A new species of silverside from the Late Miocene of NW Iran

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The genus *Atherina* (Atheriniformes, Teleostei) includes five extant brackish and marine species that inhabit the eastern Atlantic, Mediterranean Sea, Black Sea, and Caspian Sea. Several fossil species are known from the Mediterranean and Paratethyan basins. Here we describe a new fossil species, *Atherina atropatiensis* sp. nov., from Upper Miocene deposits of the intramontane Tabriz Basin in NW Iran, based on well-preserved, articulated skeletons from the Lignite Beds at Baghmisheh-Marzdaran, near Tabriz. The new fossil species closely resembles the Recent *A. boyeri*, the only extant species of *Atherina* in the Caspian Sea, from which it can be distinguished by the different relative development of the ascending and alveolar processes of the premaxilla, and the mutual relationship between pleural ribs and dorsolateral process of the basipterygium. The systematic and zoogeographic affinities of *A. atropatiensis* indicate that the Lignite Beds of the Tabriz Basin were deposited in a euryhaline environment and that a connection between the intramontane Tabriz Basin and the Eastern Paratethys (Southern Caspian Sea) once existed.

Key words: Teleostei, Atheriniformes, *Atherina*, osteology, palaeogeography, Miocene, Tabriz Basin, Iran.

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Introduction

Members of the Family Atherinidae, known commonly as silversides or sand smelts, constitute a morphologically well-defined assemblage of 12 genera and approximately 60 species of marine, brackish, and freshwater fishes of worldwide distribution (Nelson 2006). These fishes are characterized by a translucent, elongate and flattened body with a protrusible and upwardly directed mouth with small teeth, two widely separated dorsal fins, and pectoral fins inserting high on the body. The family comprises three subfamilies, the Atherininae, Atherinomorinae, and Craterocephalinae. A diversity hotspot is located in the tropical waters of the Indo-West Pacific and Australia. The genus *Atherina* includes five extant brackish and marine species that live in the eastern Atlantic, Mediterranean Sea, Black Sea and Caspian Sea. *Atherina* is relatively diverse in the fossil record, and is represented by at least eight Miocene species described from articulated skeletal remains (see Table 1), or otoliths (Nolf 1985). All fossils are from the Mediterranean and Paratethyan basins. Here, we describe a new species of the genus *Atherina* from the Upper Miocene Lignite Beds of the Tabriz basin (NW Iran).

Geographic and geological setting

The Tabriz Basin is an intramontane basin in NW Iran (Fig. 1) that developed during the Late Miocene between the colliding Arabian and Eurasian plates (McKenzie 1972; Axen et al. 2001; Allen 2004). The basin fill is composed of the Lignite Beds and Fish Beds, which primarily represent lacustrine and swamp deposits with intercalations of volcanic ash and tuffs; these deposits are overlain by Quaternary alluvial conglomerates (Rieben 1935; Reichenbacher et al. 2011). The Lignite Beds are up to 400 m thick, whereas the overlying Fish Beds may reach up to 150 m thick. Rieben (1935) stated that the Lignite Beds probably are Late Miocene in age, whereas the Fish Beds probably belong to the Pliocene. A re-evaluation of the stratigraphic position of the two beds, however, has revealed a Late Miocene age for both units (Reichenbacher et al. 2011). The fish skeletons documented herein come from the Lignite Beds.

Institutional abbreviation.—BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.

Fig. 1. Geographic overview of Iran. The studied section is near the city of Tabriz.

Material and methods

The specimens described herein are from the section Baghmi-sheh-Marzdaran, located east of Tabriz (N 38° 03'11", E 46° 23'34.6") (Fig. 2). The material comprises eight specimens that are deposited in BSPG under accession numbers 2010 XXI-4 to -11.

Osteological, meristic and morphometric characters were studied under a stereomicroscope equipped with a camera lucida. Measurements were taken with a calliper to the nearest 0.1 mm. Comparative information is derived mainly from the literature (see below). The actualistic method was applied for the palaeoecological interpretation (e.g., Etter 1994).

Systematic palaeontology

Subdivision Teleostei sensu Patterson and Rosen, 1977

Order Atheriniformes sensu Dyer and Chernoff, 1996

Family Atherinidae Risso, 1826

Genus *Atherina* Linnaeus, 1758

Type species: *Atherina hepsetus* Linnaeus, 1758.

Atherina atropatiensis sp. nov.

Figs. 2, 3, Table 1.

