fishes with otoliths in situ to 30 nominal species. These will be described in a sequence of research papers, of which this is the first one, and when finalized will represent the largest fossil fish assemblage with otoliths in situ known to date. This first part is dealing with *Atherina suchovi*. A certain part of the article is constructed to serve as an overall introduction for all following parts to set the scene and reduce unnecessary redundancy.

Several of the specimens studied represent holotypes, lectotypes, paratypes, paralectotypes or syntypes, but many others are not type-specimens of any kind and, therefore, their taxonomic allocation will be reviewed in the course of the study where appropriate. The specimens studied from the Borisyak Paleontological Institute of the Russian Academy of Sciences, Moscow were identified by Bannikov or Baykina; the material housed in the Croatian Natural History Museum mostly belongs to the collection "Sarmatian fishes of Croatia and Slavonia" described by Dragutin Gorjanović-Kramberger and includes either type-specimens of some kind or can be related to relevant type-specimens; the Andjelković collection in the Serbian Natural History Museum and the University of Belgrade is more problematic since they contain few type-specimens and many of the identifications are in need of revision.

Otoliths in situ in fossil fish are very important for paleoichthyological studies, because they provide a crucial evidence for potential parallel taxonomy (Bachmayer and Weinfurter 1965; Bedini et al. 1986; Fedotov 1971; Gaudant and Reichenbacher 2005; Schwarzhans 2014), as well as a remarkable opportunity in otolith research to calibrate fossil findings with coeval data derived from articulated skeletons, while otherwise systematic allocation of isolated fossil otoliths is restricted to comparison with extant otoliths only. Fossil fish skeletons of teleosts with otoliths in situ have traditionally been regarded to be rather rare. In 1985, Nolf listed not more than 45 species of fossil fishes recorded with otoliths in situ, and considered only 23 of them to have otoliths ‘well enough preserved or suitable oriented to show taxonomically useful features’. In Nolf (2013), the list was expanded to 96 fish species with otoliths recorded in situ, of which 45 were considered as taxonomically ‘useful’. The scarcity of fossil otoliths in situ, however, has never been exhaustively explained or challenged, even though it is evident that otoliths, which consist of aragonite are much easier dissolved during rock diagenesis or exposure compared with bones, scales and teeth. Our ongoing study, of which this is the first part, will demonstrate that fossil otoliths in situ may in fact be more common than commonly perceived and hopefully contribute to more research work in this field.

In a study dealing with otoliths in situ of the gadid *Palimphemus anceps* Kner 1862, Schwarzhans (2014) reminded about a publication by Schubert (1906), who mentioned 10 species from the Sarmatian of Dolje near Zagreb in which he had observed otoliths in situ. Tragically, the untimely death of Schubert, who perished during World War I, prevented him to work on that material. In 2010, Bannikov noted in passing that fishes from the Sarmatian of Russia and Moldavia, i.e., Eastern Paratethys almost always contain otoliths in situ, and in fact described himself a few such species—*Morone ionkoi* Bannikov 1993; *Symphodus salvus* Bannikov 1986; *Clinitrachoides gratus* (Bannikov 1989). The description of a sparid fish (*Pshekharus yesinorum* Bannikov and Kotlyar 2015) with otoliths in situ was in press by Bannikov and Kotlyar during the time of manuscript submission. Other otoliths in situ previously described from Badenian and/or Konkian-Sarmatian fishes of the Central and Eastern Paratethys were reported in *Bregmaceros albyi* (Sauvage, 1880) (in Bachmayer and Weinfurter 1965), *Micromesistius* sp. (Carnevale et al. 2006), *Palimphemus anceps* Kner 1862 (in Schwarzhans 2014), *Paratrisopterus avus* Fedotov 1971 (in Fedotov 1976), *Sparus insignis* (Prochazka 1893) (in Brzobohaty 1979), *Protonymus gontsharovae* Sytchevskaya and Prokofiev 2007 (in Sytchevskaya and Prokofiev 2007) and *Gobius elatus* Steindachner 1860 (in Schultz 2013). We took up these valuable reports to systematically search for otoliths in situ of Sarmatian fishes primarily from the collection of “Sarmatian fishes of Croatia and Slavonia” described by Dragutin Gorjanović-Kramberger from Dolje near Zagreb housed in the Croatian Natural History Museum in Zagreb, the collection assembled by Jelena S. Andjelković from excavations at the Belgrad football stadium and housed in the Serbian Natural History Museum and the University, Belgrad, and from the collection of the Borisyak Paleontological Institute of the Russian Academy of Sciences, Moscow in large part collected by Alexandre F. Bannikov.

