

NEOGENE PARATETHYAN CROAKERS (TELEOSTEI, SCIAENIDAE)

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Abstract. The fossil record of sciaenid fishes (based on both otoliths and osteological finds) from the Neogene of the Paratethys is reviewed. The species *Labrax* (= *Morone*) *multispinatus* Gorjanovič-Kramberger, 1882 from the Sarmatian of Croatia (Sv. Nedelja) that was originally described as a sea bass of the family Moronidae is re-assigned to the extant croaker genus *Argyrosomus*. Two new genera and species of sciaenid fishes are described based on a single skeleton each, namely *Landinisciaena popovi* gen. et sp. nov. from the Tarkhanian (Lower/Middle Miocene) North Shirvanskaya Formation exposed along the Pshekha River, North Caucasus, Russia, and *Croatosciaena krambergeri* gen. et sp. nov. from the Sarmatian s.s. (Middle Miocene) deposits of Dolje in the nearby of the city of Zagreb, Croatia. The holotype of the former taxon possesses a well-preserved saccular otolith *in situ* (first record of *in situ* croaker otolith in Europe) similar to the otoliths of the extant genus *Atractoscion*. The otolith-based Otnngian species *Atractoscion elongatissimus* Schwarzahns, 1993 is transferred to the genus *Landinisciaena* gen. nov. A comprehensive revision of the Neogene otolith-based sciaenid record from Paratethys resulted in the recognition of three new genera (*Chaoia* gen. nov., *Pontosciaena* gen. nov. and *Leptosciaena* gen. nov.) as well as in the description of a new species *L. caputoi* sp. nov. from the uppermost Messinian (Lago-mare phase) of Italy. A number of known otolith-based species were either synonymized or assigned to a new generic affiliation. The complex biogeographic history of the Neogene Paratethyan sciaenids (based on both otoliths and skeletal records) is discussed, resulting in the recognition of a vanished “sciaenid bioprovince”.

INTRODUCTION

Members of the family Sciaenidae, also known as croakers are shallow-dwelling suprabenthic fishes widespread in tropical and subtropical coastal and estuarine waters worldwide. A number of species of this family are restricted to freshwaters, especially in the Atlantic drainages of the Americas (Nelson et al. 2016). The Sciaenidae is a highly diverse percomorph family, including about 280 recent species belonging to approximately 70 genera (Nelson et al. 2016). While sciaenids have been traditionally regarded as percoid perciforms (Nelson 2006), recent broad-scale molecular studies placed them within the order Acanthuriformes

in the suborder Sciaenoidei together with the Emmelichthyidae (e.g., Betancur-R. et al. 2013; Near et al. 2013; Nelson et al. 2016), or as incertae sedis within the Eupercaria (Betancur-R. et al. 2017). The fossil record of croakers is mostly based on their large and thick otoliths (Schwarzahns 1993), whereas articulated fossil skeletons of the Sciaenidae are quite uncommon (see Bannikov et al. 2009). The earliest record of the Sciaenidae is a single otolith from the Ypresian Bashi Marls of Mississippi (Nolf 1995), although croaker otoliths become relatively abundant in the late Eocene, Oligocene and Neogene shallow water sediments of Europe and the Americas (e.g., Schwarzahns 1993; Nolf 1985, 2013; Aguilera et al. 2016). Skeletal remains of extinct croakers are relatively more common in the Eastern Paratethyan record compared to other re-

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gions, at least since the beginning of the Miocene. The extinct genus *Caucasisciaena* (Bannikov et al. 2009; Bannikov 2010), with the species *C. ignota* is known from the Sakaraulian (Lower Miocene, Upper Maikopian, Lower Burdigalian) of the northern Caucasus, Crimea, and Azerbaijan; the fossils belonging to this genus were initially assigned to *Perca* (Smirnov 1936) and, subsequently to *Larimus* (Daniltshenko 1960, 1980) and were referred to *Caucasisciaena* based on a unique combination of features (Bannikov et al. 2009). Several extinct croakers are known from the Sarmatian s.l. (see Bannikov 2010, 2013), of both the Eastern and Western Paratethys. Two species are known from the Sarmatian of Croatia, one of which from Dolje not far from Zagreb, is described herein for the first time (see below); the other, *Labrax* (= *Morone*) *multipinnatus* from Sv. Nedelja, Samoborsko gorje, was described as a member of the family Moronidae (Anđelković 1989; Gorjanović-Kramberger 1882) and is currently referred to the Sciaenidae (Bannikov 1992, 2010, 2013) and to the extant croaker genus *Argyrosomus* (see below). *Sciaena pimenovae* was briefly described (but not illustrated) from the Lower Sarmatian of Amvrosievka (southeastern Ukraine) together with an incomplete specimen of *Sciaena* sp. (?) (Bogatshov 1955). The location of the storage of the specimens described by Bogatshov (1955) is currently unknown, and since that time no additional specimens were collected at Amvrosievka. Another Sarmatian species, *Sciaena knyrkoi*, was described based on a single skeletal impression from the vicinity of Grozny, Chechen Republic (Daniltshenko 1980; Bannikov 2010). Menner (1948) described an incomplete croaker skeleton from the Kimmerian (=Zanclean) of the Kerch Peninsula (Crimea) as the extinct genus and species *Pseudoumbrina pcelini* Menner, 1948. The genus *Pseudoumbrina* is impossible to diagnose based on the original description and figures because of incomplete preservation of available material, and the Kimmerian taxon was tentatively referred by Bannikov (2010) to an indeterminate taxon of the family Sciaenidae, together with "*Sciaena pimenovae*". The late Neogene sciaenid genus *Carnevalella* from the eastern Black Sea Region strongly differs from the other known croakers by having a set of apomorphic characters (possession of 29 or 30 vertebrae, four supraneurals, fourth hypural fused with the terminal compound centrum, first dorsal-fin

pterygiophore located posterior to the neural spine of the third abdominal vertebra), and was assigned to the subfamily Carnevalellinae (Bannikov 2013). One of the two species of this genus, *C. impropria*, was collected from the Pontian (=Messinian) deposits of Abkhazia (Gabelia 1976) associated to a brackish fish fauna. The second species, *C. (?) tmutarakanica* Bannikov, 2013, was found in the Maeotian (=Upper Tortonian) diatomites exposed along the southern coast of the Taman Peninsula, SW Russia (Bannikov 2013). An additional croaker specimen from the same locality (Bannikov 2013: fig. 2) was not identified at genus and species level due to its poor preservation and incompleteness. Apart from the known fossil croakers listed above, there is an undescribed largely incomplete articulated skeleton from the Miocene of Coşnița, Moldavia, housed in the Natural History Museum of Kishinev. Unfortunately, up to now none of the fossil Paratethyan croaker skeletons were reported to possess the otolith *in situ*, thereby preventing the recognition of any possible link between the skeletal and the abundant otolith records (see Schwarzshans & Carnevale 2017).

The initial impetus for this paper was a discovery by one of us (AFB) of a nearly complete articulated skeleton of a croaker with the otolith *in situ* in the right bank of the Pshekha River upstream of the Shirvanskaya settlement, Krasnodar Region, NW Caucasus, SW Russia during the field campaign that took place in summer 2017.

The fossil sciaenid skeleton exhibits an otolith *in situ* and pertains to a late juvenile or to a subadult individual exhibiting a unique combination of morphological features that allow the creation of a new previously undescribed taxon. The comparative analysis of the skeletal features of this fossil with other Paratethyan croakers revealed the existence of another undescribed croaker taxon from the Sarmatian of Dolje, Croatia (mentioned above) and confirmed the sciaenid affinities of *Labrax* (= *Morone*) *multipinnatus* evidenced by Bannikov et al. (2009). At the same time, the comparative analysis of the otolith *in situ* highlighted that a taxonomic revision of the Neogene sciaenid otoliths from the Paratethys cannot be furtherly delayed. This paper thus has three goals: (1) the description of new Miocene croaker taxa from the Paratethys based on articulated skeletal remains, in one case with the otolith *in situ*; (2) a comprehensive analysis

of the Neogene otolith record of the Paratethys, with the description of three new genera and one new species; and (3) a discussion of the biogeographic history of the Neogene Paratethyan sciaenid contingent.

METHODS

The specimens were studied using stereomicroscopes (Leica M80 and Leica M165 C) equipped with a camera lucida drawing arm. Some details of the specimens examined were best seen when the specimen was moistened with alcohol. The specimens required matrix removal in order to evidence some of the skeletal features; this was achieved using thin entomological needles. Measurements were taken with a dial caliper, to the nearest 0.1 mm.

Interneural and interhaemal spaces are numbered based on the vertebra whose neural or haemal spine forms the anterior border of the space, with the first space located between the first and second neural or haemal spines (following Baldwin & Johnson 1993; Bannikov & Tyler 1995; Tyler & Bannikov 1997; etc.).

Institutional abbreviations: CNHM – Croatian Natural History Museum, Zagreb; GBA Wien – Geologische Bundesanstalt, Wien; IRSNB – Institute Royal de Sciences Naturelles de Belgique, Bruxelles; LPB – Laboratory of Paleontology, Faculty of Geology and Geography, Bucharest; MGPT-PU – Museo di Geologia e Paleontologia, Università degli Studi di Torino, Torino; NHMUK – The Natural History Museum, London; NMNH – National Museum of Natural History of the National Academy of Sciences of Ukraine, Kyiv; PIN – Borisyak Paleontological Institute of the Russian Academy of Sciences, Moscow; SMF – Naturkunde-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main; SMNS – Staatliches Museum für Naturkunde, Stuttgart. *Other abbreviations:* SL – standard length.

SYSTEMATICS

Family Sciaenidae Cuvier, 1829

The skeletal record

Remarks. Fishes of the family Sciaenidae exhibit a suite of morphological features that can be regarded as fully diagnostic of this group. In general, sciaenids are characterized by large saccular otoliths, enlarged lateral-line canals on the head and pores on the snout and lower jaws, extension of the lateral line to the tip of the caudal fin and, usually, by a large and often complex swimbladder and well-developed drumming muscles (e.g., Chao 1978). Unfortunately, the majority of these features are almost useless in the systematic examination of articulated skeletal remains since most of them cannot be observed in fossil material. Some of the

diagnoses of the family are based on a combination of both derived and plesiomorphic features (e.g., Trewavas 1977). Sasaki (1989) recognized 21 synapomorphies that support the monophyletic status of the Sciaenidae, among which at least 11 features (soft dorsal-fin base elongate, typically much longer than anal-fin base; third element of the anal fin not transformed into a spine; dorsal- and anal-fin pterygiophores bisegmental; frontals cavernous; palatine expanding ventrally; symplectic dorsally flattened, interdigitating medially with the metapterygoid; metapterygoid and quadrate interdigitating medially; supramaxillae absent; palatine toothless; second epibranchial without toothplate; one branchiostegal articulating with the posterior ceratohyal) refer to skeletal structure that are potentially observable in fossil articulated skeletons. Some of these synapomorphic skeletal features are clearly recognizable in the fossils documented below (see descriptions), thereby supporting their attribution to the family Sciaenidae. In particular, all the described taxa are characterized by a very long soft dorsal fin, two anal-fin spines, dorsal- and anal-fin pterygiophores bisegmental, and supramaxilla absent.

Genus *Landinisciaena* gen. nov.

Type Species: *Landinisciaena popovi* sp. nov., by monotypy and designation herein.

Diagnosis: Sciaenid fish with elongated body and moderately slender caudal peduncle. Maximum body depth slightly more than 25% of SL. Head moderately large, contained 3.2 times in SL. Supraoccipital crest low. Lower jaw articulation under posterior half of orbit. Mouth gape wide and terminal. Premaxilla with relatively long and narrow ascending process. Jaw teeth small and conical; few anterior premaxillary teeth enlarged as moderately developed canines. Preopercular margin with a few spines at the angle. Posttemporal without robust spines along the posterior margin. Twenty-five vertebrae (13+12). Three tiny supraneurals. Dorsal fin deeply notched, with 11 very slender exposed spines (two supernumerary) followed by 25 soft rays. Anal fin with two spines and eight rays. Second anal-fin spine thick and robust. Pectoral fin moderately long. Pelvic-fin insertion located under the pectorals. Posterior margin of caudal fin rounded. Scales ctenoid on the body, cycloid on the head. Lateral line gently convex above, descending to the vertebral column at the level of the second caudal vertebra. Sagitta relatively elongated.

Etymology: The genus is named after the Italian paleontologist Prof. Walter Landini, a mentor to one of us (GC) and valuable colleague to all of us, in recognition of his contribution to the study of Neogene croaker; and the genus *Sciaena*, gender feminine.

Composition: Type species from the Tarkhanian North Shirvanskaya Formation, North Caucasus, and otolith-based species *Landinisciaena elongatissima* (Schwarzahns, 1993) from the Ottnangian to Karpatian of the Central Paratethys and North Sea Basin.

Landinisciaena popovi sp. nov.

Figs 1; 2 F, G

Holotype: PIN 5599/1, nearly complete articulated skeleton with otolith *in situ*, in part and counterpart, 55 mm SL. Numerous minute pyrite granules are distributed throughout the skeleton, especially on the skull.

Diagnosis: As for the genus.

Etymology: The species is named in honor of Dr. Sergei V. Popov in recognition to his outstanding contribution to the Paratethyan stratigraphy and paleontology.

Referred Specimens: None.

Type Locality and Horizon: Right bank of the Pshekha River upstream of the Shirvanskaya settlement (44.368442°N; 39.796874°E), Krasnodar Region, NW Caucasus, SW Russia; Lower/Middle Miocene (terminal Burdigalian or basal Langhian), Tarkhanian regional stage, North Shirvanskaya Formation, lower subformation (Beluzhenko 2002).

The fossil was collected from Tarkhanian carbonate clays located just above the so-called “Tarkhanian marl” (or Terek layers = *Lentipecten corneus denudatus* layer) (Neveeskaya et al. 2004) characterized by a rich fauna of polyhaline mollusks (Muratov & Neveeskaya 1986; Goncharova 1989; Beluzhenko 2002; Neveeskaya et al. 2004; etc.). The fish-bearing layer corresponds to so-called “Argun layers” (Upper Tarkhanian) and consists of grey carbonate clays with abundant pteropods of the species *Spiratella tarchanensis*. Small-sized phosichthyids (*Vinciguerria merklini*) and herrings dominate the fish assemblage, although gadiforms, flatfishes, gobiids, carangids, mugilids, blenniids and scombrids can be occasionally found. Most of fish specimens are variably affected by pyrite formation, thereby suggesting anoxic conditions at the bottom during sedimentation. Plant leaves and relatively abundant insects seem to indicate a close proximity of the depositional environment to the land. The setting is therefore interpreted as a deep trough close to emerged lands, most probably represented by islands of a former archipelago of the Greater Caucasus (e.g., Popov et al. 2004).

Distribution: Tarkhanian of NW Caucasus, Pshekha River, Russia.

Measurements: (as percentage of SL): Head length: 31; maximum body depth: 25.5; snout length: 8.5; orbit diameter: 8; mandible length: 19; caudal peduncle length: 14; caudal peduncle depth: 9; predorsal (spinous dorsal) length: 38; predorsal (soft dorsal) length: 58; preanal length: 72; distance between pelvic and anal fins: 35; dorsal-fin base length: 46; spinous dorsal-fin base length: 19; anal-fin base length: 9; first dorsal-fin spine length: 4; longest dorsal-fin spine length: 14.5; first anal-fin spine length: 2; second anal-fin spine length: 11; pelvic-fin spine length: 9; longest caudal-fin ray length: 21; pectoral-fin length: 16.

Description. The body is relatively elongate, with a moderately deep caudal peduncle (Fig. 1). The caudal peduncle depth is about one third of the body depth. The head is moderately large; its length (tip of snout to posterior edge of opercle) is 1.2 times larger than the body depth. The head length is contained 3.2 times in SL. The orbit is moderate; its diameter is ca. 25% of the head length. The snout is short; its length is about 27% of the head length. The lower jaw articulation is situated under the posterior half of the orbit. The dorsal and ven-

tral profiles of the body are almost equally convex.

The neurocranial structures are difficult to interpret because of inadequate preservation (Fig. 1). The neurocranium is relatively low, with the supraoccipital crest evidently poorly developed. The frontals are the largest bones of the skull roof; their cavernous texture is not evident. The ventral projection of the frontals appears to be absent. The ethmoid block is anteroposteriorly compact and short. The parasphenoid is relatively slender and almost straight, with no dorsal flange evident. The basisphenoid and the limits of the bones of the otic region are difficult to recognize.

A relatively large and ovoid saccular otolith (sagitta) is well exposed in medial view in the counterpart (defined herein as the specimen with head to right) (Fig. 2). The maximum length of the sagitta is about 3.9 mm, representing about 7.6% of SL. Otolith length to height ratio: 2.25. The sagitta is relatively elongate and ovoid in outline. The inner face of the otolith is relatively flat with little curvature. The sulcus has a short, shallow and relatively narrow ostium and long, slightly deepened, slender cauda. The ostium has no discernable postostial lobe, and is characterized by distinctly diagonal orientation at junction with cauda; its dorsal margin has a distinct indentation at about its mid-length. Ostium length to height ratio: 1.8. The cauda is slightly longer than the ostium, and has a long horizontal section and a short downturned part. Ostium length to cauda length ratio: 0.85. The ostial - caudal interspace represents about 43 % of the sulcus length. The ventral field is smooth without ventral furrow; the area behind the downturned caudal tip is slightly wider than the cauda; the dorsal field has a broad, long, and indistinct dorsal depression. The outer face and curvature of the outer face is not visible.

The bones of the infraorbital series are not recognizable.