Etymology: Atropates is the ancient founder of the Atropatene State, which is today Azerbaijan. The name of the new species refers to the province Azerbaijan of Iran, the country of the type locality.

Type material: Holotype: BSPG 2010 XXI-4, a well preserved articulated skeleton (Fig. $3A_1$, A_2). Paratypes: BSPG 2010 XXI-5, a well preserved articulated skeleton; BSPG 2010 XXI-6 and -7, two well preserved heads; BSPG 2010 XXI-8 and -9, two moderately to well preserved articulated skeletons; BSPG 2010 XXI-10, a well preserved skeletal fragment; BSPG 2010 XXI-11, a poorly preserved articulated skeleton.
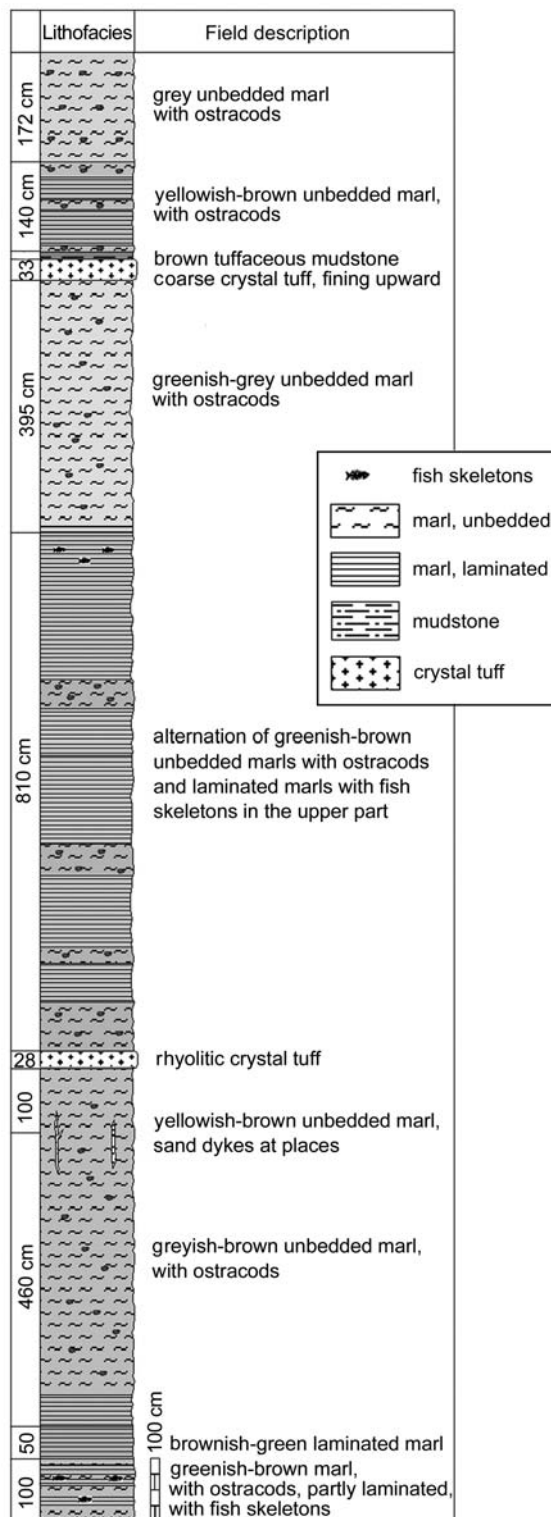