Table 1 summarizes the teleost species recorded from the Sarmatian (and Konkian) described from the Central Paratethys based on Andjelković (1989), Baciu et al. (2005) and Schultz (2013) and the Eastern Paratethys based on Carnevale et al. (2006), Bannikov (2010) and Baykina (2012, 2015). We consider the taxonomic status of the fishes from the Eastern Paratethys as modern and adequate, but the taxonomic status of the fishes from the Central Paratethys is in urgent need of review. For instance, one might readily conclude that the number of species in clupeids or gadids in the Central Paratethys could be exaggerated and that the occurrence of Mediterranean species in the isolated Middle Miocene Paratethys appears unlikely. However, it is not our target to perform a taxonomic review of the fishes concerned, except when otoliths and fishes with otoliths in situ provide for new insights. The purpose of our study is to adequately document the data, with focus on the otoliths in situ, and align skeletal and otolith-based identifications wherever possible to provide the basis for calibrating the fossil otolith record.

## Materials and methods

Among the type series of *A. suchovi* (Switchenska 1973) housed in the PIN collection, there are 10 complete specimens with otoliths in situ. Subsequent recent excavations of A. F. B. at the type locality yielded numerous complete and incomplete skeletons of *A. suchovi* (PIN collection, uncatalogized), a number of which also have the otoliths in situ. Of them, the four fish skeletons of *A. suchovi* with otoliths in situ described here are now housed at the Geological Museum of the Natural History Museum of Denmark in Copenhagen (GMUH). Comparative otolith material studied: six specimens of *Atherina gidjakensis* from the Konkian of Mangyshlak, Kazakhstan, housed at the Natural History Museum of Ukraine in Kiev (NMNH) as published by Bratishko et al. (2015) and three specimens of *Atherina austriaca* from the Serravallian of the Karaman Basin, SE-Turkey, from the collection of Schwarzhans.

The otolith-bearing specimens of *A. suchovi* studied here are incomplete, but stem from the same location

**Table 1** List of nominal skeleton-based teleost species in the Central and Eastern Paratethys during Sarmatian, Konkian and Karaganian and middle to late Badenian, respectively