The mouth is terminal with a wide gape (Fig. 1). The premaxilla has a relatively long and slender ascending process separated from the articular process. The length of the alveolar process of the premaxilla cannot be determined, as well as the presence of the postmaxillary process. Only a few of the anterior premaxillary teeth are preserved; these are small and conical, except for a couple of teeth that are somewhat enlarged and canine-like. The maxilla is too damaged to be restored. The lower jaw is relatively low; its length reaches about 59% of

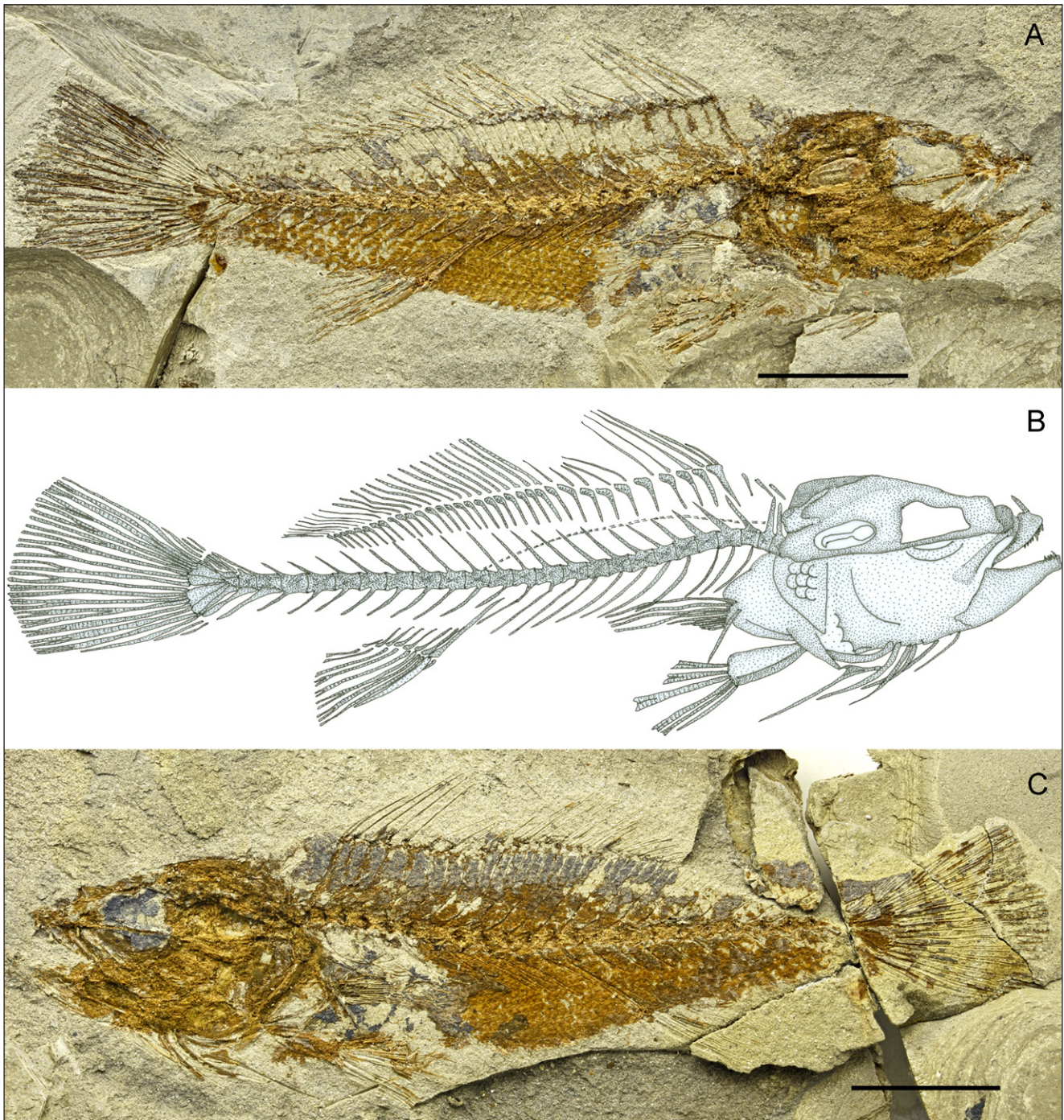


Fig. 1 - *Landinisciaena popovi* gen. et sp. nov. from the Tarkhanian of the North Caucasus, Russia. A) holotype, PIN 5599/1, right lateral view; B) reconstruction of the skeleton; C) holotype, counterpart of specimen in A. Scale bars 10 mm.

head length. It protrudes anteriorly beyond the anterior limit of the upper jaw. The dentary symphysis is relatively low, without downward projection. Only a few of the anterior mandibular teeth are preserved; these are small and conical similar to those of the premaxilla, with at least one tooth being somewhat enlarged and canine-like.

The limits of most of the bones of the suspensorium are scarcely distinguishable; however, it is

evident that the endopterygoid is flat and elongate, exposed just below the parasphenoid.

The opercular region is relatively narrow and compact. The preopercle seems to be moderately curved and possesses a few flat spines at the postero-ventral angle. The opercle is roughly triangular and is covered with cycloid scales; an opercular spine is not visible (Fig. 1 B). The subopercle and interopercle are only scarcely recognizable.

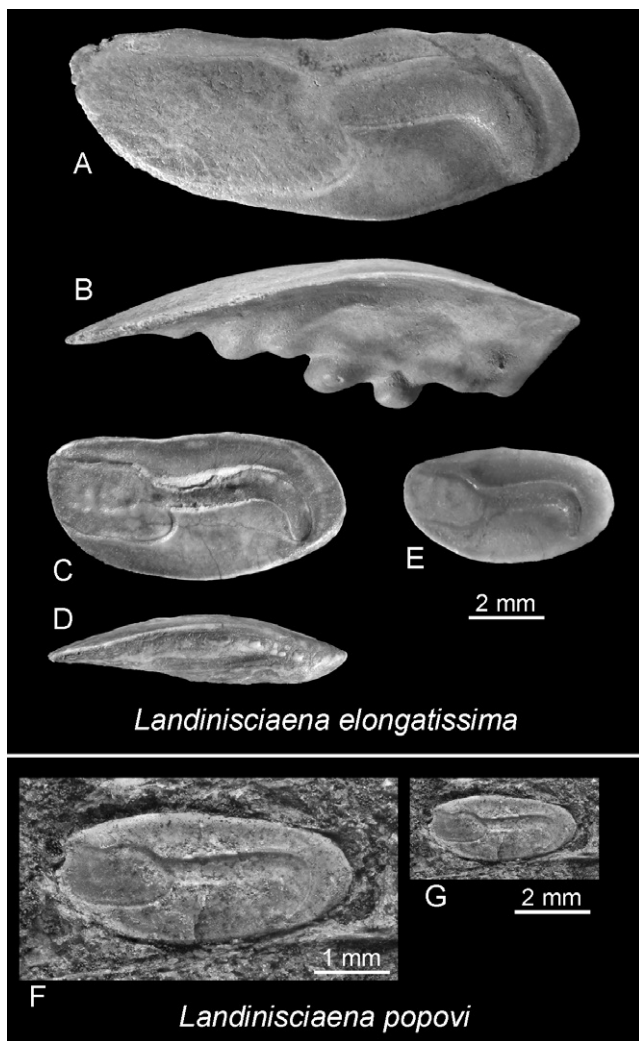


Fig. 2 - Otoliths of *Landinisciaena* gen. nov. A-E) *Landinisciaena elongatissima* (Schwarzzhans, 1993). A-B) (mirror imaged) Heistop-den-berg, Belgium, Hemmoorian, IRSNB 7096 (A inner face, B ventral view); C-D) Rhaden, Germany, Hemmoorian, SMF PO 64988 (C inner face, D ventral view); E) (mirror imaged) Ohstedt 192 m, Germany, Hemmoorian, SMF PO 64990. F-G) *Landinisciaena popovi* sp. nov. Otolith found *in situ* in holotype PIN 5599/1, Pshekha River, NW Caucasus, Tarkhanian (G lesser magnification for comparison reasons with figures 2 A-E).

The hyoid bar is hidden under fragments of other cranial bones. There are probably seven sabre-like branchiostegal rays, of which the two anterior ones are slender whereas the others are thickened. The bones of the branchial skeleton are obscured and indistinct. Below the otic region the pharyngeal teeth are recognizable; these are conical and curved and similar in size and shape to the canines-like teeth of the oral jaws.

There are 25 (13+12) vertebrae, including the urostyle. The axis of the vertebral column is gently concave and elevated anteriorly. The vertebral

centra are constricted in the middle and somewhat elongated anteroposteriorly, except for two shortened anteriormost centra. The length of the caudal portion of the vertebral column is 1.18 times greater than the length of the abdominal portion. The neural spines are inclined posteriorly, relatively short, slightly curved, and very slender, whereas those of the six anterior vertebrae are moderately expanded anteroposteriorly. The neural spines of the posteriormost abdominal and anteriormost caudal vertebrae are the longest of the series. The haemal spine of the anterior caudal vertebra is shorter than the corresponding neural spine and strongly inclined. The parapophyses are recognizable only in the posterior three abdominal vertebrae; the last parapophysis is similar to the haemal spine of the first caudal vertebra, except for its reduced length. The pleural ribs are slender and moderately elongate; these are strongly inclined posteroventrally, thereby occupying the upper half of the abdominal cavity. There is no evidence of the epineurals.

The terminal centrum consists of fused first preural centrum plus two ural centra. The parhypural, two uroneurals, five hypurals, haemal spines of the second and (perhaps) third preural centra are autogenous. The hypural diastema between the epaxial and hypaxial hypurals is very narrow. The neural and haemal spines of the third preural centrum are longer and stouter than those of the preceding vertebra. The neural spine of the second preural centrum is reduced to a short crest. There are three slender epurals, of which the first is the longest. The caudal fin is moderately long and rounded. There are 17 principal rays (I,8-7,I), whereas the precise number of procurrent rays is difficult to define. The presence of the procurrent spur (Johnson 1975, 1984) cannot be determined.

There are three short and slender posteriorly inclined supraneurals. Slight displacement of anterior two vertebrae from their natural position makes it difficult to restore the precise supraneural formula (see Ahlstrom et al., 1976), which is tentatively restored as 0/0/0+2/1+1/.

The dorsal fin is relatively long-based; it originates just above the fourth abdominal vertebra and terminates at the level the anterior portion of the eighth caudal vertebra. There is a deep notch between the spiny and soft portions of the dorsal fin. There are 11 dorsal-fin spines followed by 25 rays. The dorsal-fin spines are slender; the longest

(third and fourth) spines are 3.7 times longer than the shortest (10th) one and 3.3 times longer than the first spine. The length of the last spine equals that of the first spine. The first two dorsal-fin spines are supernumerary on the first dorsal-fin pterygiophore; these are closely spaced. The soft dorsal-fin rays are segmented and most of them are distally branched. The longest soft ray of the dorsal fin is clearly shorter than the longest dorsal-fin spine. The length of the base of the soft portion of the dorsal fin is 1.37 times longer than the base length of the spinous portion. The dorsal and anal-fin pterygiophores are bisegmental, with the medial element possibly fused with the proximal one (see Sasaki 1989). The anterior dorsal-fin pterygiophores are expanded anteroposteriorly, and bear a longitudinal thickened ridge; the succeeding pterygiophores gradually become narrower. The first to fourth dorsal-fin pterygiophores penetrate down into the interneural spaces, whereas most of the other pterygiophores terminate above the neural spines. Posteriorly in the series the soft dorsal-fin pterygiophores become more strongly inclined and of decreased length.

The anal-fin insertion is located under the fourth caudal vertebra. The length of the base of the anal fin is rather short, approximately corresponding to the length of three overlying vertebrae. The anal fin consists of two spines and eight segmented and branched rays. The second anal-fin spine is thick and about 5.2 times longer than the first spine. Both the spines are in supernumerary association on the first anal-fin pterygiophore. The second anal-fin spine is 1.3 times shorter than the longest dorsal-fin spine. The longest anal-fin ray equals in length the longest dorsal-fin spine. The anal-fin rays rapidly decrease in length posteriorly in the series. The first anal-fin pterygiophore is long and sturdy, but relatively narrow; it is strongly inclined with respect to the body axis. The succeeding anal-fin pterygiophores are slender and strongly obliquely oriented; these pterygiophores are short and terminate much below the tips of the haemal spines. The posterior pterygiophore is almost horizontally oriented.

The posttemporal lacks prominent spines along the posterior margin, possibly due to the juvenile or subadult nature of the individual; both the upper and lower arms of the posttemporal are recognizable. The morphology of the supracleithrum

cannot be determined. The cleithrum is massive and elongate; its upper part is curved anteriorly and placed just under the two anterior vertebrae. The dorsal postcleithrum is hardly recognizable, whereas the posteroventrally directed ventral postcleithrum is rib-like and slender. The coracoid is narrow, and the inter-osseous space is present ventrally between the cleithrum and coracoid. Both the scapula and pectoral radials are poorly recognizable. The base of the pectoral fin is situated approximately below the fourth vertebra, near the midlength between the vertebral column and the ventral profile of the body. The pectoral fin consists of 14 or 15 rays and is moderately long, extending posteriorly to the level of the ninth abdominal vertebra.

The basipterygia are preserved as a single series exposed in dorso-ventral view. The pelvic fin originates just under the pectoral-fin base and comprises a single spine and five distally branched rays. The pelvic fin is moderately long; the pelvic-fin spine is slender and 1.2 times shorter than the longest (second) anal-fin spine.

Moderately large scales cover the entire body and the head. Each body scale bears circuli but no radii are recognizable in the basal field. The scales are ctenoid on the body (at least ventrally) and cycloid on the head, a condition that is particularly clear on the opercle. The ctenii are not recognizable in the scales from the dorsal portion of the body. The lateral line series is gently convex anteriorly, descending to the level of the vertebral column at the level of the second caudal vertebra.

Remarks. Overall, the new fossil croaker described herein exhibits a generalized morphology lacking any of the specialized features that characterize the skeletal anatomy of many modern sciaenid taxa (see, e.g., Sasaki 1989). Moreover, due to the inadequate preservation of the head skeleton, some of the features with a potentially relevant phylogenetic information cannot be evaluated. *Landinisciaena popovi* is diagnosed by a unique combination of features that supports its recognition as a new genus and species within the Sciaenidae. The overall physiognomy of the body, as well as a series of morphometric and meristic features seem to suggest a close similarity to the extant genus *Atractoscion* (see, e.g., Song et al. 2017), from which it clearly differs by having spines along the posterior margin of the preopercle, eight rather than nine anal-fin rays, and caudal fin rounded rather than

slightly emarginate to lunate. The otolith found *in situ* in the holotypic specimen of *Landinisciaena popovi* exhibits all morphological features characteristic of a not completely developed juvenile sagitta. The combination of features observed is considerably reminiscent of that characteristic of small (juvenile) specimens of a species known as *Atractoscion elongatissimus* Schwarzshans, 1993 up to date reported from the Ottnangian to Karpatian of the Central Paratethys and time equivalent strata of the North Sea Basin. Schwarzshans (2010) figured a full ontogenetic sequence of this species from the North Sea Basin, evidencing that otoliths reach 22 mm in length and are diagnostically mature at a length of about 12 mm. The small otolith of *Landinisciaena popovi* is strikingly similar to the small sized specimens of *Atractoscion elongatissimus* reported by Schwarzshans (2010) (refigured in Fig. 2 E). However, *Landinisciaena popovi* is slightly younger stratigraphically and restricted to the Eastern Paratethys. Moreover, it differs from *Atractoscion elongatissimus* by having a mild indentation of the dorsal margin of the ostium. We therefore tentatively suggest that two species of *Landinisciaena* were present in the Paratethys during the Miocene.

Genus *Croatosciaena* gen. nov.

Type Species: *Croatosciaena krambergeri* sp. nov., by monotypy and designation herein.

Diagnosis: A relatively elongated sciaenid fish with a moderately slender caudal peduncle. Maximum body depth slightly more than 25% SL. Head relatively large, its length contained about 2.6 times in SL. Orbit relatively large. Supraoccipital crest low. Lower jaw articulation under the midpoint of the orbit. Mouth gape moderately wide and terminal. Premaxilla with long and narrow ascending process. Jaw teeth relatively small and conical, with no canines. Posterior preopercular margin with relatively large serrations. Twenty-six vertebrae (10+16). Three supraneurals. Dorsal fin with 28 elements, of which about 11 are spines (two supernumerary). Anal fin with two spines and 9 rays. Dorsal-fin spines moderately slender, whereas second anal-fin spine remarkably thick. Pectoral fin relatively short; pelvics inserted just behind pectorals. Caudal fin truncated. Scales ctenoid on the body and apparently absent on the head. Lateral line concurrent with dorsal profile of body anteriorly.

Etymology: The genus is named after Croatia and the genus *Sciaena*; gender feminine.

Composition: Type species only.

Croatosciaena krambergeri sp. nov.

Fig. 3

Holotype: CNHM 279, partially complete moderately preserved articulated skeleton, 61 mm SL.

Diagnosis: As for the genus.

Etymology: The species is named in honor of Dragutin Gorjanović-Kramberger, pioneer of the Croatian paleoichthyology.

Referred Specimens: None.

Type Locality and Horizon: Dolje, in the nearby of the city of Zagreb, Croatia; Middle Miocene, Sarmatian (=Upper Serravalian).