Fig. 2. Schematic profile of the Lignite Beds at Baghmisheh-Marzdaran, showing thicknesses, lithofacies and occurrences of fish fossils.
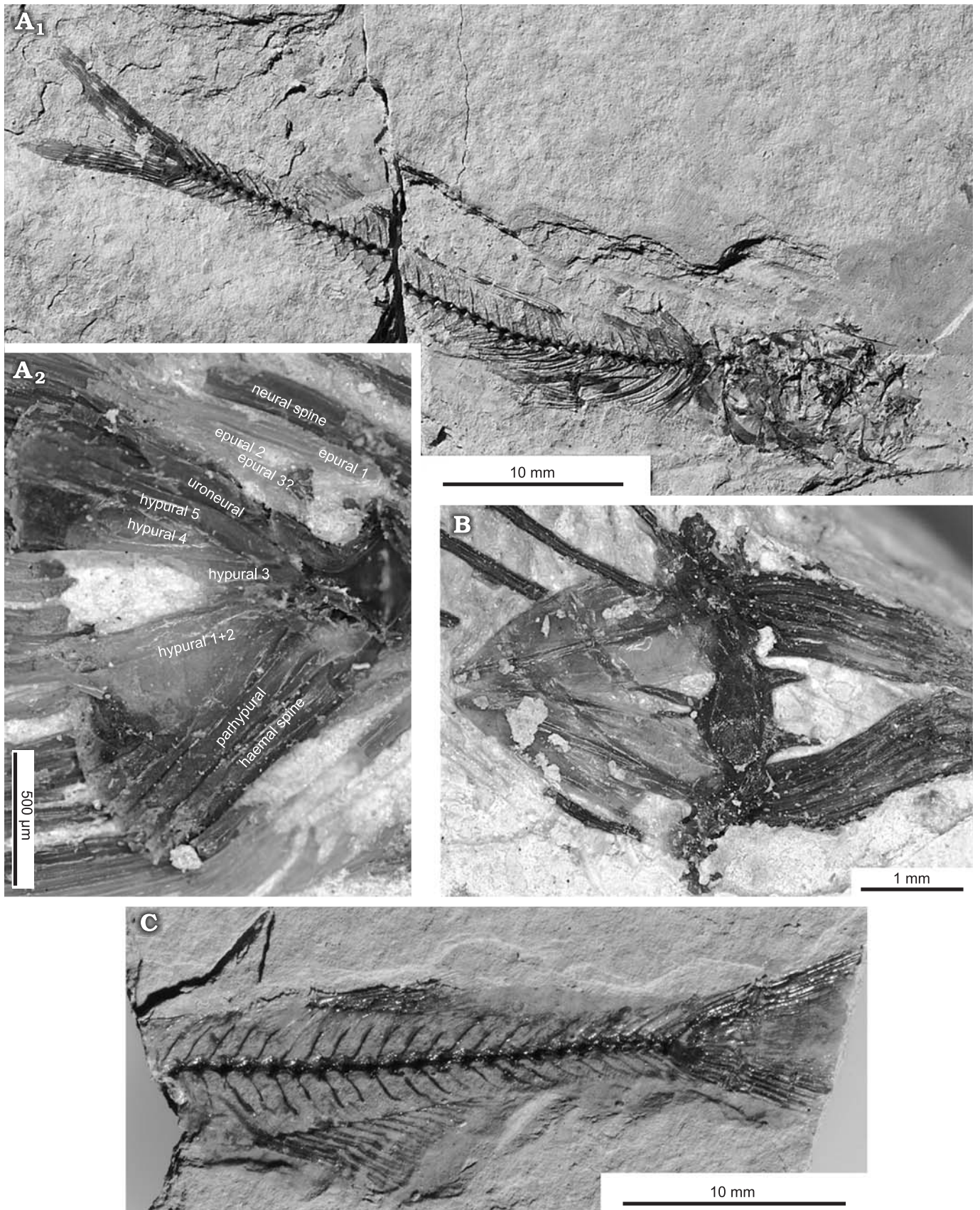
Fig. 3. Morphological characters of atheriniform fish *Atherina atropatiensis* sp. nov. from the Late Miocene Lignite Beds of the Tabriz Basin, Iran. **A**. Holotype BSPG 2010 XXI 4, general overview (A$_1$) and caudal skeleton (A$_2$). **B**. Paratype BSPG 2010 XXI 5, pelvic fins. **C**. Paratype BSPG 2010 XXI 10, showing details of the anal fin.

Type locality: Baghmisheh-Marzdaran, Tabriz Basin, NW Iran (Fig. 2).

Type horizon: Lignite Beds, Upper Miocene.

Diagnosis.—A species of *Atherina* with 42 (20+22) vertebrae; first dorsal fin with five or six spines; second dorsal fin with one slender spine plus 11 to 13 soft rays; anal fin with one spine and 16 to 18 soft rays; anterior haemal arches and spines thin and slender; ascending process of the premaxilla spatulate and slightly shorter than the alveolar (ascending/alveolar ratio = 0.83); dorsolateral process of the basipterygium closely associated to the seventh or eighth pleural rib.

Differential diagnosis.—*Atherina atropatiensis* differs from other fossil *Atherina* species by its unique combination of meristic characters and anterior haemal arches and spines that are simple and not enlarged. It differs from the Recent *Atherina boyeri* by the relative development of the ascending and alveolar processes of the premaxilla, and the mutual relationship between pleural ribs and dorsolateral process of the basipterygium.