| Central Paratethys | Eastern Paratethys |
|---|---|
| Clupeidae | |
| *Alosa crassa* Sauvage 1873* | |
| *Alosa elongata* Agassiz 1842* | |
| *Alosa* aff. *nordmani* Antipa 1906* | |
| *Alosa pinarhisarensis* Rückert-Ülkümen 1965* | |
| *Alosa sculptata* Weiler 1928 | |
| *Clupea arcuata* Kner 1863 | |
| *Clupea elongata* Steindachner 1860 | |
| *Clupea gorjensis* Huica and Gheorghiu 1962 | |
| *Clupea heterocerca* Kramberger 1883 | |
| *Clupea humilis* H.v.Meyer 1851* | ***Clupea humilis*** H.v.Meyer 1851* |
| *Clupea inflata* Vukotinovic 1870 | |
| *Clupea intermedia* Kramberger 1885 | |
| *Clupea lanceolata* H.v.Meyer 1852* | *Clupea lanceolata* H.v.Meyer 1852* |
| *Clupea maceki* Kramberger 1883 | |
| *Clupea melettaeformis* Steindachner 1860 | |
| *Clupea sarmatica* Böhm 1929 | |
| *Clupea sphaerocephala* Vukotinovic 1870 | |
| *Clupea spinosa* Rückert-Ülkümen 1965* | |
| | *Clupea stauropolitana* Bogatchov 1933 |
| *Clupea voinovi* Pauca 1929 | |
| *Etrumeus boulei* Arambourg 1927* | |
| | *Sardina tarletskovi* Baykina 2015 |
| *Sardinella beogradensis* Andjelkovic 1967 | |
| | ***Sardinella perrata*** Daniltchenko 1970 |
| *Sardinella sardinites* (Heckel 1850)* | *Sardinella sardinites* (Heckel 1850)* |
| ***Sarmatella doljeana*** (Kramberger 1883) | |
| | *Sarmatella pshekhensis* (Baykina 2012) |
| | ***Sarmatella tsurevica*** (Baykina 2012)** |
| *Sarmatella vukotinovici* (Kramberger 1883) | |
| *Stolephorus lemoinei* (Arambourg 1927)* | |
| Myctophidae | |
| *Myctophum columnae* (Sauvage 1873)* | |
| Salmonidae | |
| *Salmo ? immigratus* Kramberger 1891 | |
| Belonidae | |
| *Belone tenuis* Kramberger 1898 | |
| Bregmacerotidae | |
| ***Bregmaceros albyi*** (Sauvage 1880)*,[a] | |
| Gadidae | |
| *Brosmius elongatus* Kramberger 1883 | |
| *Brosmius fuchsianus* Kramberger 1883 | |
| *Brosmius murdjadjensis* Arambourg 1927* | |
| *Brosmius longipinnatus* (Kramberger 1880) | |
| *Brosmius strossmayeri* Kramberger 1883 | |
| ***Brosmius susedanus*** Kner 1863 | |
| *Gadus aeglefinoides* (Kner and Steindachner 1863) | |
| *Gadus extensus* (Kramberger 1891) | |

**Table 1** continued

| Central Paratethys | Eastern Paratethys |
|---|---|
| *Gadus lanceolatus* (Kramberger 1883) | |
| ***Gadus macropterygius*** (Kramberger 1883) | *Gadus macropterygius* (Kramberger 1883) |
| *Gadus minimus* (Kramberger 1885) | |
| *Gadus szagadatensis* (Steindachner 1863) | |
| | ***Micromesistius*** **sp.**[b] |
| ***Palimphemus anceps*** Kner 1862[c] | |
| | ***Paratrisopterus avus*** Fedotov 1971[d] |
| | *Paratrisopterus caspius* (Bogatchov 1929) |
| | *Paratrisopterus kiplingi* (Bogatchov 1929) |
| Syngnathidae | |
| *Syngnathus affinis* Kramberger 1891 | Syngnathid indet |
| *Syngnathus albyi* Sauvage 1817* | |
| *Syngnathus helmsii* Steindachner 1860 | |
| Holocentridae | |
| *Holocentroides moldavicus* Pauca 1931 | |
| Mugilidae | |
| | *Mugil acer* Switchenska 1959 |
| | *Mugil finitimus* Switchenska, 1973 |
| | *Mugil karaganicus* Switchenska 1973 |
| | *Mugil minax* Bogatshov 1933 |
| *Mugil radobojanus* Kramberger 1882 | |
| Atherinidae | |
| | *Atherina impropria* Switchenska 1973 |
| | *Atherina prima* Switchenska 1959 |
| *Atherina sarmatica* Kramberger 1891 | |
| | *Atherina schelkovnikovi* Bogatshov 1936 |
| | ***Atherina suchovi*** Switchenska 1973[e] |
| | *Atherina sumgaitica* Switchenska 1973 |
| Sphyraenidae | |
| | *Parasphyraena apsheronica* Switchenska 1968 |
| *Sphyraena croatica* Kramberger 1882 | |
| Scorpaenidae | |
| *Scorpaena jeanneli* Arambourg 1927* | |
| ***Scorpaena minima*** Kramberger 1882 | |
| *Scorpaena pilari* Kramberger 1882 | |
| Mullidae | |
| *Mullus gorjanovici* Andjelkovic 1969 | |
| | *Mullus moldavicus* Switchenska 1959 |
| Serranidae | |
| ***Properca sabbai*** Pauca 1929* | |
| *Serranus altus* Kramberger 1882 | |
| *Serranus dubius* Kramberger 1882 | |
| Moronidae | |
| *Morone intermedia* Kramberger 1882 | |
| | ***Morone ionkoi*** Bannikov 1993[f] |
| *Morone neumayri* (Kramberger 1882) | |
| Latidae | |
| *Lates croaticus* Kramberger 1902 | |
| | *Lates gregarius* Bannikov 1992 |