Measurements: (as percent of SL). Head length: 38; maximum body depth: ca. 25; snout length: 11; orbit diameter: 10.5; mandible length: ca. 17.5; caudal peduncle depth: 10; predorsal (spinous dorsal) length: 39; predorsal (soft dorsal) length: ca. 61; preanal length: ca. 71; distance between pelvic and anal fins: 26; dorsal-fin base length: ≤ 48 ; spinous dorsal-fin base length: ca. 22.5; anal-fin base length: 14; first dorsal-fin spine length: 4.6; longest dorsal-fin spine length: ca. 16.5; first anal-fin spine length: 6.5; second anal-fin spine length: 17; pelvic-fin spine length: 15; longest caudal-fin ray length: 21.

Description. The body is relatively elongate, with a moderately deep caudal peduncle (Fig. 3). The caudal peduncle depth is contained slightly less than three times in the maximum body depth. The head is relatively large; its length (tip of snout to posterior edge of opercle) is 1.5 times larger than the body depth. The head length is contained 2.6 times in SL. The orbit is relatively large; its diameter is ca. 27% of the head length. The snout is moderately long; its length is ca. 29% of the head length. The lower jaw articulation is located under the midlength of the orbit. The dorsal and ventral profiles of the body are almost equally convex.

The occiput of the holotype is slightly turned down post-mortem from its articulation to the backbone. The neurocranial structures are difficult to interpret because of inadequate preservation. The neurocranium is moderately low, with the supraoccipital crest evidently poorly developed. The frontals are the largest bones of the skull roof; their cavernous texture is recognizable. The ventral projection of the frontals is not evident. The ethmoid block is moderately broad. The parasphenoid is relatively slender and almost straight, with no dorsal flange evident. The basisphenoid seems to articulate with the parasphenoid. The limits of the otic bones cannot be determined.

The bones of the infraorbital series are difficult to recognize.

The mouth is moderately wide and terminal (Fig. 3). The jaw bones are badly damaged. The premaxilla has a relatively long and slender ascending process clearly separated from the articular process; the ascending process is shorter than the alveolar process; the presence of a postmaxillary process cannot be determined. A few relatively small and

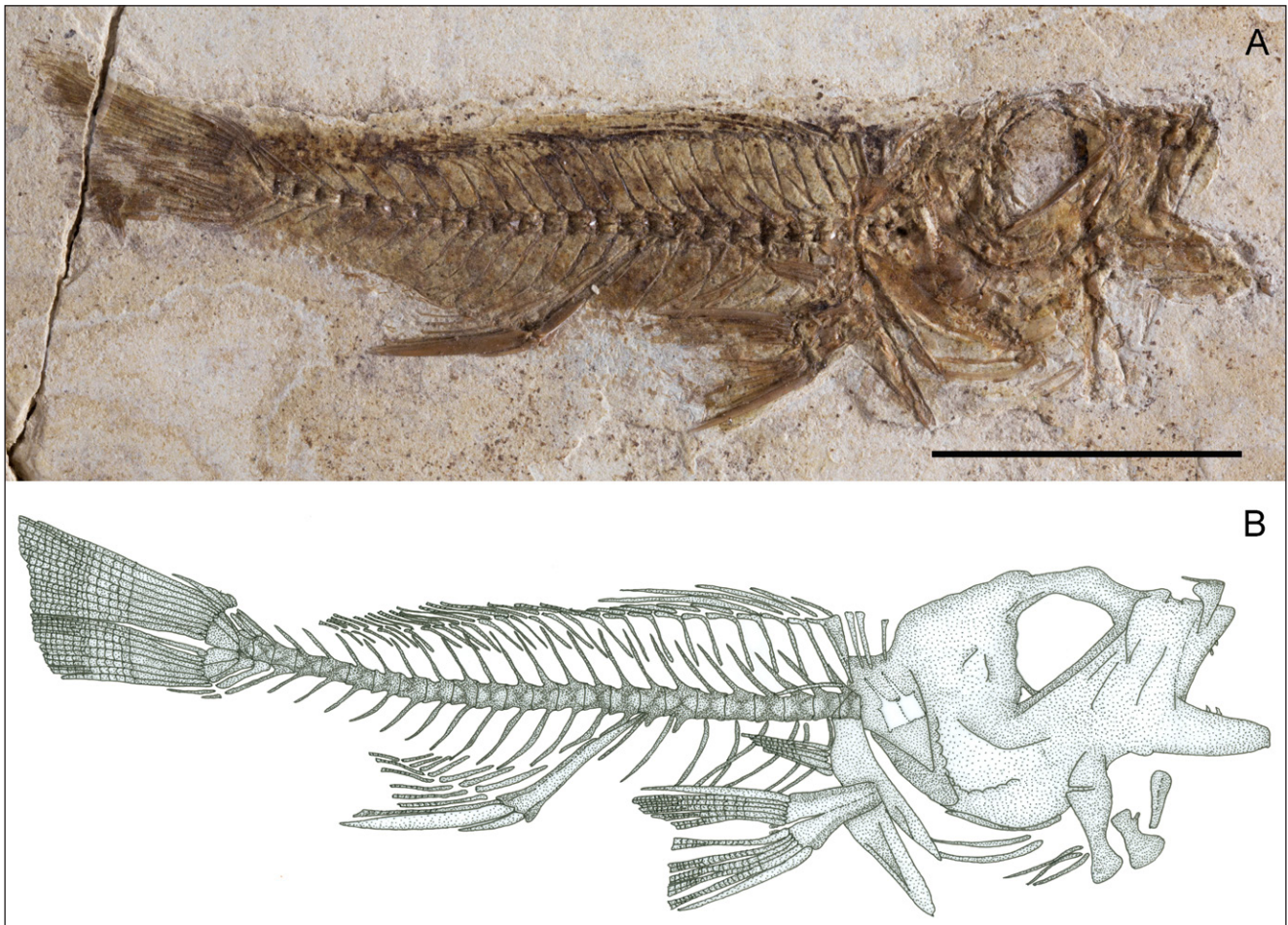


Fig. 3 - *Croatosciaena krambergeri* gen. et sp. nov. from the Sarmatian of Dolje, Croatia. A) holotype, CNHM 279, right lateral view; B) reconstruction of the skeleton. Scale bar 20 mm.

conical premaxillary teeth are scarcely recognizable; there is no evidence of canines. The maxilla is distally expanded. The lower jaw is poorly preserved. Overall, the mandible length is less than half of head length. Few of the mandibular teeth are preserved mostly as impression only; these are relatively small and conical, with no evidence of canines.

The limits of the majority of the bones of the suspensorium are scarcely distinguishable.

The opercular region is relatively wide. The preopercle appears to be crescent shaped and characterized by relatively large serrations along its posterior margin. The horizontal and vertical arms of the preopercle seem to be almost equal in length. The opercle, subopercle and interopercle are only scarcely recognizable.

The hyoid bar is inadequately preserved, with bones preserved mostly as impression only. The ceratohyal is not pierced by the “beryciform foramen”. There are about seven sabre-like branchiostegal

rays, disarticulated from the hyoid bar. The basihyal is narrow and rod-like. The bones of the branchial skeleton and the pharyngeal teeth are not exposed.

The vertebral column seems to comprise 26 (10+16) vertebrae, including the urostyle. Only eight posterior abdominal vertebrae are clearly recognizable and the neural spine of the anteriormost vertebra precedes the second dorsal-fin pterygiophore. However, since the vertebral column of sciaenids contains at least ten abdominal vertebrae (Sasaki, 1989), and not less than two neural spines are situated before their first dorsal-fin pterygiophore (see Johnson, 1984; Bannikov, 2013), we presume that the two anteriormost vertebrae are not exposed. The axis of the vertebral column is almost straight. The vertebral centra are subrectangular, longer than high and constricted in the middle. The length of the caudal portion of the vertebral column is 1.75 times greater than the reconstructed length of the abdominal portion. The neural spines are inclined

posteriorly, moderately long, straight or slightly curved, and relatively slender. The neural spines of the posteriormost abdominal and anteriormost caudal vertebrae are longest. The haemal spines of the two anterior caudal vertebrae are shorter than the opposite neural spines and the succeeding haemal spines. The parapophyses are recognizable only in the posterior two abdominal vertebrae. The ribs are slender and moderately elongate; these are moderately inclined posteroventrally, thus occupying the upper half of the abdominal cavity. Only a single element of the epineural series is recognizable.

The caudal skeleton is poorly preserved. However, it seems that the caudal skeleton has the structure typical for the generalized percoids, with the terminal centrum composed of first preural centrum fused to the two ural centra, plus parhypural, (two) uroneurals, five hypurals and haemal spines of second and third preural centra autogenous. The neural and haemal spines of the third preural centrum are somewhat longer and stouter than those of the preceding vertebra. The neural spine of the second preural centrum is reduced to a short crest. Among the epurals, only the first one is clearly recognizable. The caudal fin is moderately long and probably truncated (perhaps its lower lobe is incomplete distally). The caudal fin consists of 17 (I,8-7,I) principal rays plus not less than six dorsal and four ventral procurrent rays. The presence of the procurrent spur is difficult to determine.

There are three robust supraneurals slightly expanded distally. However, since the first two vertebrae are not exposed, the precise supraneural formula cannot be recognized.

The dorsal fin is relatively long-based; it originates over the third or fourth vertebra. The posterior portion of the dorsal fin is poorly preserved; 26 pterygiophores seem to be present in the fin. Since the first two dorsal-fin spines are supernumerary on the first pterygiophore, therefore, the fin likely contained 28 elements in origin, of which 11 should have been spines and 17 segmented and distally bifurcated rays. The dorsal-fin spines are moderately strong; the longest (fourth) spine is 3.6 times longer than the first one. The longest ray of the dorsal fin is obviously shorter than the longest dorsal-fin spine. The base of the soft portion of the dorsal fin seems to be almost equal in length to the base of the spiny portion. The dorsal-fin pterygiophores are bisegmental. The anterior dorsal-fin pterygiophores

are expanded anteroposteriorly, and bear a central longitudinal thickened ridge; the succeeding pterygiophores become gradually shorter and narrower. The ventral shafts of one or two of the dorsal-fin pterygiophores insert into the interneural spaces. Posteriorly in the series the dorsal-fin pterygiophores become more strongly inclined.

The anal fin originates under the fourth or fifth caudal vertebra. The base of the anal fin is moderately short, corresponding to the length of about five vertebrae. The anal fin consists of two spines and nine branched rays. The second anal-fin spine is remarkably thick, being about 4.1 times longer than the first anal-fin spine. Both the spines are in supernumerary association on the first anal-fin pterygiophore. The second anal-fin spine is almost as long as the longest dorsal-fin spine. The first anal-fin ray seems to be slightly shorter than the second anal-fin spine. The succeeding rays rapidly decrease in length posteriorly in the series. The first anal-fin pterygiophore is exceptionally long and sturdy, wedge-shaped, strongly inclined with respect to the body axis with its proximal tip almost contacting the vertebral column. The second and successive anal-fin pterygiophores are slender, and strongly inclined, their size rapidly decreases in length posteriorly in the series. Each of the anal-fin pterygiophores usually occupies a single interhaemal space, except for the posterior three that are closely associated to each other in the sixth interhaemal space.

The bones of the pectoral girdle are poorly preserved. The posttemporal and the postcleithra are not recognizable. The cleithrum is moderately massive and elongate. The coracoid seems to be very narrow. An inter-osseous space can be observed ventrally between the cleithrum and coracoid. Both the scapula and pectoral-fin radials are scarcely recognizable. The pectoral-fin base is located just under the fourth and fifth vertebrae, above the midpoint between the vertebral column and the ventral profile of the body. The pectoral fin seems to be narrow at the base and relatively short; the total complement of the pectoral-fin rays cannot be determined.

The basipterygia are dorso-ventrally exposed. The pelvic fin inserts just behind the pectoral-fin base and contains a single spine and five branched rays. The pelvic fin is relatively long; the pelvic-fin spine is strong and 1.2 times shorter than the long-

est (second) anal-fin spine.

Relatively large scales cover the entire body including the head. The limits of the individual scales are not recognizable; some radii are distinguishable in the basal field of the trunk scales. The body is covered with ctenoid scales, whereas they appear to be absent on the head. Only the anterior portion of the lateral line is recognizable; it follows the dorsal profile of the body.

Remarks. As discussed above, *Croatosciaena krambergeri* is based on a single and moderately well-preserved specimen measuring about 61 mm SL, characterized by a partially recognizable skeletal anatomy. It is defined by a unique combination of morphological and meristic features that justify its placement as a new genus and species within the family Sciaenidae. Some of the distinctive features of *Croatosciaena krambergeri* can be regarded phylogenetically informative (see Sasaki 1989), including: frontal not projecting downward, basisphenoid articulates with the parasphenoid, canines absent in the oral jaws, preopercular spines present, and pectoral fin very short. In any case, the skeletal structure and body aspect of *Croatosciaena krambergeri* appear to be rather generalized, lacking the majority of the distinctive features that define the subfamilial or tribal clades recognized by Sasaki (1989); for this reason, it is extremely difficult to determine any possible phylogenetic relationship of *Croatosciaena krambergeri* with other sciaenid taxa.

Genus *Argyrosomus* de la Pylae, 1835

Argyrosomus multipinnatus
(Gorjanović-Kramberger, 1882)

Fig. 4

1882 *Labrax multipinnatus* Gorjanović-Kramberger, p. 99, pl. 23, fig. 3.

1989 *Morone multipinnata* (Gorjanović-Kramberger, 1882) - Anđelković, pl. 12, fig. 2.

Lectotype: CNHM 44, single plate, complete articulated skeleton without caudal fin, 252 mm SL.

Diagnosis: A species of *Argyrosomus* with relatively elongated body and a moderately slender caudal peduncle. Maximum body depth almost equals to head length. Head relatively small, 3.6 times in SL. Orbit relatively small. Supraoccipital crest low. Lower jaw articulation under anterior half of the orbit. Mouth gape barely wide and terminal, slightly oblique. Jaws of equal length. Premaxilla with relatively short ascending process. No large canines. Mandible length about 12% SL. Preopercular margin posteriorly with moderate serrations. 25 (11+14) vertebrae. Three supraneurals. Dorsal fin slightly

notched, with 11 exposed spines and 24 soft rays. Anal fin extremely short based with two spines and 6 (?) rays. Dorsal-fin spines moderately strong. Second anal-fin spine notably robust, its length reaching about 10% SL. Pectoral fin relatively short; pelvics inserted below pectorals. Scales cycloid or weakly ctenoid on the body and cycloid on the head.

Referred Specimens: Apparently none. Gorjanović-Kramberger (1882: 99) reported the existence of the second poorly preserved specimen from Podsused, Croatia. We have been unable to locate such a specimen.

Type Locality and Horizon: Sveta Nedelja, Samoborsko gorje, NW Croatia; Middle Miocene, Sarmatian (=Upper Serravalian).

Measurements: (as percent of SL). Head length: 28; maximum body depth: ca. 26.5; snout length: 8; orbit diameter: 7.5; mandible length: ca. 12; caudal peduncle depth: 9; caudal peduncle length: 12; predorsal (spinous dorsal) length: 36; predorsal (soft dorsal) length: 56.5; preanal length: 75; distance between pelvic and anal fins: 41; dorsal-fin base length: 54; spinous dorsal-fin base length: 20; anal-fin base length: 6; length of the first dorsal-fin spine: 3; length of the longest dorsal-fin spine: >10; length of the first anal-fin spine: 3; length of the second anal-fin spine: 10

Description. The morphology of this species was described in detail by Gorjanović-Kramberger (1882: 99) to whom we refer.

Remarks. The fossil exhibits several morphological features that justify its inclusion within the genus *Argyrosomus*, including a fairly elongated body, mouth terminal, jaws equal anteriorly, large canines absent, preopercle serrated, 11+14 vertebrae, 11 dorsal-fin spines, and pectoral fin relatively short (see, e.g., Griffiths & Heemstra 1995).

Most of the distinctive features of extant species of *Argyrosomus* concern the morphology of the saccular otolith and structure of the swimbladder and its appendages (see Griffiths & Heemstra 1995). Unfortunately, all of these features cannot be determined in the fossil due to inadequate preservation. Nevertheless, there is substantial morphometric and meristic evidence that supports the recognition of the fossil as a representative of an additional species of the genus *Argyrosomus*, including dorsal fin with 24 (vs 25-30 in extant species) rays; mandible relatively short, reaching 12% (vs 13.5-18 in extant species) of SL; anal fin extremely short, being about 6% (vs 21-19% in extant species) SL; and second anal-fin spine considerably elongate and robust, its length measuring about 10% SL (see, e.g., Griffiths & Heemstra 1995). In particular, *Argyrosomus multipinnatus* differs from the extant Atlantic-Mediterranean species *A. regius* (Asso, 1801) by having 24 vs 26-30 dorsal-fin rays, a more compact mandible (mandible length 12% vs 14-16% SL), anal fin remarkably short (anal-fin length 6% vs 14-



Fig. 4 - *Argyrosomus multipinnatus* (Gorjanović-Kramberger, 1882) from the Sarmatian of Dolje, Croatia. Lectotype, CNHM 44, left lateral view. Scale bar 20 mm.

18% SL), and second anal-fin spine considerably developed (2nd anal-fin spine 10% vs 7.0-8.9% SL).