Measurements (based on the holotype).—Standard length: 43.2 mm; total length: 51.7 mm. Other measurements as percentage of standard length: Head length: 20.6; head depth: 15.3; maximum body depth: 11.6; predorsal (1st fin) distance: 42.8; predorsal (2nd fin) distance: 58.6; prepelvic distance: 37.7; prepectoral distance: 22.9; caudal peduncle length: > 18.

Geographic and stratigraphic range.—Known from the type locality and horizon.

Description

The body is elongate, slender and laterally compressed, with a relatively long caudal peduncle (Fig. 3A$_1$). The head is moderately elongate and pointed, its length is contained approximately five times the SL. The orbit is large, located approximately at the middle of head length. Mouth terminal. The gape is slightly oblique, relatively short, extending posteriorly up to the level of the anterior margin of the orbit (Fig. 4).

The neurocranium is moderately deep with a large orbital region (Fig. 4). The dorsal surface of the skull is smooth, devoid of crests. The frontals are the largest bones of the skull roof. The prominent supraorbital sensory canal is particularly well exposed in specimens BSPG 2010 XXI-6 and -7 (Fig. 4). The frontals broadly extend backwards replacing the parietals, which appear to be absent. The ethmoid region is rather short. The rostral ethmoid region appears to be excavated dorsally, forming a fossa for the ascending process of the premaxilla and its originally associated rostral cartilage. The lateral ethmoid is columnar and characterized by a posterior laminar wing. The mesethmoid is short and thickened. The vomer is not exposed in the specimens examined. A straight and robust parasphenoid is visible in the lower third of the orbit. A small basisphenoid is also present. The otic and occipital sectors of the neurocranium are extremely damaged and unclear in all the specimens examined, except for what appears to be a short lateral wing of the sphenotic, which appears to be present in specimens BSPG 2010 XXI-5 and -6.

A badly damaged nasal is partially preserved in specimens BSPG 2010 XXI-6 and -7. The lachrymal is thin and roughly quadrangular in shape, with a shallow notch extending along its posterior border for the articulation with the lateral ethmoid (see Dyer and Chernoff 1996). The second and third infra-orbital bones are thin, laminar, subrectangular in shape. The infraorbital and preopercular sensory canals are disconnected.

The general structure of the upper jaw indicates high protrusibility (Fig. 4). The premaxilla has a moderately elongate alveolar process and a slightly shorter antero-posteriorly enlarged and spatulate ascending process (ascending/alveolar ratio: 0.83). The articular process of the premaxilla is stout and pointed, while the postmaxillary process is poorly developed. Premaxillary teeth are short, curved and pointed. The maxilla is elongate with a thick and rounded anterior articular head; this bone has an anterior shelf that partially overlaps the premaxilla (see Alexander 1967). The dentary is thick with a prominent coronoid process arising from the posterior sector of its alveolar arm. The dentary teeth are similar to those of the premaxilla. The angulo-articular is nearly triangular with a shallow concave anterior margin. The retro-articular is small and compact.

The suspensorium is elongate to span the orbit. The thick and straight hyomandibula is characterized by two scarcely separated articular heads. The symplectic is nearly rectangular in outline. The quadrate is a shallow triangular bone with a posteriorly thickened margin which terminates ventrally in a massive articular head. The metapterygoid is partially preserved in specimen BSPG 2010 XXI-5, showing a nearly quadrangular shape. The ectopterygoid is elongate and laminar, while the endopterygoid is relatively large and ovoid in shape. Pterygoid teeth are not visible but their presence in origin cannot be excluded. The palatine is short, lacking a dorsally directed anterior process (see Dyer and Chernoff 1996).

The hyoid bar is well preserved in specimens BSPG 2010 XXI-6 and -7 (Fig. 4). The hypohyals are minute. The anterior ceratohyal is robust with a thick dorsal margin and a broad concavity occupying the anterior half of its ventral portion. The posterior ceratohyal is roughly triangular with a gently curved posteroventral margin. There are six sabre-like branchiostegal rays of which the four anterior articulate with the anterior ceratohyal. The urohyal is large, elongate and triangular in shape. The posterodorsal processes of the urohyal (see e.g., Chernoff 1986) are absent.