**Table 1** continued

| Central Paratethys | Eastern Paratethys |
|---|---|
| Priacanthidae | |
| *Priacanthus croaticus* (Kramberger 1885) | |
| Carangidae | |
| *Caranx haueri* Kramberger 1882 | |
| ***Caranx longipinnatus*** Kramberger 1882 | |
| *Seriola gracilis* Böhm 1942 | |
| Centracanthidae | |
| | *Naslavcea fundata* (Bannikov 1990) |
| Sparidae | |
| | ***Pshekharus yesinorum*** Bannikov and Kotlyar 2015[g] |
| *Boops roulei* Arambourg 1927* | |
| | *Sparus? brevis* (Lednev 1914) |
| *Sparus brusinai* (Kramberger 1882) | *Sparus brusinai* (Kramberger 1882) |
| ***Sparus insignis*** (Prochazka 1893)[h] | |
| *Sparus intermedius* (Kramberger 1902) | |
| Sciaenidae | |
| | *Sciaena knyrkoi* Daniltshenko 1980 |
| *Sciaena? multipinnata* (Kramberger 1882) | |
| | *Sciaena pimenovae* Bogatshov 1955 |
| Pomacentridae | |
| *Chromis savornini* Arambourg 1927* | |
| Polynemidae | |
| | *Polydactylus frivolus* Bannikov 1989 |
| Labridae | |
| | ***Symphodus salvus*** Bannikov 1986[i] |
| ***Symphodus woodwardi*** (Kramberger 1891) | |
| Scombridae | |
| *Auxis croaticus* Kramberger 1882 | |
| *Auxis minor* Kramberger 1882 | |
| *Auxis thynnoides* Kramberger 1882 | |
| *Auxis vrabcensis* Kramberger 1882 | |
| | *Scomber caucasicus* (Bogatshov 1933) |
| *Scomber priscus* Kramberger 1882 | |
| *Scomber sarmaticus* Kramberger 1882 | |
| *Scomber steindachneri* Kramberger 1882 | |
| Callionymidae | |
| ***Callionymus macrocephalus*** Kramberger 1882 | ***Callionymus macrocephalus*** Kramberger 1882 |
| | ***Protonymus gontsharovae*** Sytchevskaya and Prokofiev 2007[j] |
| Trachinidae | |
| *Trachinus dracunculus* Heckel 1849 | |
| | ***Trachinus* sp.** |
| Blenniidae | |
| *Blennius fossilis* Kramberger 1891 | |
| Clinidae | |
| | ***Clinitrachoides gratus*** (Bannikov 1989)[k] |
| Gobiidae | |
| *Gobius brivesi* Arambourg 1927* | |
| ***Gobius elatus*** Steindachner 1860[l] | |

**Table 1** continued

| Central Paratethys | Eastern Paratethys |
|---|---|
| *Gobius oblongus* Steindachner 1860 | |
| ***Gobius pullus*** Kramberger 1882 | |
| *Gobius viennensis* Steindachner 1860 | |
| | *"Gobius"* sp. |
| | ***Pomatoschistus* sp.**[b] |
| Caproidae | |
| *Proantigonia octacantha* Kramberger 1882 | |
| *Proantigonia radobojana* Kramberger 1882 | |
| | *Proantigonia dagestanica* Baciu, Bannikov and Tyler 2005 |
| Bothidae | |
| | *Arnoglossus ovalis Switchenska 1981* |
| | ***Bothus* sp.** |
| ***Rhombus bassanianus*** Kramberger 1883 | |
| *Rhombus parvulus* Kramberger 1883 | |
| ***Rhombus serbicus*** Andjelkovic 1966 | |
| *Rhombus stamatini* Pauca 1931 | |
| Pleuronectidae | |
| | *Platichthys svitschenskajae* (Dzhafarova 1976) |
| Soleidae | |
| *Achirus mediterraneus* Arambourg 1927* | |
| *Microchirus abropteryx* (Sauvage 1870)* | |