The otolith record

Remarks. Sciaenid otoliths are mostly large, robust and easily recognized by their distinctive sulcus morphology characterized by a wide ostium and a steeply curved slender cauda. Because of their diversity, large size and species-specific morphology, they are commonly used also in ichthyological literature to separate the extant taxa of the family (e.g., Chao 1978). Due to their somewhat spectacular appearance, sciaenid otoliths have been commonly recorded from Neogene strata worldwide, including the Paratethyan realm. However, many of the Paratethyan records are in need of revision. The original material described by Schubert (1902) was reviewed by Nolf (1981) and that of Weinfurter (1952) by Nolf & Brzobohaty (2009). All the material was also discussed in the comprehensive review compiled by Schwarzhans (1993). However, other original material was not available for any of these revisions and new material has been collected and described since the publication of these studies. Here, we present a review of the sciaenid otoliths described by Pana (1977, 1982, 1995) from the late Neogene deposits of Romania as well as of the specimens figured in Gorjanović-Kramberger (1891) from the late Pannonian (Portaferrian) of Croatia. However, other Neogene Paratethyan sciaenid otoliths have still not been available for review, particularly those described by Lörenthey (1906), Pobedina (1956) and Djafarova (2006). Among the papers containing records of sciaenid otoliths published after the

monographic review of Schwarzhans (1993), those of Bratishko et al. (2015), Djafarova (2006) and Rückert-Ülkümen (1996) are of particular interest. Unfortunately, the material described by Djafarova (2006) was not available for review. In addition, there is a large collection of Bessarabian otoliths from the Crimea currently under study by Bratishko and Schwarzhans. Thanks to the kind support of Andriy Bratishko, these Bessarabian sciaenids are also included in the present study.

One of the main aspects of the otolith-based sciaenid taxonomy in the older literature is that several species were identified based on worn or juvenile specimens. Many sciaenid otolith morphologies are subject to considerable ontogenetic changes, with negative implications in the attempts to identify juvenile specimens. However, there are some sciaenids characterized by relatively small otoliths that can be recognized due to their aberrant morphology or based on a reasonably complete ontogenetic sequence. Another problematic aspect commonly observed in older literature is a proliferation of names due to an inadequate understanding of the intraspecific variability. These aspects have also been addressed in the reviews of Nolf (1981) and Schwarzhans (1993). Finally, there is an ongoing dispute in otolith literature about the usage of otolith-based fossil genera versus open generic nomenclature or the usage of undefined collective genus group names [see discussions in Schwarzhans (2012) and Nolf (2013)]. We are opting here for the usage of otolith-based fossil genus group names where appropriate, because the two other systems in use are not, or not fully, conformable with the ICZN rules (Tracey 2014). Moreover,

we believe that the usage of unambiguous generic names in otolith description is useful to support nomenclatural stability. We are aware, however, that this practice may create parallel taxonomy for skeleton-based and otolith-based data, at least until such time that otoliths are found *in situ*. We believe that the situation has advanced to a state where seeking of a clarification from the ICZN committee may be beneficial.

The following text is bipartite, consisting of (1) an annotated alphabetic list of sciaenid otolith-based species recorded from the Paratethys since Ottnangian /Kotsakhurian (late Burdigalian) including their review history and the view of their current status as adopted herein, and of (2) a descriptive part for the species documented in this work or for which the status has been changed.

Annotated list of Neogene (since Ottnangian/Kotsakhurian stages) Paratethyan sciaenid otolith-based species. Species names are listed in alphabetic order with original generic allocation or first usage in Paratethyan reference, then authority, figure and stratigraphic age, followed by brief review history, or comments in the absence of reviews, and finally current or new status as adopted herein. Valid species are in bold. Occasionally described sciaenid lapilli are not reported herein, since we believe that those identifications are not supported by distinctive diagnostic morphologies.

abrupta Schubert, 1902, *Otolithus* (*Sciaenidarum*) *corii*. Schubert (1902, pl. 10, fig. 21), Badenian. - Reviewed by Nolf (1981) and rejected based on inadequate preservation; reviewed by Schwarzhans (1993) and regarded as a synonym of *Argyrosomus corii* (Schubert, 1902). - Current status: synonym of ***Argyrosomus corii* (Schubert, 1902)**.

acuterostratus Rückert-Ülkümen, 1996, *Serranus*. Rückert-Ülkümen (1996, pl. 2, figs. 4-6), Sarmatian s.l. - Under review by Bratishko & Schwarzhans (in preparation) and considered a valid species of the family Sciaenidae. - New status: valid as ***Pontosciaena acuterostrata* (Rückert-Ülkümen, 1996)**.

alsheimensis Weiler, 1963, *Umbrina* cf. Pana (1965, pl. 4, figs. 125-126), Dacian. - Reviewed herein. - New status: ***Trewasciaena dobrogiaca* (Pana, 1977)**.

angulata Schubert, 1902, *Sciaena irregularis*. Schubert (1902, pl. 10, fig. 8), Pannonian E. - Re-

viewed by Nolf (1981) and rejected based on inadequate preservation; reviewed by Schwarzhans (1993) and regarded as a synonym of *Trewasciaena kokeni* (Schubert, 1902). - New status: we follow Nolf in rejecting this nominal species, since it is occurred sympatrically with a single *Trewasciaena*, a single *Chaoia* and two different *Umbrina* species and it is difficult to determine which species it should be related to.

angulata Schubert, 1902, *Sciaena*. Pana (1977, pl. 5, figs. 15-16; 1995, pl. 4, figs. 5-8), Dacian. - Reviewed herein. - New status: ***Trewasciaena dobrogiaca* (Pana, 1977)**.

azerbaidjanicus Djafarova, 2006, *Otolithus* (*Mugilidarum*). Djafarova (2006, pl. 11, fig. 4, non fig. 3, non pl. 12, fig. 2), middle Sarmatian s.l. - Comment: Djafarova (2006) figured three specimens under this name, which actually belong to two different species; one of these from the Chokrakian actually represents a mugilid and another corresponds to an aberrant sciaenid of the genus *Leptosciaena* from the Sarmatian. Djafarova (2006) did not provide any information about the type specimen. The Sarmatian otolith figured herein is highly characteristic and therefore we have tentatively accepted that one as name giving specimen. - New status: provisionally referred to as ***Leptosciaena azerbaidjanica* (Djafarova, 2006)**.

cirrosa (Linnaeus, 1758), *Umbrina* aff. Cziczter et al. (2008, fig. 12), Pannonian C. - Comment: a reasonably well-preserved specimen of slightly more than 9 mm in length. - New status: ***Umbrina subcirrhosa* (Schubert, 1902)**.

cirrosa (Linnaeus, 1758), *Umbrina* cf. Brzobohaty et al. (2007, pl. 7, fig. 6), Badenian. - Comment: An incomplete specimen of the genus *Umbrina*, probably *U. subcirrhosa* (Schubert, 1902). - New status: probably ***Umbrina subcirrhosa* (Schubert, 1902)**.

cirrosa (Linnaeus, 1758), *Umbrina*. Reichenbacher (1998, pl. 3, fig. 2), Karpatian. - Comment: a well-preserved specimen of *Umbrina* without post-central umbo on the outer side as seen in extant specimens of *U. cirrosa*. - New status: ***Umbrina subcirrhosa* (Schubert, 1902)**.

cirrhosoides Schubert, 1902, *Corvina?* Schubert (1902, pl. 10, fig. 4), Nolf (1981, pl. 3, fig. 10), Schwarzhans (1993, figs. 124-125), Jovanović et al. (2010, pl. 2, fig. 3), Schultz (2013, pl. 90, figs. 3-4), Pannonian E and Portaferrian. - Reviewed by Nolf (1981) and Schwarzhans (1993) and considered valid

as *Umbrina cirrhosoides*. - Current status: valid as ***Umbrina cirrhosoides* (Schubert, 1902)**.

claybornensis Koken, 1888, *Otolithus* (*Sciaenidarum*) aff. Schubert (1902, pl. 10, fig. 13 and text-fig. 2), Schultz (2013, pl. 90, fig. 2; as *Umbrina* sp.), Badenian. - Reviewed by Nolf (1981) and considered an unidentifiable eroded sciaenid otolith (Koken described this species from the Eocene of the USA). - Current status: invalid reference.

***compacta* Schubert, 1902.** *Sciaena?* Schubert (1902, pl. 10, fig. 11), Schwarzhans (1993, figs. 275-277), Schultz (2013, pl. 89, fig. 8), Ottnangian. - Reviewed by Nolf (1981) and rejected because of the lack of the anterior tip of the otolith; reviewed by Schwarzhans (1993) and considered valid as *Miracorvina?* *compacta* (Schubert, 1902). - Current status: valid as ***Miracorvina?* *compacta* (Schubert, 1902)**.

***corii* Schubert, 1902,** *Otolithus* (*Sciaenidarum*). Schubert (1902, pl. 10, fig. 20), Schwarzhans (1993, figs. 257-260), Schultz (2013, pl. 89, figs. 5, 7, 9), Badenian. - Reviewed by Schubert (1906) and considered as synonym of *Sciaena pecchiolii* (Lawley, 1876), together with the subspecies *Otolithus* (*Sciaenidarum*) *corii abrupta* Schubert, 1902. *Sciaena pecchiolii* is regarded as a subjective synonym of the extant *Argyrosomus regius* (Asso, 1810) following Schwarzhans (1993); reviewed by Nolf (1981) and tentatively synonymized with *Argyrosomus* aff. *regius*; reviewed by Schwarzhans (1993) and considered valid as *Argyrosomus corii* (Schubert, 1902). - Current status: valid as ***Argyrosomus corii* (Schubert, 1902)**.

dacica Pana, 1977, *Corvina*. Pana (1977, pl. 5, figs. 1-12; 1995, pl. 4, figs. 12-15), Dacian. - Reviewed herein. - New status: synonym of ***Trewasciaena dobrogiaca* (Pana, 1977)**.

depressus Schubert, 1902, *Otolithus* (*Sciaenidarum*). Schubert (1902, pl. 10, fig. 19), Badenian. - Reviewed by Nolf (1981) and rejected as based on an eroded and fragmentary otolith. - Current status: species rejected.

***dobrogiaca* Pana, 1977,** *Corvina*. Pana (1977, pl. 3, figs. 1-11, pl. 4, figs. 1-4; 1995, pl. 5, figs. 1-3), Dacian. - Reviewed herein. - New status: valid as ***Trewasciaena dobrogiaca* (Pana, 1977)**.

dubius Schubert, 1902, *Otolithus* (*Sciaenidarum*). Schubert (1902, text-fig. 5), Schultz (2013, pl. 90, fig. 8; as *Sciaenidae* indet.), Badenian. - Reviewed by Nolf (1981) and rejected as based on an eroded and fragmentary otolith. - Current status: species rejected.

***elongatissimus* Schwarzhans, 1993,** *Atracoscion*. Schwarzhans (1993, fig. 78), Ottnangian. - New status: valid as ***Landinisciaena elongatissima* (Schwarzhans, 1993)**.

excissus Schubert, 1902, *Sciaena?* Schubert (1902, pl. 10, fig. 17), Pannonian E. - Reviewed by Nolf (1981) and Schwarzhans (1993) and considered as synonym of *Trewasciaena kokeni* (Schubert, 1902) [Nolf (1981) tentatively though and proposing rejection of species because of poor preservation]. - Current status: synonym of ***Trewasciaena kokeni* (Schubert, 1902)**.

excissus Schubert, 1902, *Sciaena* aff. Djafarova (2006, pl. 15, figs. 2-4), Akchagylian. - Comment: Well-preserved otoliths that perfectly match coeval otoliths known from Turkmenistan (Schwarzhans 1993) and *Trewasciaena dobrogiaca* (Pana, 1977). - New status: ***Trewasciaena dobrogiaca* (Pana, 1977)**.

fuchsi Schubert, 1902, *Otolithus* (*Sciaenidarum*). Schubert (1902, fig. 3), Nolf (1981, pl. 3, fig. 7), Schultz (2013, pl. 89, fig. 3; as *Sciaenidae* indet.), Badenian. - Reviewed by Nolf (1981) and considered a valid species despite some erosion and of uncertain generic relationships. - Current status: nominally valid species but of doubtful nature.

gemmoides Schubert, 1902, *Otolithus* (*Sciaenidarum*). Schubert (1902, pl. 10, fig. 14), Badenian. - Reviewed by Nolf (1981) and rejected as based on an extremely eroded otolith. - Current status: species rejected.

***getica* Pana, 1995,** *Corvina*. Pana (1995, pl. 5, figs. 7-9), Dacian. - Reviewed herein (name mentioned without description in Pana, 1982). - New status: valid as ***Umbrina getica* (Pana, 1995)**.

gibberula Koken, 1884, *Corvina* aff. Schubert (1902, pl. 10, fig. 5), Badenian. - Reviewed by Nolf (1981) and considered an unidentifiable eroded sciaenid otolith. - Current status: invalid reference.

gracilis Schubert, 1902, *Otolithus* (*Sciaenidarum*). Schubert (1902, pl. 10, fig. 22), Badenian. - Reviewed by Nolf (1981) and rejected based on poor preservation; reviewed by Schwarzhans (1993) and considered as synonym of *Argyrosomus corii* (Schubert, 1902). - Current status: synonym of ***Argyrosomus corii* (Schubert, 1902)**.

incisus Radwanska, 1984, *Argyrosomus*. Radwanska (1984, pl. 3, figs. 1-2), Badenian. - Reviewed by Radwanska (1992) as *Argyrosomus regius* (Asso, 1801); reviewed by Schwarzhans (1993) and found to be eroded but considered as synonym of *Argyro-*

somus corii (Schubert, 1902). - Current status: synonym of ***Argyrosomus corii* (Schubert, 1902)**.

irregularis Koken, 1884, *Sciaena*. Schubert (1902, pl. 10, fig. 7), Badenian. - Reviewed by Nolf (1981) and considered an unidentifiable eroded sciaenid otolith. - Current status: invalid reference.

irregularis Koken, 1884, *Sciaena*. Pana (1965, pl. 4, figs. 133-134), Dacian. - Reviewed herein. - New status: ***Trewasciaena dobrogiaca* (Pana, 1977)**.

irregularis Koken, 1884, *Sciaena* aff. Brzobohaty et al. (2007, pl. 7, fig. 4), Badenian. - Comment: Apparently an eroded specimen of the genus *Umbrina*. - Current status: invalid reference.

karagiensis Bratishko, Schwarzhans & Reichenbacher, 2015, *Genyonemus?* Bratishko et al. (2015, figs. 7.3-7.8), Konkian. - New status: valid as ***Leptosciaena karagiensis* (Bratishko, Schwarzhans & Reichenbacher, 2015)**.

kirchbergensis Koken 1891, *Sciaena*. Koken (1891, not figured), Weiler (1966, fig. 46), Martini (1981, pl. 3, figs. 13-16), Schwarzhans (1993, figs. 126-127), Reichenbacher (1993, pl. 11, fig. 172), Ottangian. - Reviewed by Schwarzhans (1993) and considered valid as *Umbrina?* *kirchbergensis*; reviewed by Reichenbacher (1993) and considered valid as *Sciaena kirchbergensis*. - Current status: valid as ***Sciaena?* *kirchbergensis* Koken, 1891**.

kittli Schubert, 1902, *Otolithus* (*Sciaenidarum*). Schubert (1902, text-fig. 4), Nolf & Brzobohaty, (2009, pl. 6, fig. 1; as *Sciaenidae* indet.), Schultz (2013, pl. 89, fig. 2; as *Sciaenidae* indet.), Badenian. - Reviewed by Nolf (1981) and Nolf & Brzobohaty (2009) and considered an unidentifiable eroded sciaenid otolith. A very similar otolith, however, is figured by Brzobohaty et al. (2007) as *Umbrina* aff. *ronchus* Valenciennes, 1843, which because of its very large ostium and small cauda may represent a species of the genus *Sciaena*. - Current status: unresolved, doubtful species.

kokeni Schubert, 1902, *Otolithus* (*Sciaenidarum*). Schubert (1902, pl. 10, fig. 18), Nolf (1981, pl. 3, figs. 8-9), Schwarzhans (1993, figs. 171-175, non figs. 176-177), Schultz (2013, pl. 91, figs. 1-5), Pannonian E and Portaferrian. - Reviewed by Nolf (1981) and Schwarzhans (1993) and considered as valid. Schwarzhans (1993) placed the species in the then newly established fossil otolith-based genus *Trewasciaena*. - Current status: valid as ***Trewasciaena kokeni* (Schubert, 1902)**.

kokeni (Schubert, 1902), *Trewasciaena* aff.