The gill arches are partially preserved in specimens BSPG 2010 XXI-5 to -7. The ceratobranchials are elongate and slightly curved. The epibranchials are slender, with short uncinate processes. The pharyngobranchials are crushed and difficult to recognize. A large nearly triangular (?upper) pharyngeal jaw with a broad alveolar surface is preserved in BSPG 2010 XXI-7. Thin and elongate branchiospines articulate along the posterior surface of the gill bones.

The preopercle is a L-shaped bone with vertical and horizontal arms of approximately the same length (Fig. 4). The vertical arm has an anterior thickening, which extends also on the posterior portion of the horizontal arm. The interopercle is laminar and elongate, with a rounded ventral pro-
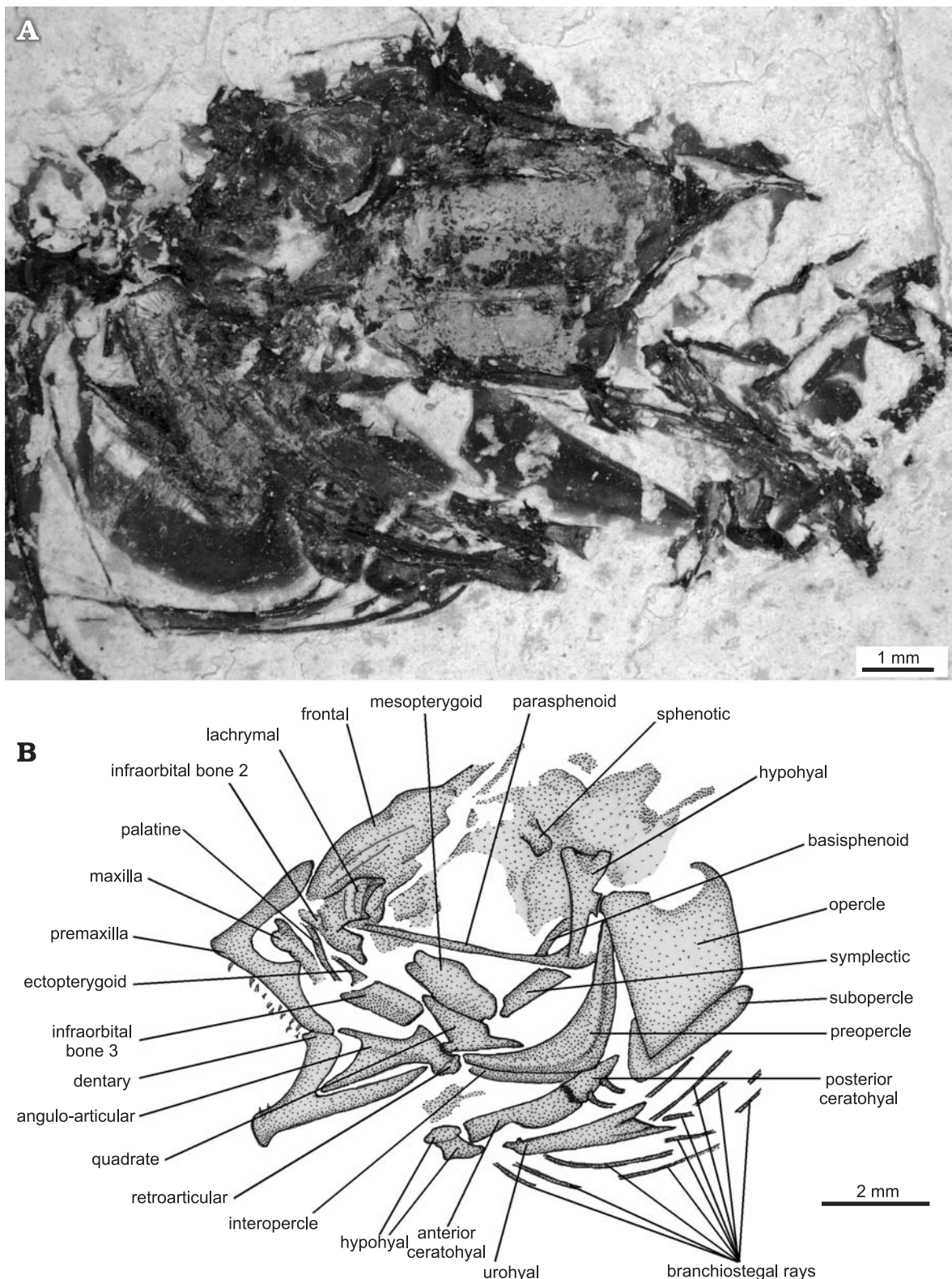
Fig. 4. Skull of atheriniform fish *Atherina atropatiensis* sp. nov. from the Late Miocene Lignite Beds of the Tabriz Basin, Iran. **A**. Digital image of the paratype BSPG 2010 XXI-7. **B**. Drawing of specimen BSPG 2010 XXI-6.

file. The opercle is quadrangular with curved posterior and ventral margins. The articular process of the opercle is short with a slightly concave articular surface. The subopercle extends along the ventral margin of the opercle; it possesses a rounded ventral margin and is characterized by a relatively short and thin anterior vertical apophysis.