Central Paratethys based on Andjelković (1989), Baciu et al. (2005) and Schultz (2013); Eastern Paratethys based on Carnevale et al. (2006), Bannikov (2010), Bannikov and Kotlyar (2015) and Baykina (2012, 2015). The systematic follows Nelson (2006)

Skeletons with otoliths in situ are shown in bold

* Originally described from outside Paratethys and identity of referred fishes in the Paratethys questionable

** Isolated otolith attributed to skeleton-based species based on taxonomic evidence

*Superscript alphabets* refer to published otoliths in situ: [a] Bachmayer and Weinfurter (1965) from the lower Badenian of Austria; [b] Carnevale et al. (2006) from the Sarmatian of Russia; [c] Schwarzhans (2014) from the middle Badenian of Poland; [d] Fedotov (1971) from the Sarmatian of Moldavia; [e] this paper; [f] Bannikov (1993, 2009) from the Sarmatian of Moldavia; [g] Bannikov and Kotlyar (2015) from the Sarmatian of Russia; [h] Brzobohaty (1979) from the late Badenian of Slovakia (species identified on basis of the otolith in situ) [i] Bannikov (1986) from the Sarmatian of Moldavia; [j] Sytchevskaya and Prokofiev (2007) from the Konkian of Russia; [k] Bannikov (1989) from the Sarmatian of Moldavia; [l] according to Schultz (2013) from the Sarmatian of Austria

mentioned above and containing only a single atherinid species (Bannikov 2009). Moreover, the studied otoliths are identical to those of the complete specimens, including those of the type series.

Otoliths were first identified on the skeleton-bearing slabs by visual inspection. When considered well enough preserved they were carefully cleaned trying to keep any damage to fish or otolith at a minimum. Since otoliths are often fragile and rather soft we commonly left them in the rock after having cleaned the surface of its inner face as much as possible. By this, fracturing of the otoliths or severance was kept to a minimum. As a consequence of this procedure, no lateral views of otoliths of *A. suchovi* are produced. In addition, the otolith specimen is maintained associated with the skeleton to reduce the risk of potential future loss or damage or any uncertainty about the correlation between otolith and articulated skeleton. The morphological terminology of otoliths was established by Koken (1891) with amendments by Weiler (1942) and Schwarzhans (1978). The morphometric measurements of otoliths follow Schwarzhans (2013). Documentation of otoliths is provided by photographs. All otoliths are shown from the right side. Left otoliths are mirror imaged and annotated accordingly ('reversed').

Abbreviations used are: general: institution acronyms see above, *vs* versus, skeletons: *SL* standard length, *TL* total length, *HL* head length, *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 numerals denote spiny fin rays, Arabic numerals denote branched fin rays; otoliths: *OL* otolith length, *OH* otolith height, *OT* otolith thickness, *SuL* sulcus length, *OsL* ostium length, *OsH* ostium height, *CaL* cauda length, *CaH* cauda height.

## Systematic paleontology

Class Osteichthyes Huxley 1880
Division Teleostei Müller 1846
Order Atheriniformes Rosen 1964
Family Atherinidae Risso 1827
Genus *Atherina* Linnaeus 1758
*Atherina suchovi* Switchenska 1973
(Figure 1a–d)
1954 *Atherina sarmatica* Gorjanovic-Kramberger 1891—Ionko: pl. 1, Fig. 4.
1973 *Atherina suchovi* Switchenska—Switchenska: pl. 5, Figs. 5, 6, pl. 6, Figs. 1–5, pl. 7, Figs. 1–3.
1980 *Atherina suchovi* Switchenska 1973—Switchenska: pl. 15, Figs. 4–5.
2009 *Atherina suchovi* Switchenska 1973—Bannikov: pl. 11, Fig. 1
2010 *Atherina suchovi* Switchenska 1973—Bannikov: pl. 2, Fig. 3

### Remark

The spelling of 'Switchenska' follows the transliteration from the Polish root of the name.