Schwarzhans (1993, figs. 176-177, non figs. 171-174), stratigraphy unresolved, probably Kimmerian or Akchagylian. - Reviewed herein. - New status: ***Trewasciaena dobrogiaca* (Pana, 1977)**.

kokeni (Schubert, 1902), *Trewasciaena*. Jovanić et al. (2010, pl. 2, figs. 1.2), Portaferrian. - Reviewed based on photograph in literature. - New status: ***Trewasciaena dobrogiaca* (Pana, 1977)**.

levis Schubert, 1902, *Sciaena?* Schubert (1902, pl. 10, fig. 9), Pannonian E. - Reviewed by Nolf (1981) and rejected based on inadequate preservation; reviewed by Schwarzhans (1993) and considered as a synonym of *Trewasciaena kokeni* (Schubert, 1902). - Current status: synonym of ***Trewasciaena kokeni* (Schubert, 1902)**.

loczyi Lörenthey, 1906, *Otolithus* (*Sciaenidarum*). Lörenthey (1906, pl. 2, fig. 8; pl. 3, figs. 23, 24 as *Ot.* (*Sciaenidarum*) aff. *loczyi*), Transdanubian [8.3-8.1 Ma according to Sztano et al. (2013)]. - Comment: A 6 mm long specimen that is consistent to *Trewasciaena kokeni* (Schubert, 1902) in all the pertinent characters; the specimens referred and figured as *Ot.* (*Sciaenidarum*) aff. *loczyi* exhibit the same morphological features. - New status: synonym of ***Trewasciaena kokeni* (Schubert, 1902)**.

moguntina (Koken, 1891), *Morone*. Pana (1965, pl. 4, figs. 129-130, 135-137), Maeotian. - Reviewed herein. - New status: ***Pontosciaena 'sigmoilinoidea'* (Pobedina, 1956)**.

moguntina Weiler, 1942, *Sciaena*. Pana (1965, pl. 3, figs. 99-100, ?111-112), Dacian. - Reviewed herein. - New status: ***Umbrina getica* (Pana, 1995)**.

moguntiniformis Pana, 1977, *Sciaena*. Pana (1977, pl. 2, figs. 1-12), Pana, 1995 (pl. 4, figs. 1-4), Portaferrian and Dacian. - Reviewed herein. - New status: valid as ***Chaoia moguntiniformis* (Pana, 1977)**.

nolfi Reichenbacher, 1998, *Atractoscion?* Reichenbacher (1998, pl. 3, figs. 1, 3), Schultz (2013, pl. 89, figs. 4, 6), Karpatian. - Comment: A probable specimen of *Landinisciaena elongatissima*. This species also occurs in the Hemmoorian (Ottangian to early Badenian) of the North Sea Basin and a complete ontogenetic series has been figured by Schwarzhans (2010). - New status: synonym of ***Landinisciaena elongatissima* (Schwarzhans, 1993)**.

ottangensis Martini, 1983, *Atractoscion*. Martini (1983, pl. 1, figs. 9-16), Ottangian. - Reviewed by Schwarzhans (1993) and regarded as synonym of *Argyrosomus similis*. - Current status: synonym of

***Argyrosomus similis* (Weiler, 1966).**

ovata (Koken, 1891), *Corvina*. Pana (1965, pl. 4, figs. 131-132), Pana (1995, pl. 4, figs. 9-11), Dacian. - Reviewed herein. - New status: ***Trewasciaena dobrogiaica* (Pana, 1977).**

pannonicus Lörenthey, 1906, *Otolithus* (*Sciaenidarum*). Lörenthey, (1906, pl. 2, fig. 7), Transdanubian [8.3-8.1 Ma according to Sztano et al. (2013)]. - Comment: A strongly eroded juvenile specimens belonging to an indeterminate taxon of the family Sciaenidae. - Current status: species rejected.

pecchioli Lawley, 1876, *Sciaena*. Weiler (1950, pl. 3, fig. 13), and Smigielska (1979, pl. 7, fig. 2), Badenian. - Reviewed by Radwanska (1992) and Schwarzhans (2010) and regarded as synonym of *Umbrina polonica* (Radwanska, 1984). - Current status: ***Umbrina polonica* (Radwanska, 1984).**

plena Schubert, 1902, *Umbrina?* Schubert (1902, pl. 10, fig. 6), Pannonian E. - Reviewed by Nolf (1981) and regarded as synonym of the extant *Umbrina cirrhosa* (Linnaeus, 1758); reviewed by Schwarzhans (1993) and referred to *Umbrina cirrhosoides* (Schubert, 1902). - Current status: synonym of ***Umbrina cirrhosoides* (Schubert, 1902).**

polonica Radwanska 1984, *Argyrosomus*. Radwanska (1984, pl. 4, figs. 1-3), Radwanska (1992, pl. 28, figs. 1-2; as *Sciaena polonica*), Badenian. - Current status: valid as ***Umbrina polonica* (Radwanska 1984).**

regius (Asso, 1801), *Argyrosomus*. Radwanska (1992, pl. 27, figs. 1-2), Badenian. - An eroded specimen reviewed by Schwarzhans (1993) and regarded as synonym of *Argyrosomus corii* (Schubert, 1902). - Current status: ***Argyrosomus corii* (Schubert, 1902).**

regius (Asso, 1801), *Argyrosomus*. Brzobohaty et al. (2007, pl. 7, figs. 1-2), Badenian. - Comment and new status: likely belonging to ***Argyrosomus similis* (Weiler, 1966).**

rhombus Valenciennes, 1843, *Umbrina* aff. Brzobohaty et al. (2007, pl. 7, fig. 5), Badenian. - Comment: resembling *Otolithus* (*Sciaenidarum*) *kittli* Schubert, 1902 and probably a representative of the genus *Sciaena*. - New status: unresolved, invalid reference.

rumana Pana, 1977, *Corvina*. Pana (1977, pl. 4, figs. 5-15, 5, figs. 13-14), Pana (1995, pl. 5, figs. 4-6), Dacian. - Reviewed herein. - New status: synonym of ***Trewasciaena dobrogiaica* (Pana, 1977).**

rybnicensis Radwanska, 1992, *Sciaena*. Rad-

wanska (1992, pl. 29, figs. 1-5), and Brzobohaty et al. (2007, pl. 7, fig. 3), Badenian. - Current status: valid as ***Sciaena rybnicensis* Radwanska, 1992.**

schuberti Lörenthey, 1906, *Otolithus* (*Sciaenidarum*). Lörenthey (1906, pl. 2, fig. 6), Transdanubian [8.3-8.1 Ma according to Sztano et al. (2013)]. - Comment: A 5 mm long specimen resembling *Umbrina subcirrhosa* in all the pertinent characters. - New status: synonym of ***Umbrina subcirrhosa* (Schubert, 1902).**

sigmoilinoidea Pobedina, 1956, *Otolithus* (*Percidarum*). Pobedina (1956, pl. 28, fig. 3), refigured by Djafarova (2006; pl. 12, fig. 1; as *Otolithus* (*Mugilidarum*) *sigmoilinoidea*), Maeotian. - Reviewed herein on the basis of material from the Maeotian of Romania referred by Pana (1965) to as *Morone moguntina*. - New status: valid as ***Pontosciaena 'sigmoilinoidea'* (Pobedina, 1956).**

similis Weiler, 1966, *Sciaena*. Weiler (1966, figs. 43-44), Martini, (1983, pl. 1, figs. 1-8; as *Atracoscion similis*), Schwarzhans (1993, figs. 262-264), Ottnangian. - Reviewed by Schwarzhans (1993) and referred to as *Argyrosomus similis*. - Current status: valid as ***Argyrosomus similis* (Weiler, 1966).**

simplex Schubert, 1902, *Otolithus* (*Sciaenidarum*) *corii*. Schubert (1902, text-fig. 1), Badenian. - Reviewed by Nolf (1981) and rejected based on inadequate preservation. - Current status: species rejected.

speciosus Koken, 1884, *Sciaena* aff. Schubert (1902, pl. 10, fig. 10), Badenian. - Reviewed by Nolf (1981) and regarded as synonym of *Trewasciaena kokeni* (Schubert, 1902). - Current status: invalid reference.

styriacus Weinfurter, 1952, *Otolithus* (*Sciaenidarum*). Weinfurter (1952, pl. 1, fig. 6), Nolf & Brzobohaty (2009, pl. 6, fig. 2; as Sciaenidae indet.), Schultz (2013, pl. 89, fig. 1; as Sciaenidae indet.), Badenian. - Reviewed by Schwarzhans (1993) and referred to as a valid species, *Pogonias styriacus*; reviewed by Nolf & Brzobohaty (2009) and considered a non-diagnostic and strongly eroded sciaenid otolith. - Current status: We maintain the provisional attribution as ***Pogonias styriacus* (Weinfurter, 1952)**, suggesting that further scrutiny is necessary to conclusively verify its affinities to *Otolithus* (*Sciaenidarum*) *fuchsi* Schubert, 1902.

subcirrhosa Schubert, 1902, *Umbrina*. Schubert (1902, pl. 10, fig. 3), Schwarzhans (1993, figs. 103-107), Schultz (2013, pl. 90, fig. 6), Pannoni-

an E. - Reviewed by Nolf (1981) and regarded as synonym of the extant *Umbrina cirrosa* (Linnaeus, 1758); reviewed by Schwarzhans (1993) and referred to as *Umbrina subcirrhosa* based on its elongate outline and absence of an umbo on the outer face. - Current status: valid as ***Umbrina subcirrhosa* Schubert, 1902.**

subgemma Schubert, 1902, *Otolithus* (*Sciaenidarum*). Schubert (1902, pl. 10, fig. 15), Badenian. - Reviewed by Nolf (1981) and rejected because of inadequate preservation. - Current status: species rejected.

subsimilis Schubert, 1902, *Otolithus* (*Sciaenidarum*). Schubert (1902, pl. 10, fig. 12), Schultz (2013, pl. 90, fig. 1; as *Umbrina* sp.), Badenian. - Juvenile specimen reviewed by Nolf (1981) and Schwarzhans (1993) and rejected based on inadequate preservation. - Current status: species rejected.

suzini Bratishko, Schwarzhans & Reichenbacher, 2015, *Trewasciaena*. Bratishko et al. (2015, figs. 7.9-7.14), Konkian. - Current status: valid as ***Trewasciaena suzini* Bratishko, Schwarzhans & Reichenbacher, 2015.**

telleri Schubert, 1902, *Sciaena?* Schubert (1902, pl. 10, fig. 16), Pannonian E. - Reviewed by Nolf (1981) and Schwarzhans (1993) and regarded as synonym of *Trewasciaena kokeni* (Schubert, 1902). - Current status: synonym of ***Trewasciaena kokeni* (Schubert, 1902).**

telleri Schubert, 1902, *Sciaena*. Djafarova (2006, pl. 15, fig. 1), Apsheronian. - Comment: A well-preserved otolith extremely similar to the extant *Argyrosomus regius*. - New status: probably belonging to ***Argyrosomus regius* (Asso, 1801).**

Description of otolith-based species

Genus *Argyrosomus* de la Pylaie, 1835

Remarks. *Argyrosomus* otoliths are characterized by a vertical and partially straight posterior rim that runs very close to the posterior, downturned part of the cauda, shallow and nearly straight dorsal and ventral rims, massive postventral umbo on the outer face, a sulcus with large and wide ostium occupying most of the anterior region of the inner face, and a cauda in which the downward bent posterior stretch is about as long as the horizontal anterior part. There are two otolith-based species

recorded from the middle Miocene of the Central Paratethys, *Argyrosomus similis* (Weiler, 1966) and *A. corii* (Schubert, 1902). The distribution of *Argyrosomus similis* ranges from the Ottnangian to the early Badenian, while *A. corii* is only known from the Badenian, at least up to middle Badenian times. *Argyrosomus corii* can be distinguished from *A. similis* primarily because of the more compressed shape clearly expressed by the lower ratio otolith length : otolith height (1.5-1.7 vs 1.9-2.15). A third otolith-based *Argyrosomus* species has been documented by Djafarova (2006) (as *Sciaena telleri* Schubert, 1902) from the Apsheronian of Azerbaijan; this is reinterpreted herein as representing a record of the extant *A. regius* (Asso, 1801).

Genus *Chaoia* gen. nov.

Type Species: *Sciaena moguntiniformis* Pana, 1977.

Etymology: Named in honor of Ning Labbish Chao in recognition of his outstanding contributions to the knowledge of extant Sciaenidae. Dr. Chao was one of the first researchers that recognized and emphasized the use of otolith morphology in the systematic studies of sciaenids.

Diagnosis: A large growing otolith-based genus of the family Sciaenidae characterized by the following combination of characters: otoliths up to 14 mm in length. Otolith length to height ratio: 1.6-2.0, increasing with size. Posterior rim rounded to slightly tapered, dorsal and ventral rims shallow. Weak postcentral umbo on outer face. Inner face distinctly bent. Ostium wide, occupying nearly full width of the anterior part of inner face, with moderate postostial lobe. Ostium length to height: 1.1-1.2. Cauda long and narrow, with the anterior, horizontal part about as long as the downturned posterior part. Space between the rear margin of the ostium and the downturned portion of the cauda moderately wide, measuring about 24-28% of sulcus length.

Discussion. The otoliths of this genus show a typical sciaenid sulcus morphology similar to that characteristic of many extant genera. However, the slender physiognomy, wide ostium, wide ostial - caudal interspace and weak postcentral umbo on the outer face, concur to distinguish *Chaoia* from extant genera. Otoliths of *Sciaena* and *Umbrina* exhibit a similar sulcus configuration, but are always more compressed (otolith length to height 1.2-1.6 vs 1.6-2.0), and except for *U. cirrosa* (and a few Paleogene species erroneously referred to *Umbrina*; see below), show a narrower ostial - caudal interspace. The morphologically similar fossil '*Sciaena*' *kirchbergensis* of problematic generic allocation, has a very narrow ostial - caudal interspace (13-15% of sulcus length vs 24-28%) and a massive umbo on the

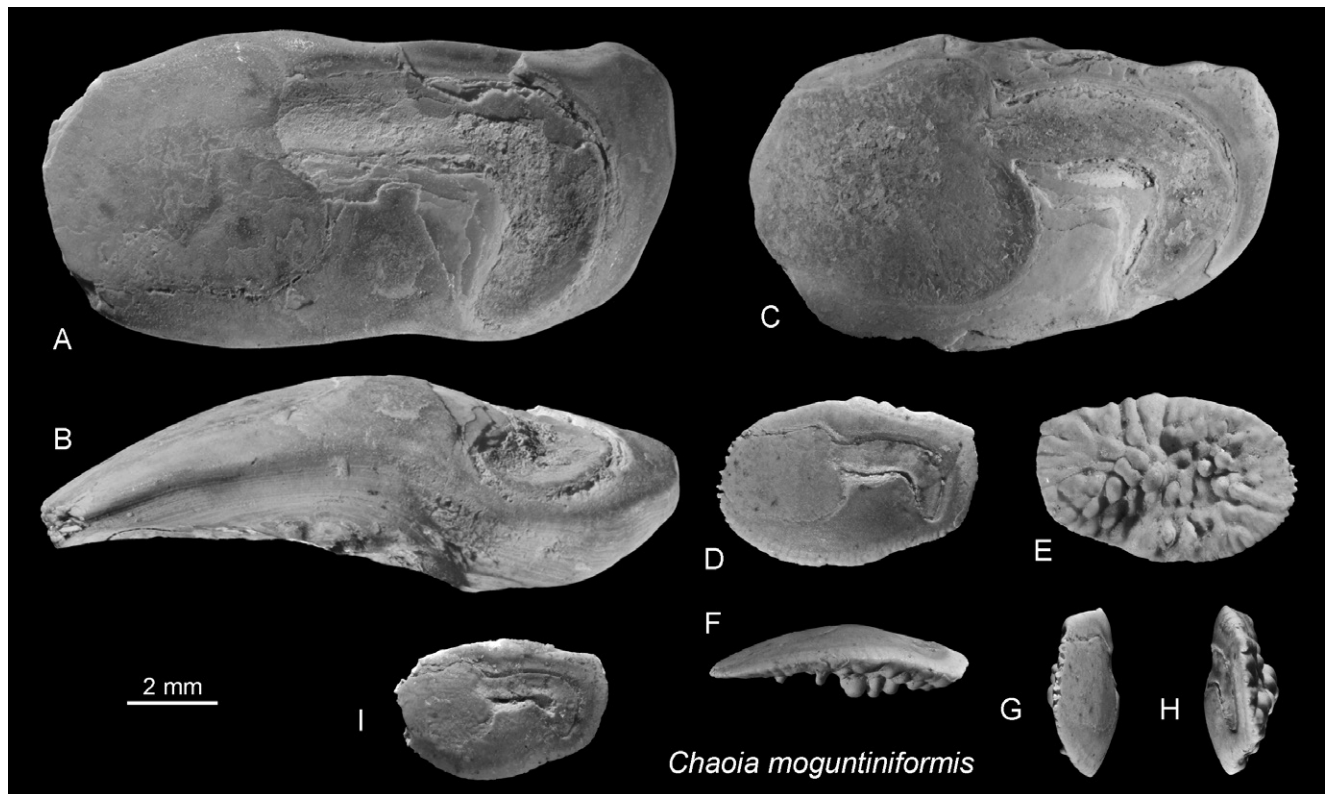


Fig. 5 - *Chaioia moguntiniformis* (Pana, 1977). A-B) Okrugljak, Croatia, Portaferrian, CNHM 109.3 (A inner face, B ventral view); C) Vösendorf, Austria, Pannonian E, SMNS 80556-2; D-H) (mirror imaged) holotype, Oltina 2C, Romania, Parscovian, Dacian, LPB II P/o 0050 (D inner face, E outer face, F ventral view, G anterior view, H posterior view); I) paratype, Oltina 2C, Romania, Parscovian, Dacian, LPB II P/o 0051.

outer face compared to *Chaioia*. A wide ostium and a moderate ostial - caudal interspace is found in *Argyrosomus* and small-sized otoliths of these two genera can be very similar. Large *Argyrosomus* otoliths, however, always show a distinctive high and vertical posterior rim and an anteriorly obliquely oriented and narrowing ostium. They also show a massive umbo on the outer face. *Atractoscion* and the fossil *Landinisciaena* probably show the highest degree of similarity in shape and general sulcus morphology. *Chaioia* differs from them in the short and wide ostium (ostium length to height: 1.1-1.2 vs 1.7-2.2) and the absence of a massive umbo on the outer face. The otoliths of the fossil *Trewasciaena* are usually less elongate (1.2-1.7 vs 1.6-2.0), and thinner without umbo on the outer face and with a narrower ostium and a wider ostial - caudal interspace (30-40% vs 24-28%). The relationships of *Chaioia* are unresolved, although an affinity to the *Umbrina* or *Trewasciaena* group cannot be excluded. We assume that *Chaioia* represents an endemic Paratethyan sciaenid genus.

Composition. *Chaioia moguntiniformis* (Pana,

1977) from the Dacian of the Eastern Paratethys and the Pannonian and Portaferrian of the Central Paratethys.