The vertebral column is slightly curved in its abdominal portion and consists of 42 (20+22) vertebrae (Fig. 3A$_1$). The

vertebral centra are rectangular, longer than high, slightly constricted in the middle, and characterized by one or two horizontal ridges along their lateral surface. The neural arches of vertebrae two to five with a large anteroposteriorly expanded plate; these neural arches appear to be not meeting in the midline to form a spine. The neural spines of vertebrae six to eight (or nine?) are spatulate distally. Well-developed neural prezygapophyses progressively reduced in size posteriorly arise from the anterior margin of the basal portion of the neural arches. The neural prezygapophyses of the anterior abdominal vertebrae are bifid. The neural spines are straight, thin and obliquely oriented, becoming thickened in the posterior portion of the caudal region. The haemal arches, spines and prezygapophyses are similar in morphology to their neural counterparts. Slender and elongate pleural ribs insert along the lower third of the abdominal centra, beginning on the third. Epineural bones thin.

The caudal fin is deeply forked and consists of 17 principal rays, plus eight dorsal and 12 ventral procurrent rays. The caudal skeleton consists of a robust autogenous parhypural, a large triangular hypaxial hypural plate (hypurals 1+2) fused to the last centrum, three autogenous epaxial hypurals, a large uroneural fused to the urostyle, and two (or three) epurals (Fig. $3A_2$). The neural spine of the penultimate vertebra is reduced to a short crest. The autogenous haemal spine of the penultimate vertebra is greatly enlarged. The haemal spine of the antepenultimate vertebra is also autogenous; this structure is bifid in the holotype, with the anterior spine preserved as impression only. Haemal arches of both the penultimate and antepenultimate vertebrae are greatly expanded into a crest characterized by delicate serrations along their anteroventral margin.

Supraneural bones absent. The first dorsal fin inserts at the level of the 14th vertebra and consists of five or six spines supported by four or five pterygiophores. The second dorsal fin contains a single spine plus 11 to 13 soft rays. The two dorsal fins are separated by a large gap, which equals the length of eight vertebrae; in the endoskeleton, this gap is filled in part by rayless pterygiophores.

The anal fin inserts in advance to the second dorsal-fin origin (Fig. 3C). It consists of one spine plus 17–18 soft rays, supported by 16–17 pterygiophores.

The pectoral fin inserts high along the lateral side of the body and consists of ten rays. The cleithrum is a large, crescent-shaped bone with a thickened anterior margin, and a small laminar process emerging from its posterodorsal margin. The coracoids is a broad posteriorly curved lamina. The scapula and posttemporal are poorly preserved and difficult to recognize. A single postcleithrum is recognizable. There are four hourglass-shaped pectoral-fin radials.

The pelvic fin consists of one spine plus five rays. The basipterygia are strongly ossified elongate bones with a thickened central axis and an enlarged distal portion characterized by an irregular posterior margin (Fig. 3B). Medially, each basipterygium possesses a thin and pointed anteromedial spine, a stout posteromedial spine (sensu Stiassny 1990), and an irregular posterodorsally oriented dorsolateral process, the latter closely associated to the seventh or eighth pleural rib.

The body is covered by thin deciduous cycloid scales.

Discussion

Taxonomic interpretation.—The taxonomic interpretation of fossil atherinid fishes is problematic. This diverse group of tropical to temperate fishes contains a number of anatomically conservative species, which are distinguishable from each other by delicate skeletal structures, as well as by characters related to muscles and ligaments (see Dyer and Chernoff 1996), which are not normally adequately preserved. Nevertheless, our morpho-anatomical study indicates several features that indicates that the Iranian material represents a new species of the genus *Atherina*.

The specimens show a number of features typical of atherinomorphs (Parenti 1993), including the absence of supraneurals, neural arches of vertebrae two through five that are anteroposteriorly expanded into a flat quadrangular plate, dorsolateral process of the basipterygia associated with the distal tips of pleural ribs, and reduced number of infraorbital bones.