### Material

4 partially complete articulated skeletons with 5 otoliths in situ from Naslavcea, northern Moldavia, Middle Miocene, Serravallian, Early Sarmatian (Volhynian), collected, identified and donated by A. Bannikov, now housed at GMUH VP-9505-9508.

### Short description of fish

Maximum body depth 17–21 % SL; head length 25–30 % SL. Orbit diameter 32–42 % HL. Premaxillary length exceeds orbit diameter. Ascending premaxillary process longer than alveolar ramus. First dorsal-fin origin placed above the 13 or 14th vertebra; interdorsal (D1–D2) space equals 5–6 vertebrae. Anal fin inserts in advance of the second dorsal-fin origin by about 2 rays. Preanal length 62–68 % SL. Vertebrae 39–40 (18–19 + 20–22). D1 = VI–VII, D2 = I + 10–11; A = I + 12–14.

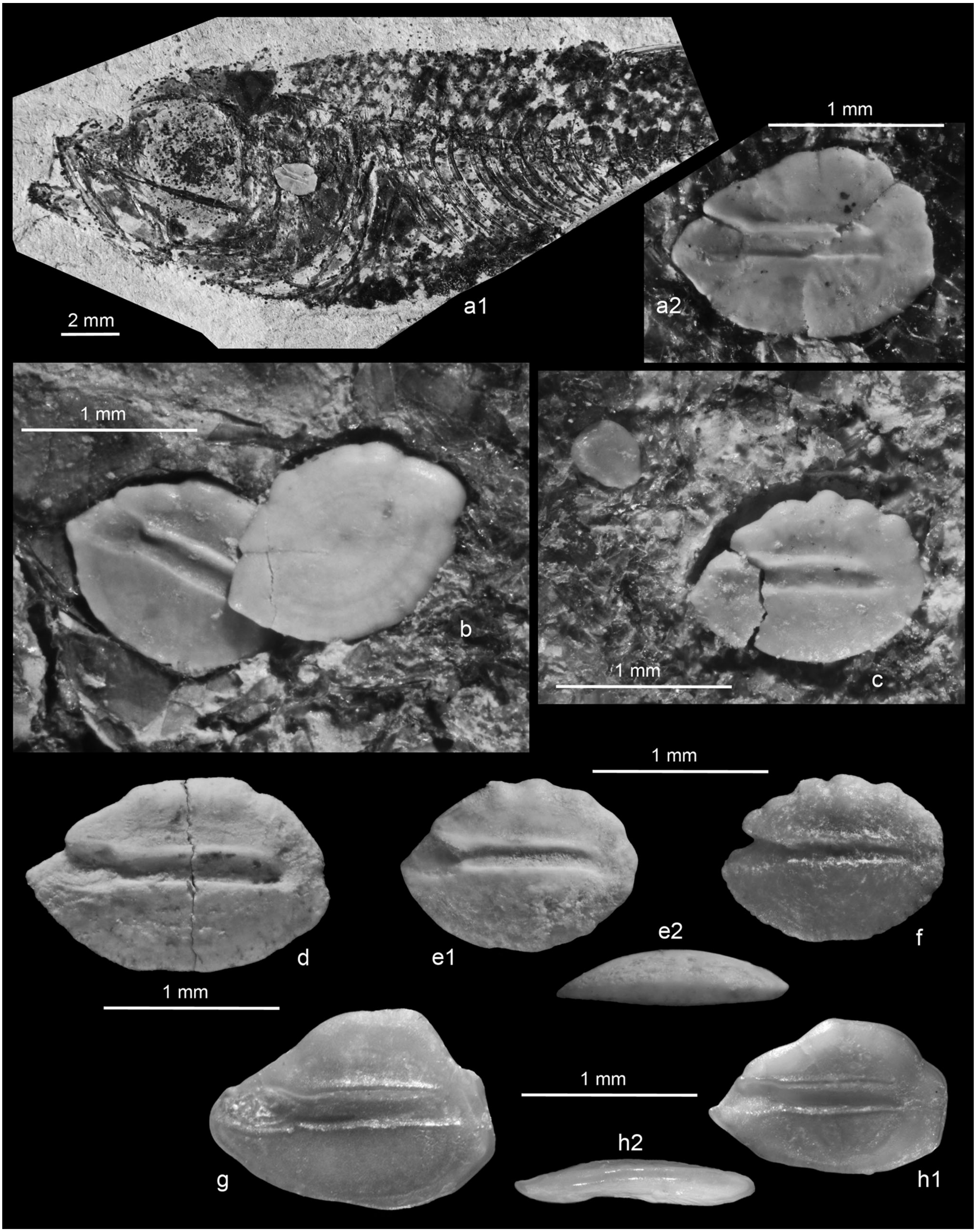
### Description of otoliths in situ (3 specimens measured)