Chaioia moguntiniformis (Pana, 1977)

Figs. 5 A-I

1977 *Sciaena moguntiniformis* Pana, pl. 2, figs. 1-12

1995 *Sciaena moguntiniformis* Pana, 1977 - Pana, pl. 4, figs. 1-4

Studied Material: Eight specimens from the collection assembled and studied by Pana (1977), including the type series of *Sciaena moguntiniformis*, all from the upper Dacian, Parscovian of Romania. An additional, large specimen from Gorjanović-Kramberger's collection, CNHM 109.3, from the Portaferrian of Okrugljak near Zagreb, Croatia (Okrugljak Formation in Vrsaljko et al. 2011), and one specimen from Pannonian of Vösendorf, Austria, SMNS 80556-2.

Diagnosis: Otoliths relatively slender with an otolith length to height ratio of 1.55 in specimens up to 6 mm and up to 2.0 in specimens up to 14 mm of length. Dorsal and ventral rims equally shallow. Pronounced angle at junction of dorsal and posterior rims. Ostium wide, distinctly longer than wide (ostium length to height ratio: 1.1-1.3). Moderately deep postostial lobe. Ostial - caudal interspace equals 28-30% of sulcus length.

Distribution: *Chaioia moguntiniformis* is known from the Dacian of Romania (western part of the Eastern Paratethys), the Pannonian E and the Portaferrian of the Central Paratethys.

Description. Moderately large otoliths reaching sizes of at least 14 mm (specimen from Okrugljak, Fig. 5 A-B), although the largest specimen recorded by Pana (1977) reaches 5.6 mm (Fig. 5 D-H). The dorsal and ventral rims are shallow, gently curved without prominent angles except at junction between dorsal and posterior rims. The maximum depth of the otolith occurs at about its midlength or slightly anterior to it. The anterior rim is broadly rounded; the posterior part of the otolith is more slender compared to the anterior part, and is characterized by a blunt posterior rim. All the rims are smooth or finely crenulated in specimens smaller than 6 mm.

The inner face is distinctly bent. The sulcus has a wide and shallow ostium, longer than wide. The rear margin of the ostium shows a strong dorsal flexure and a very deep ventral flexure, with a moderately developed postostial lobe. The cauda is narrow, slightly deepened, about as long or slightly shorter than the ostium; it is steeply curved posteriorly with an anterior horizontal stretch slightly longer than the downturned posterior part. The ventral field is smooth, with ventral line sometimes visible as the termination edge of the radial ornamentation along the otolith margin. The dorsal field has a narrow and indistinct depression. The outer face is more or less flat, with intense ornamentation in small specimens of less than 6 mm in length, becoming smooth in the specimen of 14 mm length; the postcentral umbo is extremely reduced or absent.

Remarks. All the records of *Chaoia moguntiniformis* from Romania, including the holotype, are smaller than 6 mm. A singular find from the Portaferrian of Croatia is much larger, reaching a length of 14 mm and most likely represents a truly adult specimen. Another specimen from the Pannonian E from Vösendorf in the SMNS collection reaches a length of about 12 mm. The largest specimen is more elongate (otolith length to height: 1.95 vs 1.55-1.7) and possesses flat dorsal and ventral rims. Both the large available specimens share a much reduced ornamentation along the otolith rims and the outer surface. These differences may be related to a combination of intraspecific variability and ontogenetic changes, which are consistent with the patterns observed in extant sciaenid otoliths. However, additional comparative information would be desirable in order to conclusively

clarify the taxonomic status of this taxon. In any case, the smaller Romanian specimens are regarded as diagnostic at the species level.

Genus *Leptosciaena* gen. nov

Type Species: *Genyonemus? karagiensis* Bratishko, Schwarzahns & Reichenbacher, 2015.

Etymology: From the Greek word leptos = slender, small, and the generic name *Sciaena*, in reference to the slender and relatively small size of the otoliths of this genus.

Diagnosis: A fossil otolith-based genus of the family Sciaenidae with the following combination of characters: small otoliths not exceeding 6 mm in length. Otolith length to height ratio: 1.6-2.4. Posterior rim rounded, dorsal and ventral rims shallow, nearly straight. No distinct postcentral umbo on outer face. Inner face mildly bent. Ostium relatively narrow and short, without postostial lobe. Cauda long and narrow; the anterior, horizontal part of cauda about twice as long as short, with downturned posterior part. Space between the rear margin of the ostium and the downturned portion of the cauda very wide, 30-45% of sulcus length.

Discussion. The otoliths of this genus can be recognized from those of other Paratethyan sciaenids by having a widened, shallow ostium and a steeply downturned caudal tip. However, when compared to the majority of sciaenid otoliths, the ostium appears relatively small and the horizontal stretch of the cauda is comparatively long, resembling the condition observed in the extant genus *Genyonemus*, to which the type species was tentatively placed originally, as well as that characteristic of *Menticirrhus*, *Leiostomus*, but also the fossil otolith-based genus *Trewasciaena*. *Leptosciaena* shows a trend in reduction of the size of the ostium with *L. caputoi* n. sp. documenting the most extreme reduction within the lineage (see below).

Composition. *Leptosciaena karagiensis* (Bratishko, Schwarzahns & Reichenbacher, 2015) from the Konkian of the Eastern Paratethys, *L. 'azerbaidjanica'* (Djafarova, 2006) from the Maotian of the Eastern Paratethys (originally described as *Otolithus (Mugilidarum) azerbaijanicus*; regarded as provisionally valid, see discussion above), and *L. caputoi* n. sp. from the uppermost Messinian (Lago-mare phase) of Italy.

Leptosciaena 'azerbaidjanica' (Djafarova, 2006)

Fig. 6 F

2006 *Otolithus (Mugilidarum) azerbaijanicus* Djafarova, pl. 11, fig. 4 (non pl. 11 figs. 1-3, pl. 12, fig. 2)

Remarks. No material was available for review. The provisional acceptance of the species is entirely based on a single specimen figured by Djafarova (2006) (Fig. 6 F), which clearly represents an otherwise unknown sciaenid belonging to the genus *Leptosciaena*.

Distribution. Maeotian of Azerbaijan.

***Leptosciaena caputoi* sp. nov.**

Figs 6 G-M

2006 Sciaenidarum sp. nov. - Carnevale, Caputo & Landini, figs. 3 C-I.

2017 Sciaenidarum sp. nov. - Colombero et al., 2017, figs. 5.15-5.16.

2018 Sciaenidarum sp. nov. - Carnevale et al., 2018, fig. 3 P.

Holotype: Fig. 6 H-I, MGPT-PU 130338, Capanne di Bronzo, Montecalvo in Foglia syncline, Marchean Apennines, Italy; Colombacci Formation, upper Messinian, between 5.5 and 5.3 Ma, Late Miocene.

Paratypes: 15 specimens, MGPT-PU 130339, from the type locality.

Diagnosis: Otolith length to height ratio: 1.6-1.7; otolith height to thickness: 2.0-2.3. Ostium relatively small, oval in shape, without postostial lobe; ostium length to cauda length: 0.85-0.9. Caudal tip bent downward at about 90°, less than half the length of anterior horizontal section. Ostial - caudal interspace: 40-45% of sulcus length.

Referred Specimens: 84 specimens from the type locality. Moreover, 28 specimens have been collected from Moncucco Torinese, Piedmont, Italy; Cassano Spinola Formation, upper Messinian, Late Miocene.

Etymology: Named after the geologist Dorian Caputo, friend and former student of one of us (GC), in recognition of his multiple contributions to the interpretation of the Lago Mare event in Italy.

Distribution: Latest Messinian, Lago Mare phase, northern and central Italy.

Description. Relatively small, compact and robust otoliths measuring up to about 5.2 mm in length (holotype 4.4 mm). Dorsal rim irregularly undulating, mostly flat with prominent, rounded postdorsal angle close to the junction with the posterior rim. The ventral rim is moderately deep, with its deepest point distinctly anterior to its midlength. The anterior rim is rounded, its tip slightly dorsally shifted, resembling a rostrum. Excisura-like indentation sometimes present at about midlength of the dorsal margin of the ostium. The posterior rim has a broadly rounded tip at about mid-section; the dorsal section is straight and obliquely inclined towards the postdorsal angle.

The inner face is almost flat. The sulcus is distinctly suprmedian. The ostium is oval in

shape, somewhat narrowing anteriorly, without postostial lobe; it is very slightly depressed, in some cases characterized by a precaudal depression. The cauda is long, narrow, deepened, with its rear part bent downward forming an angle of 70° to 90° with the horizontal part. The horizontal section of the cauda is nearly three times as long as the downturned section; the ventral margin of the horizontal section is often slightly convex. A feeble ventral furrow is occasionally present very close to the ventral rim of the otolith. The dorsal field has a broad and ventrally well-marked depression above the anterior part of the cauda. The outer face is distinctly convex, smooth and without umbo.

Remarks. *Leptosciaena caputoi* exhibits a number of characters that are not commonly found in sciaenid otoliths, such as an oval ostium without postostial lobe and a short downturned part of the cauda. The ostial opening in a broadly rounded rostrum-like feature is more typical for sciaenids, but, also in this case, the development of an excisura-like indentation along the mid-dorsal section of the ostium is unusual. Carnevale et al. (2006) reported these characters in the first description of these otoliths, and compared them with those of certain extant sciaenids with similarly small ostium and short downturned cauda, like *Seriplus* and certain *Cynoscion* species, concluding that the placement within the Sciaenidae is justified despite the unusual combination of plesiomorphic characters.

Our understanding of the Paratethyan sciaenid otoliths have increased since the publication of that paper and we now interpret the otoliths in question as possible derived members of the endemic Paratethyan lineage of *Leptosciaena* comprising small sciaenid fishes characterized by a gradual reduction of certain “sciaenid” characters. When comparing the earliest member (*Leptosciaena karagiensis*) with *L. caputoi* it becomes evident how the ostium has been reduced in size and also the downturned portion of the cauda. In addition, *L. caputoi* differs from its congenics in having a more compressed shape (otolith length to height: 1.6-1.7 vs 2.0-2.4) and a considerable thickness.

Leptosciaena caputoi is exclusively known from the Lago Mare phase of the Messinian salinity crisis, in Italy. Considering its position as the possible terminal member of an endemic Paratethyan genus (*Leptosciaena*), it is reasonable to hypothesize

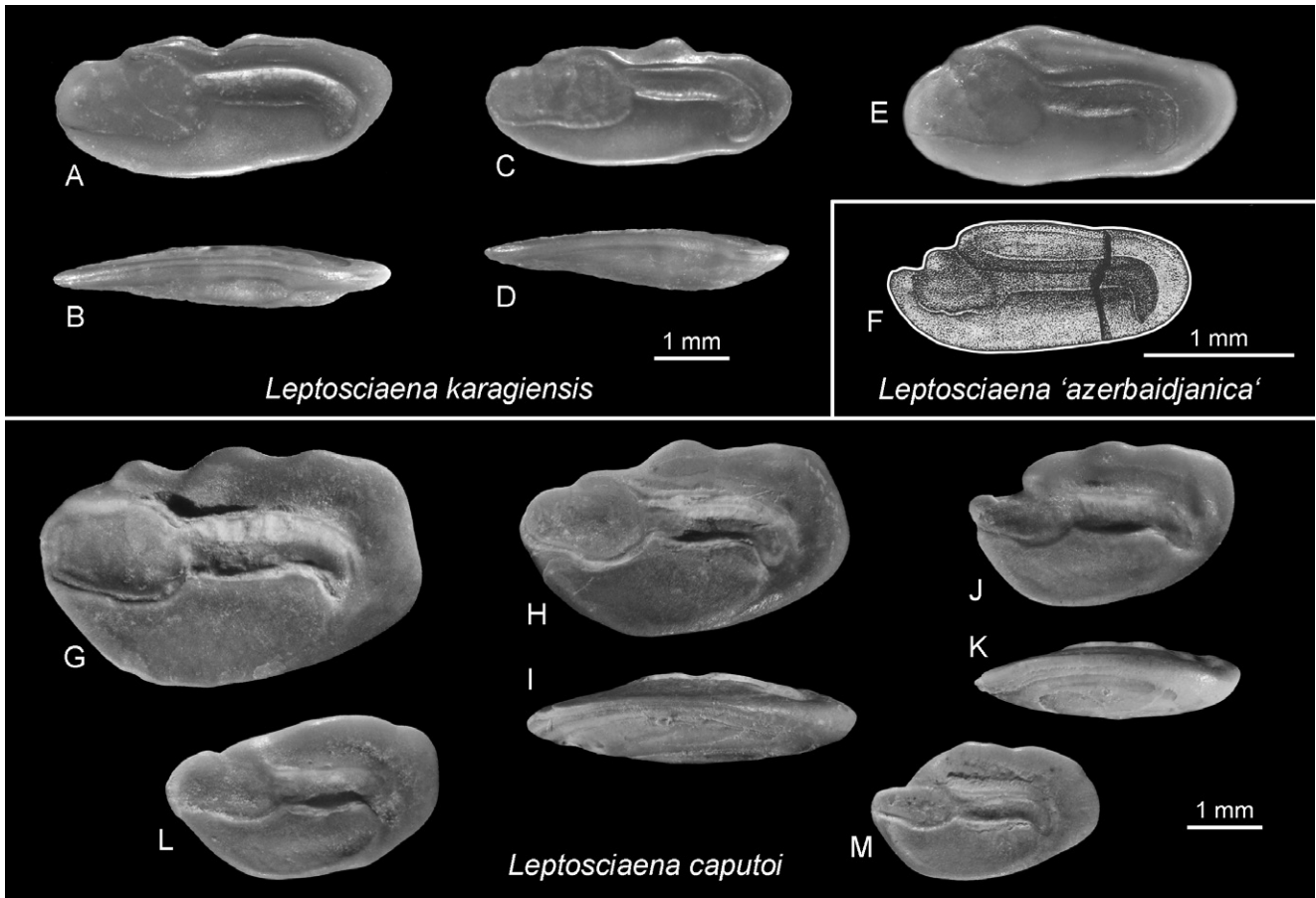


Fig 6 - *Leptosciaena* gen. nov. A-E - *Leptosciaena karagiensis* (Bratishko, Schwarzahns & Reichenbacher, 2015). Karagaily, Kazakhstan, Konkian; C-D) holotype, NMNH 2532/058 (D ventral view); A-B, E) paratypes, NMNH 2532/056 and 059 (B ventral view). F - *Leptosciaena 'azerbaidjanica'* (Djafarova, 2006). Azerbaijan, Maeotian, refigured from Djafarova (2006). G-M - *Leptosciaena caputoi* sp. nov., Capanne di Bronzo, Italy, latest Messinian; H-I) holotype, MGPT-PU 130338 (I ventral view); G, J-M) paratypes, MGPT-PU 130339 (K ventral view) (G, J, K mirror imaged).

that this species must have had the opportunity to migrate into the Mediterranean during the late Miocene. Unfortunately, our knowledge of the Maeotian and Pontian otoliths as the most relevant time intervals for the search of a direct link with the Paratethyan realm is very poor. We do not know yet, whether *L. caputoi* was also present in the Eastern Paratethys during the upper Messinian or represented an endemic expatriate in the Mediterranean from a former Paratethyan stock as a result of some earlier immigration.

***Leptosciaena karagiensis* (Bratishko, Schwarzahns & Reichenbacher, 2015)**

Figs 6 A-E

2015 *Genyonemus?* *karagiensis* Bratishko et al., fig. 7.3-7.7.

Material: No new material studied. Figured specimens are reproduced from Bratishko et al. (2015).

Distribution: Konkian of Mangyshlak (Kazakhstan).

Genus *Pontosciaena* gen. nov.

Type Species: *Serranus acuterostratus* Rückert-Ülkümen, 1996.

Etymology: Named after Pontos (Greek), in reference to the Ponto-Caspian Basin, and the generic name *Sciaena*.

Diagnosis: A fossil otolith-based genus of the family Sciaenidae with the following combination of characters: Comparatively small sciaenid otoliths reaching up to 7 mm in length. Otolith length to height ratio 1.8 in very small specimens (<2 mm length) up to 3.3 in the largest known specimen (7.1 mm length), thereby evidencing a considerable ontogenetic allometry. Posterior tip expanded, often pointed, dorsal and ventral rims shallow, curved. Otolith very thin, with nearly flat inner face and no postcentral umbo on outer face. Ostium long, relatively narrow, without postostial lobe. Cauda long and narrow, with very long anterior, horizontal part and very short, downturned posterior part. Space between rear margin of ostium and downturned portion of cauda very wide, measuring 30-40% of sulcus length.

Composition: *Pontosciaena acuterostrata* (Rückert-Ülkümen, 1996) from the Sarmatian s.l. of the Eastern Paratethys, and tentatively *P. sigmoilinoidea* (Pobedina, 1956) from the Maeotian of the Eastern Paratethys (see discussion below).

Discussion. The otoliths of *Pontosciaena*

na are remarkable for their slender overall shape and thin aspect as well as for the narrow ostium without postostial lobe, and the short downturned part of the cauda. Because of this combination of features, it was not recognized as a sciaenid by Rückert-Ülkümen (1996). Similar otoliths were described by Müller (1999) from the lower Miocene deposits of the Atlantic Coastal Plain and referred to the genus *Genyonemus* – *G. calvertensis* Müller, 1999 and *G. ? pertenuis* Müller, 1999. The latter species, in particular, resembles *Pontosciaena acuterostrata* in being very slender and thin. However, additional figures published in Nolf (2013) revealed differences with *Genyonemus pertenuis* showing a more spatulate ostium with a mild postostial lobe, and a more strongly curved cauda. We consider *Pontosciaena* as an endemic Paratethyan genus, although it appears likely that it derived from forms similar to *Genyonemus* that possibly immigrated from the NW Atlantic.