The inclusion of the studied specimens within the "atherinoid" fishes is justified by several morphological features, including the general physiognomy, presence of six branchiostegal rays (Rosen 1964), possession of small teeth (Starks 1899), infraorbital series constituted by the three anterior elements only (Chernoff 1986; Stiassny 1990), epibranchials uncinate (see Rosen and Parenti 1981), first pleural rib inserting on the third vertebra (Rosen 1964), and basipterygia bearing anteromedial and posteromedial spines (Stiassny 1990).

The absence of neurocranial crests (Gosline 1962), possession of a developed basisphenoid (Starks 1899), absence of parietals (see Ivantsoff et al. 1987), presence of an articular notch along the posterior margin of the lachrymal (Dyer and Chernoff 1996), as well as certain meristic values (vertebral number, fin formulae) support the assignment of the specimens to the family Atherinidae.

Finally, the attribution of the specimens to the genus *Atherina* is based on several diagnostic features typical of living species of this genus, such as the presence of a maxillary ventral shelf (e.g., Alexander 1967), preopercular and infraorbital sensory canals disconnected (Dyer and Chernoff 1996), dorsally directed anterior palatine process absent (Dyer and Chernoff 1996), and dorsolateral process of the basipterygium oriented posterodorsally (Dyer and Chernoff 1996).

Comparisons.—The genus *Atherina* includes five extant species (*A. breviceps*, *A. boyeri*, *A. hepsetus*, *A. lopeziana*, *A. presbyter*, see Table 1) that live in brackish and shallow marine waters of the eastern Atlantic, from Scandinavia to South Africa, Mediterranean Sea, Black Sea and Caspian Sea, plus seven skeleton-based extinct species (*A. cavalloi*, *A. impropria*, *A. prima*, *A. sarmatica*, *A. schelkovnikovi*, *A. suchovi*, *A. sumgaitica*, see Table 1) from the Miocene of the Mediterranean (e.g., Gaudant 1981; Landini and Sorbini 1989) and Paratethys (Gorjanović-Kramberger 1891; Switshenskaja

Table 1. Meristic characters, zoogeography, and stratigraphic age of the known fossil and Recent *Atherina* species and *Atherina atropatiensis* sp. nov. Abbreviations: A, anal fin, D1, first dorsal fin; D2, second dorsal fin. Data are compiled from Gorjanović-Kramberger (1891), Rossignol and Blache (1961), Kiener and Spillmann (1969), Switshenskaja (1973), Gaudant (1981), and Ivantsoff (2003).

Species	Vertebrae	D1	D2	A	Geographic distribution	Stratigraphy
Atherina atropatiensis sp. nov.	42	V–VI	I, 11–13	I, 17–18	Tabriz Basin	Maeotian
Atherina cavalloi Gaudant, 1979	48	X	I, 10	I, 12	Paleomediterranean	Messinian
Atherina impropria Switshenskaja, 1973	38–39	V	I, 10–11	I, 12	Eastern Paratethys	Sarmatian
Atherina prima Switshenskaja, 1959	38–39	IV–V	?	I, 12–14	Eastern Paratethys	Karaganian
Atherina sarmatica Gorjanovic-Kramberger, 1891	44	VII	I, 11	I, 15	Central Paratethys	Sarmatian
Atherina suchovi Switshenskaja, 1973	39–40	VI	I–II, 10–11	II, 12–13	Eastern Paratethys	Sarmatian
Atherina sumgaitica Switshenskaja, 1973	40–41	VI	I, 10–11	I, 11–12	Eastern Paratethys	Karaganian
Atherina schelkovnikovi Bogachev, 1936	40–43	V	I, 10–12	I, 12–14	Eastern Paratethys	Sarmatian
Atherina boyeri Risso, 1810	40–47	VI–IX	I, 9–15	I, 12–18	Eastern Atlantic (North Sea to Mauritania), Mediterranean, Black Sea, Caspian Sea	Messinian to Recent
Atherina breviceps Valenciennes, 1835	?	V–VIII	I, 11–15	I, 15–18	Namibia to Natal, South Africa	Recent
Atherina hepsetus Linnaeus, 1758	53–57	VII–X	I, 10–12	I, 11–13	Eastern Atlantic (Spain to Morocco), Mediterranean, Black Sea	Recent
Atherina lopeziana Rossignol and Blache, 1961	40–42	VI–VIII	I, 11–13	I, 14–17	Eastern Atlantic (Gulf of Guinea)	Recent
Atherina presbyter Cuvier, 1829	46–52	VII–IX	I, 11–14	I, 14–17	Eastern Atlantic (North Sea to Mauritania), Mediterranean	Recent