Moderately elongate otoliths to slightly larger sizes than 1.5 mm length. OL:OH = 1.4–1.5. Outline: regularly oval without prominent angles and short, but mostly pointed rostrum. Dorsal rim irregularly undulating or crenulated; ventral rim slightly shallower than dorsal rim and very regularly curved, smooth. Posterior rim rounded or blunt, usually pronounced ventral of caudal tip. Excisura and antirostrum weak. Inner face slightly convex with narrow, slightly supramedian and moderately deep sulcus. Cauda moderately narrow, nearly straight, just very slightly bent at termination, which is at moderate distance from posterior tip of otolith. Ostium slightly wider than cauda and short; CaL:OsL = 1.85–2.0. Dorsal depression long, ventrally marked by well-developed crista superior, dorsal margin indistinct; ventral furrow indistinct. Outer face nearly flat, rather smooth.

### Comparison

Bratishko et al. (2015) listed three fossil otolith-based species of *Atherina*. One of these, *A. austriaca* Schubert 1906, ranges from the uppermost Burdigalian (Karpatian) to Serravallian of the Central Paratethys (e.g., Brzobohaty and Stancu 1974; Brzobohaty 1994; Brzobohaty et al. 2003) and the Mediterranean (Schwarzhans 2014), *A. gidjakensis* (Pobedina 1956) (with *A. kalinoraensis* Rückert-Ülkümen and Kaya 1993 representing a junior synonym) ranges from the Karaganian to Pannonian of the Eastern Paratethys and is also mentioned from the Pontian of the Vienna Basin (Brzobohaty 1992), and *A. mutila* Rückert-Ülkümen 1996 is known from the Sarmatian to Pontian of the Thrace Basin. Otoliths of *A mutila* (not figured herein) can be easily distinguished by their elongate shape (OL:OH = 1.8–1.9) and very long cauda reaching close to the posterior tip of the otolith. This species may belong to a different atherinid genus.

With respect to the other two species the differences are subtle, but consistent: otoliths of *A. austriaca* (Fig. 1e, f)


2 mm
a1
1 mm
a2
1 mm
b
1 mm
c
1 mm
d
e1
e2
f
1 mm
1 mm
g
h2
h1

◀**Fig. 1** Middle Miocene, Serravallian *Atherina* otoliths from the Mediterranean and the Paratethys. **a–d** *Atherina suchovi* Switchenska, 1973, early Sarmatian of Naslavcea, Moldavia. All otoliths are sagittal otoliths and shown from *inner face*, if not mentioned otherwise. **a1** Fish specimen 1 (GMUH VP-9505) with otolith in situ (reversed); **a2** close-up view of otolith of the same specimen (reversed). **b** Close-up view of fish specimen 2 (GMUH VP-9506) with both sagittal otoliths in situ, *upper* one shown from the *outer face* (reversed). **c**. Close-up view of fish specimen 3 (GMUH VP-9507) showing fractured sagittal otolith and small, triangular lapillus otolith (*upper left*), both in situ. **d** Extracted otolith from fish specimen 4 (GMUH VP-9508), fractured during recovery process (reversed). **e–f** *Atherina austriaca* Schubert, 1906, late Serravallian of Seyithasan, Karaman Basin, Turkey, coll. Schwarzhans (reversed). **e2** Ventral view of same otolith as **e1**. **g–h** *Atherina gidjakensis* (Pobedina, 1956), Konkian, Karagaily, Mangyshlak, Kazakhstan, NMNH 2532/031 and/034 (reversed; refigured from Bratishko et al. 2015). **h2** Ventral view of same otolith as **h1**