Pontosciaena acuterostrata
(Rückert-Ülkümen, 1996)

Fig. 7 A-E

- 1996 *Serranus acuterostratus* Rückert-Ülkümen, pl. 2, figs. 4-6.
 2009 *Serranus acuterostratus* Rückert-Ülkümen, 1996 - Üner & Öngen, pl. 3, fig. 4.
 2013 “*Percoidens*” *acuterostratus* (Rückert-Ülkümen, 1996) - Nolf, pl. 193.
 2017 ? *Genyonemus?* sp. Bratishko, Kovalchuk & Schwarzshans, figs. 3.5-8.

Studied Material: Ten specimens from the Bessarabian of Jurkino, Crimea (courtesy of Andrei Bratishko).

Distribution: *Pontosciaena acuterostrata* is known from the Sarmatian s.l. (Bessarabian of the Crimea) of the Eastern Paratethys.

Description (based on otoliths 5-7 mm in length). The otoliths are thin and elongate, the largest known specimen being 7.1 mm long. Otolith length to height ratio: 2.7-3.3; otolith height to thickness ratio: 3.0-3.6. The dorsal and ventral rims are shallow, the ventral rim regularly curved, while the dorsal rim has a broadly rounded medio-dorsal angle. The anterior rim is broadly rounded, sometimes with feebly recognizable excisura, more commonly without incisions. The posterior rim is variably expanded, in some cases being very long and pointed. The otolith rims are smooth or very finely crenulated in smaller specimens.

The inner face is almost flat to slightly bent

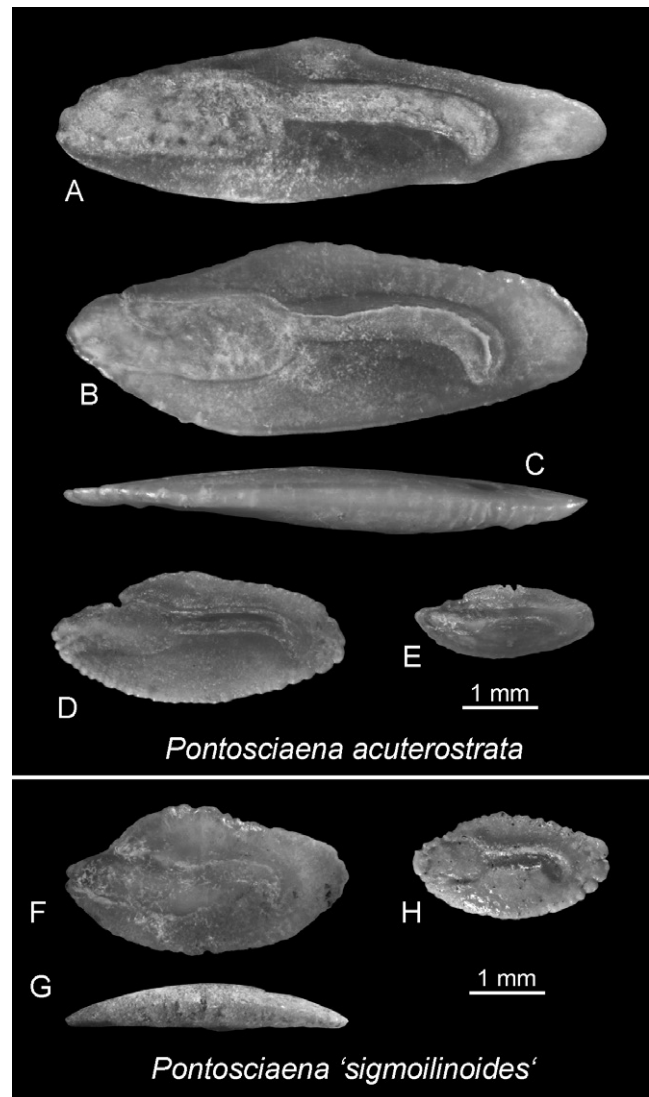


Fig. 7 - *Pontosciaena* gen. nov. A-E - *Pontosciaena acuterostrata* (Rückert-Ülkümen, 1996). Jurkino, Crimea, Bessarabian (figures courtesy A. Bratishko; mirror imaged) (C ventral view). F-H - *Pontosciaena 'sigmoilinooides'* (Pobedina, 1956). F-G) Rusavet, Romania, Macotian, LPB II P/o 0031 (G ventral view); H) (mirror imaged) Plopeasa, Romania, Macotian, LPB II P/o 0030.

horizontally and rather smooth. The sulcus has a shallow, moderately wide, oval ostium; the ostium is anteriorly rounded, and posteriorly lacks a postostial lobe. The ostial widening is stronger ventrally. The dorsal ostium margin is often slightly depressed anteriorly. The cauda is not as long as the ostium, narrow, somewhat deepened, with long horizontal stretch and very short downturned posterior part. Ostium length to height ratio: 2.1-2.5, ostium length to cauda length ratio: 1.05-1.15, distance of ostial/caudal interspace in percentage of the total length of the sulcus: 35-40%. The ventral field is smooth without a ventral furrow;

the dorsal field has a narrow, short and indistinct dorsal depression. The outer face is smooth and nearly flat.

Ontogeny. *Pontosciaena acuterostrata* shows a pronounced allometric development. The specimens measuring between 1.8 and 4.3 mm in length have an otolith length to height ratio of 2.2 to 2.45, whereas those from 4.3 to 4.6 mm in length (including the type-series) show a ratio of 2.5 to 2.6, while those in the range of 5.0 to 7.1 mm in length show a ratio ranging between 2.7 and 3.3. The diagnostic maturity seems to be reached at a length of about 4.5 mm (the length of the holotype), indicating that *P. acuterostrata* likely was a small-sized species. Other ontogenetic changes such as the loss of a fine marginal crenulation, development of the pointed posterior tip and expression of the dorsal and ventral rims are all within the expected range of variation.

Pontosciaena 'sigmoilinoides' (Pobedina, 1956)

Fig. 7 F-H

1956 *Otolithus (Percidarum) sigmoilinoides* Pobedina, pl. 28, fig. 3.

1965 *Morone moguntina* (Koken, 1891) - Pana, pl. 4, figs. 129-130, 135-137.

2006 *Otolithus (Mugilidarum) sigmoilinoides* (Pobedina, 1956) - Djafarova, pl. 12, fig. 1 (refigured from Pobedina, 1956).

Studied Material: Two juvenile specimens from the collection of Pana (described in 1965 as *Morone moguntina*), one specimen from the Sarmatian/Maeotian interval exposed at valea Plopeaso, Romania (LPB II P/o 0030) and one specimen from the Maeotian 1 of valea Rusavet, Romania (LPB II P/o 0031).

Distribution: Sarmatian to Maeotian of Romania and Azerbaijan.

Discussion. The holotype described by Pobedina (1956) from the Maeotian of Azerbaijan was reported to be 4 mm long. The two specimens from the Pana's undescribed collection are characterized by a length of 2.6 and 3.8 mm. Therefore, all the available specimens must be regarded as not fully diagnostically mature compared to those of *Pontosciaena acuterostrata* described above. Anyway, they closely resemble *P. acuterostrata*, but differ from it in being less compressed and in having the ostium as long as the cauda or slightly shorter (vs slightly longer than the cauda). However, additional material significantly larger than 4 mm in length would be necessary to provide a reliable re-definition of *P. sigmoilinoides*, whose validity is regarded herein as provisional.

Genus *Trewasciaena* Schwarzahns, 1993

Diagnosis: Large otoliths reaching a length of more than 20 mm in certain species. Otolith length to height ratio: 1.3-1.8. Posterior rim rounded, sometimes with angular expansion at the joint between dorsal and posterior rims; dorsal and ventral rims shallow, gently curved. No distinct postcentral umbo on outer face. Inner face distinctly convex. Ostium moderately narrow but rather short (usually shorter than cauda), with distinct and small postostial lobe. Cauda long and narrow; the anterior, horizontal part of the cauda about as long or slightly longer than the downturned posterior part. Downturned part of the cauda broadly curved and often pointing forward at its tip. Space between rear margin of the ostium and downturned portion of the cauda moderately wide to wide, measuring between 30 and 40% of sulcus length (mostly >33%).

Composition: *Trewasciaena dobrogiaca*, *T. kokeni*, *T. suzini* and *T. moguntina*.

Remarks. A new diagnosis is necessary due to the changed composition of the genus because certain species formerly referred to *Trewasciaena* - *Sciaenops eastmani* Dante, 1953, *Sciaena? irregularis* (Koken, 1884) and *S.? bavarica* (Schwarzahns, 1993) - are currently placed elsewhere, and *Trewasciaena dobrogiaca* (Pana, 1977) is included and re-described below.

The wide interspace between the ostium and the downturned part of the cauda as well as the lack of a distinct postcentral umbo on the outer face are the most prominent features of the genus. This redefinition allows to exclude from *Trewasciaena* the two Oligocene species *Sciaena? irregularis* and *S.? bavarica*, which are now considered as sciaenids of uncertain generic allocation characterized by a combination of predominantly plesiomorphic characters. The justification for the generic allocation of *Sciaenops eastmani* is discussed in Schwarzahns (2010).

Therefore, *Trewasciaena* in its current definition is restricted to a stratigraphic range from early Miocene to Pleistocene in brackish to freshwater settings from the Mainz Basin in the Northwest to the Caspian Basin in the East. It contains a well-defined Paratethyan lineage comprising *T. suzini* from the Konkian of the Eastern Paratethys, *T. kokeni* from the Late Miocene of the Central Paratethys, and *T. dobrogiaca* from the early Pliocene to the middle Pleistocene of the Eastern Paratethys. A more slender morphotype with a lower postdorsal angle appears to be confined to *T. moguntina* from the early Miocene of Mainz Basin.

The distinction of *Trewasciaena* otoliths from those of *Umbrina* is primarily focused on the width of the ostial - caudal interspace, which ranges from

30 to 40% of the sulcus length in *Trewasciaena* versus between 17 and 30% of the sulcus length in otoliths of extant *Umbrina* species. Additional minor differences such as the anteriorly inclined dorsal margin of the ostium in many *Umbrina* species or the stronger curvature of the inner face of *Umbrina* otoliths are not always unequivocal for distinction. Otoliths with a similar wide ostial - caudal interspace and weakly bent inner face are those of the New World genus *Ctenosciaena* Fowler & Bean, 1924. Anyhow, the affinities of *Trewasciaena* and its possible relationships to *Umbrina* or *Ctenosciaena* remain obscure and will be probably resolved only when an otolith *in situ* associated to the articulated skeletal remains will be available for study and a comprehensive review of the various extant species of the genus *Umbrina* will be realized. It must also be pointed out that many of the so-called *Umbrina* otoliths from the Paleogene are also characterized by an ostial - caudal interspace of >30% of the sulcus length. These forms represent plesiomorphic sciaenid otolith morphologies of unknown generic affinity and should neither be recorded as *Trewasciaena* nor *Umbrina* spp. but rather as *Sciaena?* spp., following the suggestion of Janssen (2012), thereby providing indication that they may represent an undescribed fossil genus of the Sciaenidae.

Trewasciaena dobrogiaca (Pana, 1977)

Fig. 8 K-S

- 1891 ? Otoliti: Gorjanović-Kramberger, pl. 3, fig. 6.
 1965 *Umbrina* cf. *alsheimensis* Weiler, 1963 - Pana, pl. 4, figs. 125-126.
 1965 *Sciaena irregularis* Koken, 1884 - Pana, pl. 4, fig. 133-134.
 1965 *Corvina onata* (Koken, 1891) - Pana, pl. 4, figs. 131-132.
 1977 *Corvina dobrogiaca* Pana, pl. 3, figs. 1-11, pl. 4, figs. 1-4.
 1977 *Corvina rumana* Pana, pl. 4, figs. 5-15, pl. 5, figs. 13-14.
 1977 *Corvina dacica* Pana, pl. 5, figs. 1-12.
 1977 *Sciaena angulata* Schubert, 1902 - Pana, pl. 5, figs. 15-16.
 1995 *Sciaena angulata* Schubert, 1902 - Pana, pl. 4, figs. 5-8.
 1995 *Corvina onata* (Koken, 1891) - Pana, pl. 4, figs. 9-11.
 1995 *Corvina dacica* Pana, 1977 - Pana, pl. 4, figs. 12-15.
 1995 *Corvina dobrogiaca* Pana, 1977 - Pana, pl. 5, figs. 1-3.
 1995 *Corvina rumana* Pana, 1977 - Pana, pl. 5, figs. 4-6.
 2006 *Sciaena* aff. *excissus* Schubert, 1902 - Djafarova, pl. 15, figs. 2-4.
 2010 *Trewasciaena kokeni* (Schubert, 1902) - Jovanović et al., pl. 2, figs. 1.2.

Studied Material: A total of 34 otoliths from the collection of Pana, including all the specimens examined for the papers published in 1965 and 1977, as well as the holotypes of *Corvina dobrogiaca*, *C. rumana* and *C. dacica*, all from the upper Dacian, Parscovian. Two further specimens from Cheleken, Turkmenistan [NHMUK P.11225; labeled as from the Apsheron Series, Pontian (inconclusive stratigraphy, probably not younger than Akchagylia and not older than Kimmerian); figured in Schwarzahans (1993)].

Diagnosis: Otoliths relatively compressed with an otolith length to height ratio of 1.25-1.45. Dorsal rim shallow, with low mediadorsal angle and angle at joint with posterior rim. Ostium wide, about as wide as long or wider (ostium length to height ratio: 0.85-1.05). Postostial lobe weak. Ostial - caudal interspace 35-40% of sulcus length.

Distribution: *Trewasciaena dobrogiaca* is common in the Dacian of Romania and has also been recorded from the Akchagylia of Azerbaijan by Djafarova (2006) (as *Sciaena* aff. *excissus* Schubert, 1902). Two specimens figured by Schwarzahans (1993) as *T. aff. kokeni* from the Cheleken Peninsula of Turkmenistan also represent *T. dobrogiaca* and are the largest specimens so far known. The specimens have been labeled as derived from the Pontian deposits of the Apsheron Series. However, according to Junek (2004), the Pontian is not exposed at Cheleken. The core of an eroded anticline at Cheleken contains the upper part of the "Red series", corresponding to the upper part of the Kimmerian (late Zanclean to Piacenzian). Given the Akchagylia record from Azerbaijan, we assume that the geological age of these two specimens will not be younger than Akchagylia and not older than late Kimmerian.

Jovanović et al. (2010) figured otoliths of *T. kokeni* from the Portaferrian of Orešac-Udovice and Sastavci, Serbia, which perfectly match *T. dobrogiaca* in proportions and for this reason are regarded as members of the latter species. The localities are described by Jovanović et al. (2010) as representing the latest brackish phase in the Central Paratethys, i.e. probably younger than the Croatian locality of Okrugljak I, from where Gorjanović-Kramberger (1891) described some otoliths. However, Gorjanović-Kramberger (1891) also figured a small otolith of about 5 mm length from the freshwater Paludina beds from Sibirj, Slavonia (Serbia) which in fact represents the only sciaenid otolith so far recorded from the Paludina Lake. Its short ostium and the wide ostial - caudal interspace resembles *Trewasciaena dobrogiaca*, to which we tentatively refer this record.

Trewasciaena dobrogiaca probably evolved in the Eastern Paratethys separately from the Central Paratethyan *T. kokeni* and migrated into the Central Paratethys during the latest brackish stage of the Central Paratethys through a short lived connection between these basins.

Description. Large otoliths reaching sizes of at least 16 mm (specimens from Cheleken), although largest specimen recorded from Pana equals a length of 8.1 mm (Fig. 8 K-N). The dorsal rim is shallow, nearly horizontal, often with reduced mediadorsal angle and rounded angle at the junction with posterior rim; the latter becomes stronger in large specimens. The ventral rim is deeply and regularly rounded. The anterior rim is broadly rounded, while the posterior rim is nearly vertically cut. All the rims are smooth.