1973; Anđelković 1989). All these species show marked morphological variability (e.g., Kiener and Spillmann 1969; Boscolo 1970; Switshenskaja 1973; Bamber and Henderson 1985; Mistri and Colombo 1988) and can be distinguished from each other mostly based on meristic features (Table 1), premaxillary and dentary configuration, and relative enlargement of the anterior haemal arches (Borsieri 1904; Schultz 1948; Kiener and Spillmann 1969; Switshenskaja 1973). A comparative analysis of the potentially diagnostic features of *Atherina atropatiensis* sp. nov. has revealed that this form differs from all other congeners, except *A. boyeri*, in having a unique combination of meristic values (Table 1) and anterior haemal arches and spines that are simple and not enlarged.

Atherina boyeri is a highly heterogeneous and polymorphic species that displays a wide range of morphometric and meristic values, broadly overlapping those of other species, often related to various environmental conditions (Kiener and Spillmann 1969, 1972); the morphology of the anterior haemal arches and spines is also highly variable in this eurytopic species, ranging from thick and chunky to thin and slender (Kiener and Spillmann 1969). In spite of considerable morphological similarity, however, *Atherina atropatiensis* sp. nov. and *A. boyeri* are readily distinguished by the different relative development of the ascending and alveolar processes of the premaxilla, with higher values of the ascending/alveolar ratio in the former than the latter (0.83 vs 0.58–0.69) (Bamber and Henderson 1985), and the dorsolateral process of the basipterygium, which is closely associated with the seventh or eighth pleural rib in *A. atropatiensis* sp. nov., and the sixth in *A. boyeri* (Kiener and Spillmann 1969).

Moreover, Bogachev (1962) described a new taxon *Prolebias schelkovnikovi* from the Neogene sediments near Tabriz that may be another *Atherina*. The proportions and meristic values are similar to those of *Atherina atropatiensis*

sp. nov., but it differs in having a lower number of abdominal vertebrae (17 rather than 20) and higher number of principal rays in the caudal fin (20 rather than 17). This may then be a second *Atherina* species from the Tabriz Basin: the name *Prolebias schelkovnikovi* is not available for this species because Bogachev (1936) described a different *Atherina* species with the same name in an earlier study (see also Table 1). Further fossils from the Tabriz Basin are required before a new name is provided for "*Prolebias*" [= *Atherina*] *schelkovnikovi* Bogachev, 1962.

Paleoenvironmental implications

The fossil assemblages from the Lignite Beds at Baghmisheh-Marzdaran in the Tabriz Basin have yielded a relatively low number of taxa of fishes, bivalves, gastropods, ostracods, diatoms and a single benthic foraminifer (Reichenbacher et al. 2011). Remains of aquatic macroplants apparently belonging to *Typha* sp. and *Nelumbo protospeciosa* Saporta, 1891 were recorded from the western side of the Baghmisheh-Marzdaran section (Negin park section, unpublished data by the Iranian co-authors). Most of the fossil fishes recovered from Baghmisheh-Marzdaran can be assigned to *Atherina atropatiensis*; rarer are *Aphanius persicus* (Priem, 1908) and the pharyngeal teeth of the cyprinid taxa aff. *Leuciscus*, aff. *Scardinius*, and Cyprinidae gen. et sp. indet.

The depositional environment of the Lignite Beds at Baghmisheh-Marzdaran included lacustrine as well as euryhaline settings as the fossil assemblages show a mixed composition of freshwater, brackish and marine-euryhaline forms (Reichenbacher et al. 2011). The occurrence of a fossil species of *Atherina*, possibly closely related to the extant *Atherina boyeri*, provides additional support for the assumption of euryhaline environments, because species of the genus

Atherina are common today in coastal marine and brackish fish communities of the eastern Atlantic-Mediterranean-Paratethyan realm. Moreover, the current geographic distribution of extant and fossil *Atherina* species strongly suggests that the Tabriz Basin of the Late Miocene was connected to the Southern Caspian Basin of the Eastern Paratethys at times (see also Reichenbacher et al. 2011), and that it was not an isolated intramontane basin as indicated in former palaeogeographic reconstructions (e.g., Popov et al. 2004, 2006).

Acknowledgements

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