differ from those of *A. suchovi* in being slightly more compressed (OL:OH = 1.3–1.4 vs 1.4–1.5), more regularly oval in outline with a short rostrum and a continuously crenulated dorsal rim, and a thinner and longer cauda, the latter expressed in a higher ratio CaL: OsL of 2.1–2.4 (vs 1.85–2.0). Moreover, they are thicker and show a more convex inner face. Much more similar to *A. suchovi* is the coeval *A. gidjakensis* from the Eastern Paratethys (Fig. 1g, h). Both species share a similar irregularly developed dorsal rim, a rather wide cauda and a mildly convex inner face. Despite the rather strong morphological variability observed in the otoliths of both species, a few consistent differences seem to hold. Otoliths of *A. gidjakensis* tend to be slightly more elongate than those of *A. suchovi* (OL:OH = 1.45–1.6 vs 1.4–1.5), are characterized by a longer cauda (CaL: OsL = 1.85–2.3 vs 1.85–2.0) a remarkably strong rostrum, a ventral rim which is deepest well behind its midlength (vs at its midlength) and a coarsely ornamented, but not crenulated dorsal rim with a high, broadly undulating bulge (stronger than the most coarsely ornamented specimen of *A. suchovi* as depicted in Fig. 1a1, a2). These observed subtle differences correlate in character and magnitude to those observed in otoliths of the three extant European species *A. boyeri* Risso 1810, *A. hepsetus* Linnaeus, 1758 and *A. presbyter* Cuvier 1829 as figured by Chaine (1958), Lombarte et al. (2006) and Nolf et al. (2009). We, therefore, conclude that *A. gidjakensis* and *A. suchovi* are different species.

## Discussion

Carnevale et al. (2011) listed and compared the five known recent species of the genus, all from the Atlantic and Mediterranean and the eight skeleton-based fossil species of the genus. Of the fossil ones, all but one (*Atherina cavalloi* Gaudant 1979 from the Messinian of the Mediterranean) have been described from the Paratethys: two from the Karaganian of the Eastern Paratethys (*Atherina prima* Switchenska 1959 and *A. sumgaitica* Switchenska 1973), two from the Sarmatian of the Eastern Paratethys (*Atherina impropria* Switchenska 1973 and *A. suchovi* Switchenska 1973), one from the Sarmatian of the Central Paratethys (*Atherina sarmatica* Gorjanovic-Kramberger 1891), and two from the Maeotian and Pontian of the Caspian Basin s.l. (*Atherina atropatiensis* Carnevale, Haghfarshi, Abbasi, Alimohammadian and Reichenbacher, 2011 and *A. schelkovnikovi* Bogatshov 1936). In addition, *A. colchidica* Gabelaia 1971 is known from the Lower Pliocene (?) of Abkhasia. Bannikov (2010) synonymized *A. sumgaitica* with *A. prima*. It seems logical to expect that any of those three fossil otolith-based *Atherina* species would correlate with some of the respective skeleton-based species once otoliths in situ have been retrieved. In the case of *A. suchovi*, however, no such correlation presents itself.

Several other cases of atherinid otoliths in situ have been recorded from species of the fossil genus *Hemitrichas* Peters 1877 from brackish and freshwater rocks of the Upper Rhine Valley of Germany by Keller et al. (2002) and Gaudant and Reichenbacher (2005) (see also extensive discussion about *Hemitrichas* in Reichenbacher 2000). Their otoliths are readily distinguished from any of the *Atherina* otoliths discussed here by their very short rostrum and ostium, the strongly convex inner face and the deep cauda.

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