The inner face is moderately bent along its horizontal axis, less bent along its vertical axis. The sulcus has a wide, shallow ostium, often shorter than wide or with equal width and length. The rear margin of the ostium shows a strong dorsal flexure and a ventral flexure about twice as deep, albeit with weak postostial lobe. The cauda is narrow, slightly deepened, about as long or slightly longer

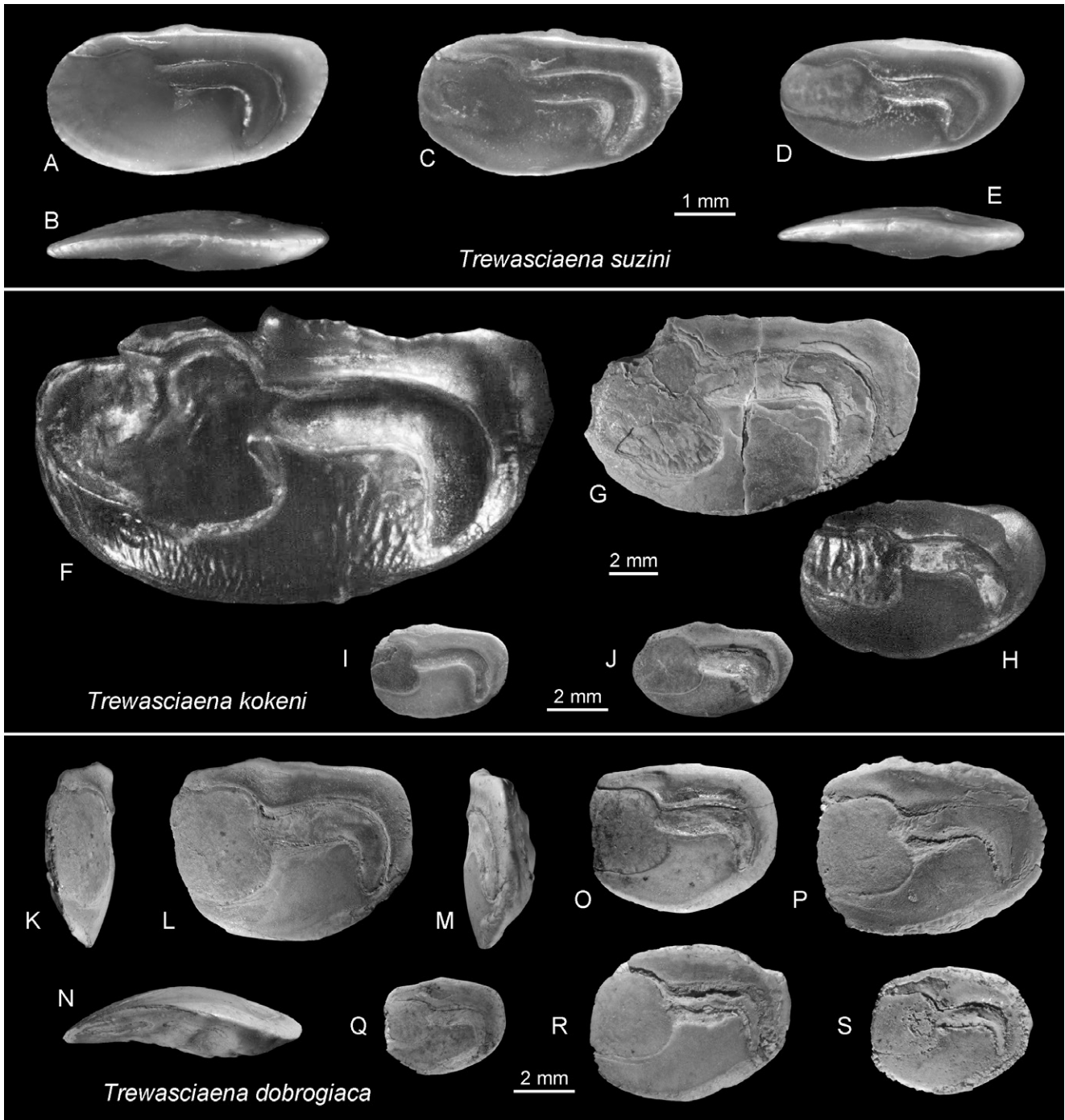


Fig. 8 - *Trewasciaena* Schwarzzhans, 1993. A-E - *Trewasciaena suzini* Bratishko, Schwarzzhans & Reichenbacher, 2015. Karagaily, Kazakhstan, Konkian; D) holotype NMNH 2532/063 (E ventral view); A-B, C) paratypes NMNH 2532/061 and 062 (B ventral view). F-J - *Trewasciaena kokeni* (Schubert, 1902). F) Brunn am Gebirge, Austria, Pannonian E, holotype (reproduced from Schultz, 2013, mirror imaged), GBAWien 1902/01/23; G) (mirror imaged) Okrugeljak, Croatia, Portaferrian, CNHM 109.1; H) Brunn am Gebirge, Austria, Pannonian E) holotype of *Sciaena? telleri* (reproduced from Schultz, 2013, mirror imaged), GBAWien 1902/01/21; I) (mirror imaged) Moncucco Torinese, Italy, terminal Messinian, MGPT-PU130336; J) (mirror imaged) Capanne di Bronzo, Italy, terminal Messinian, MGPT-PU 130337. K-S - *Trewasciaena dobrogiaca* (Pana, 1977). Romania, Parscovian, Dacian; K-N) (mirror imaged), O, R) types of *Corvina dobrogiaca*, Oltina (R holotype, LPB II P/o 0044), (K-N, O paratypes, LPB II P/o 0045) (K anterior view, L inner face, M posterior view, N ventral view); P, S) types of *Corvina rumana* (S holotype, Oltina, LPB II P/o 0046), (P paratype, Runcu, LPB II P/o 0036); Q) specimen described as *Sciaena aff. angulata* in Pana (1977), Oltina, LPB II P/o 0054.

than ostium, steeply curved posteriorly with the anterior horizontal stretch being slightly longer than the downturned posterior part. The ventral field is

smooth, sometimes with a weak ventral line close to ventral margin of the otolith and posteriorly turning upwards to the tip of the cauda. The dorsal field

exhibits a narrow, indistinct depression. The outer face is more or less flat, with little ornamentation and scarcely pronounced postcentral umbo.

Discussion. Based on our observation of a relatively large sample of specimens, it is difficult to understand how Pana (1965, 1977) managed to describe this species under seven different species names [also Schubert (1902) introduced five different species for *Trewasciaena kokeni*]. *Trewasciaena dobrogiaca* resembles *T. kokeni* on many aspects, related to sulcus proportions, otolith outline, and a relatively flat outer face. However, *Trewasciaena dobrogiaca* clearly differs from *T. kokeni* in having a more compressed shape expressed in the otolith length to height ratio of 1.25 to 1.45 (vs 1.55-1.75) as well as in the shape of the ostium, which is as high or higher than long (vs longer than high in *T. kokeni*). Both these species possibly belong to a distinct lineage within the genus *Trewasciaena*.

Trewasciaena kokeni (Schubert, 1902)

Fig. 8 F-J

- 1902 *Otolithus (Sciaenidarum) kokeni* Schubert, pl. 10, fig. 18.
 1902 *Sciaena? excisus* Schubert, pl. 10, fig. 17.
 1902 *Sciaena? levis*: Schubert, pl. 10, fig. 9.
 1902 *Sciaena? telleri*: Schubert, pl. 10, fig. 16.
 1906 *Otolithus (Sciaenidarum) loczyi*: Lörenthey, pl. 2, fig. 8.
 1906 *Otolithus (Sciaenidarum) aff. loczyi*: Lörenthey, pl. 3, figs. 23, 24.
 1981 "genus aff. *Umbrina*" *kokeni* (Schubert, 1902) - Nolf, pl. 3, figs. 8-9.
 1993 *Trewasciaena kokeni* (Schubert, 1902) - Schwarzghans, figs. 171-75 (non figs. 176-177).
 2006 *Umbrina* sp. Carnevale, Caputo & Landini, fig. 3 B.
 2008 *Umbrina* sp. Carnevale et al., fig. 3 M.
 2013 *Trewasciaena kokeni* (Schubert, 1902) - Schultz, pl. 91, figs. 1-5.
 2017 "*Trewasciaena*" sp. Colombo et al., fig. 5.15.
 2018 *Trewasciaena* sp. Carnevale et al., fig. 3 R.

Studied Material: Two specimens from collection of Gorjanović-Kramberger, CNHM 109.1-2, from the Portaferrian of Okrugljak near Zagreb, Croatia (Okrugljak Formation in Vrsaljko et al., 2011). Six specimens from Moncucco Torinese and Capanne di Bronzo, Lago Mare phase of the Messinian salinity crisis (roughly between 5.5 and 5.3 Ma), Italy. Schubert's type-material was studied for the sciaenid monographic review published by Schwarzghans (1993). Two photographs from Schultz (2013) have been used here for documentary purposes.

Distribution: Pannonian of the Central Paratethys and late Messinian (Lago Mare phase) of Italy.

Discussion. These are the youngest unambiguous records of *T. kokeni*. Jovanović et al. (2010) have recorded otoliths from the Portaferrian of Serbia that are referred herein to as *T. dobrogiaca* (see above). Lörenthey (1906) figured specimens synonymized herein with *T. kokeni* from the Transdanubian (Pan-

nonian H), according to a recent stratigraphic review of the localities by Sztano et al. (2013), who identified a time interval of 8.1 to 8.3 Ma. It is uncertain, whether both these species coexisted in the Central Paratethys during the Portaferrian, or the occurrence of *T. dobrogiaca* postdates that of *T. kokeni*, a possibility that appears more likely based on the observations by Jovanović et al. (2010). However, there are also records of *T. kokeni* from the Lago Mare phase of the Messinian salinity crisis in the Mediterranean, which indicate that this species extends into younger strata. The occurrence of these fossils in the Lago Mare phase also indicates that opportunistic migration of *T. kokeni* must have taken place from the Paratethys into the Mediterranean during the late Miocene.

Trewasciaena suzini Bratishko, Schwarzghans & Reichenbacher, 2015

Figs 8 A-E

2015 *Trewasciaena suzini*: Bratishko et al., figs. 7.9-7.14.

Remarks. No new material studied. *Trewasciaena suzini* represents a slender, relatively small species (up to 6 mm length) of *Trewasciaena*, exclusively known from the Konkian of Kazakhstan in the Eastern Paratethys.

Genus *Umbrina* Cuvier, 1817

Discussion. *Umbrina* is a speciose and widespread genus of the family Sciaenidae. Schwarzghans (1993) recognized four different otolith morphologies within the genus, suggesting that *Umbrina* as currently defined may contain several distinct lineages. Most otoliths of extant *Umbrina* species, however, share a relatively narrow ostial - caudal interspace measuring 17-25 % of the sulcus length, although in one species, *Umbrina cirrosa*, this parameter regularly ranges from 23 to almost 30 %. The three *Umbrina* species from the Neogene of the Paratethys discussed below all show a similarly wide ostial - caudal interspace.

Umbrina cirrhosoides (Schubert, 1902)

Fig. 9 A-B

- 1891 Otoliti Gorjanović-Kramberger, pl. 3, fig. 5.
 1902 *Corvina? cirrhosoides* Schubert, pl. 10, fig. 4.
 1902 *Umbrina? plena* Schubert, pl. 10, fig. 6.

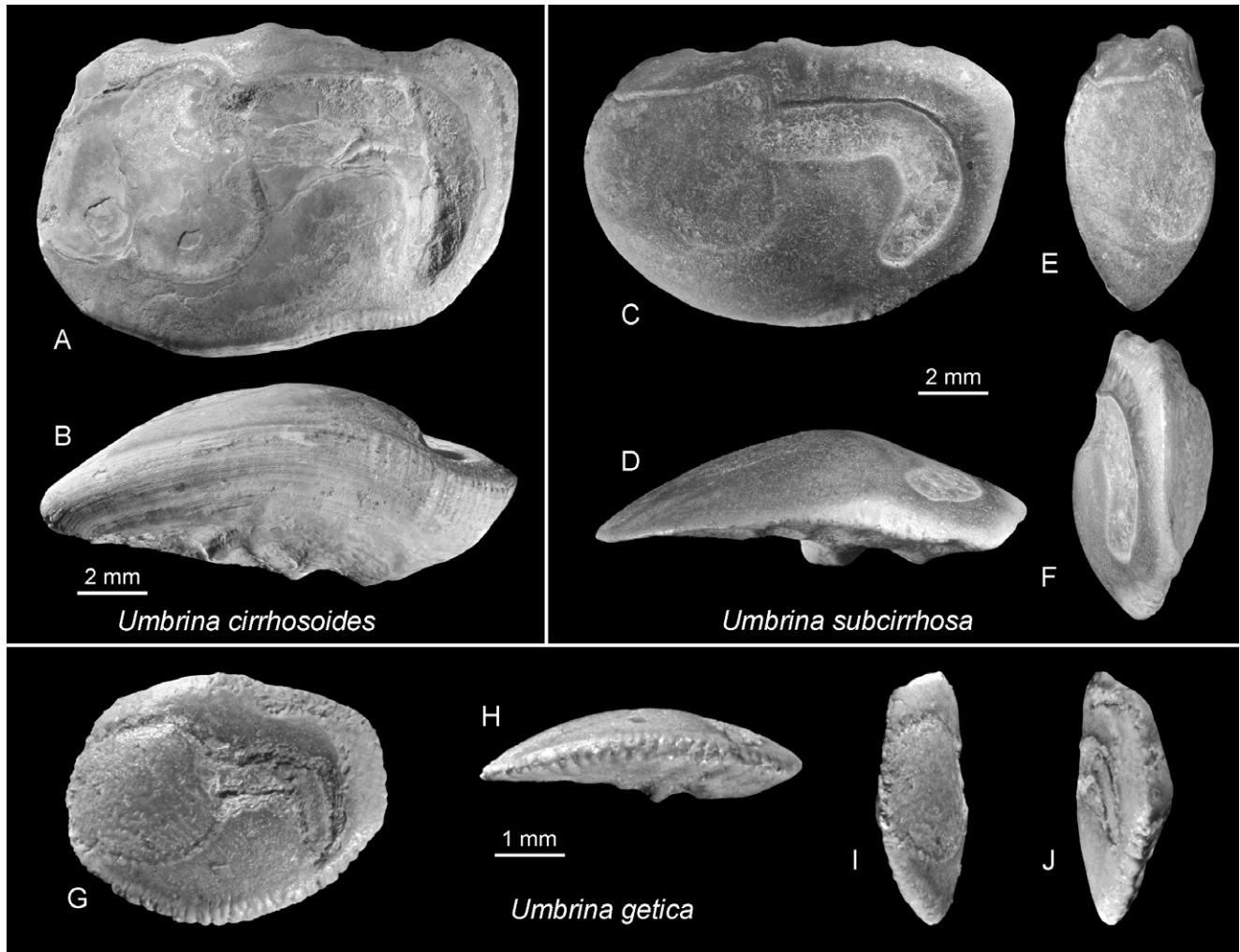


Fig. 9 - *Umbrina* Cuvier, 1817. A-B - *Umbrina cirrhosoides* (Schubert, 1902). Okrugljak, Croatia, Portaerrian, CNHM 109.4 (A inner face, B ventral view). C-F - *Umbrina subcirrhosa* Schubert, 1902. Okrugljak? (location uncertain), Croatia, Portaerrian? (stratigraphy uncertain), CNHM 109.5 (C inner face, D ventral view, E anterior view, F posterior view). G-J - *Umbrina getica* (Pana, 1995). Tircov, Romania, Parscovian, Dacian, LPB II P/o 0035a (G inner face, H ventral view, I anterior view, J posterior view).

- 1981 *Umbrina cirrhosoides* (Schubert, 1902) - Nolf, pl. 3, fig. 10.
 1993 *Umbrina cirrhosoides* (Schubert, 1902) - Schwarzahns, figs. 124-125.
 2010 *Umbrina cirrhosoides* (Schubert, 1902) - Jovanović et al., pl. 2, fig. 3.
 2013 *Umbrina cirrhosoides* (Schubert, 1902) - Schultz, pl. 90, figs. 3-4.

Studied Material: A single large specimen from the collection of Gorjanović-Kramberger, CNHM 109.4, from the Portaerrian of Okrugljak near Zagreb, Croatia (Okrugljak Formation in Vrsaljko et al., 2011). This specimen probably corresponds to that figured in Gorjanović-Kramberger (1891) judging from the proportions as given by him in the somewhat schematized drawing.

Distribution: *Umbrina cirrhosoides* is a relatively long ranging Central Paratethyan species, recorded from the late Badenian to the Portaerrian (Jovanović et al. 2010).

Discussion. *Umbrina cirrhosoides* resembles certain *Trevasciaena* species with a pronounced angle at the joint between the dorsal and posterior rims and a relatively wide ostial - caudal interspace. However, the spatulate ostium, which narrows anteriorly with

inclined dorsal and ventral sulcus margins clearly differs from the ostium characteristic of *Trevasciaena*. Therefore, we maintain *Umbrina cirrhosoides* within the genus *Umbrina*. Other diagnostic characters of the species are the lack of a postcentral umbo on the outer face, and the flat ventral rim that becomes even concave between the ostium and the cauda in large specimens.

Umbrina getica (Pana, 1995)

Fig. 9 G-J

- 1965 *Sciaena moguntina* Weiler, 1942 - Pana, pl. 3, figs. 99-100, ?111-112.
 1995 *Corvina getica* Pana, pl. 5, figs. 7-9.

Studied Material: Two specimens from the Dacian of valea Tircov, Romania, described by Pana (1965) as *Sciaena moguntina* Weiler, 1942. The type material of Pana (1995) was not available for study.

Distribution: Dacian of Romania.

Description. Small, oval shaped otoliths with maximum size of 4.4 mm in length. Otolith length to height ratio: 1.3. The dorsal and ventral rims are regularly curved, the ventral rim being deeper. The anterior rim is broadly rounded; the posterior rim is rounded, but much less high than the anterior one; no pronounced angle is present at the junction between dorsal and posterior rims. All the rims are finely crenulated.

The inner face is distinctly convex. The ostium is large and wide, ovoid in outline, shallow, and lacking a postostial lobe. The cauda is short, narrow, slightly deepened; its horizontal section is about as long as its vertically inclined posterior section. Length ostium to cauda ratio: 1.4; ostial - caudal interspace 27 % of sulcus length. The ventral field is smooth, with fine line at the termination of the marginal ornamentation. The dorsal field has an indistinct dorsal depression. The outer face is flat with little ornamentation.

Discussion. The available specimens as well as those figured by Pana (1995) do not appear to be adult specimens and seem to lack some of the diagnostic features typical of otoliths pertaining to large adult individuals. Therefore, we regard the status of the validity of *Umbrina getica* as provisional, until additional, large specimens will be available for further investigations. Nevertheless, *U. getica* shows a few characters of possible diagnostic value, including the oval outline without marked angles, the large and ovoid ostium without postostial lobe (although the latter can be an ontogenetic artifact and large specimens could potentially have a postostial lobe), the small sized cauda, and the rather wide ostial - caudal interspace. Overall, the morphological features concur to support the assignment of this species to the genus *Umbrina*.

Umbrina subcirrhosa Schubert, 1902

Fig. 9 C-F

- 1902 *Umbrina subcirrhosa* Schubert, pl. 10, fig. 3.
 1906 *Otolithus (Sciaenidarum) schuberti* Lörenthey, pl. 2, fig. 6.
 1993 *Umbrina subcirrhosa* Schubert, 1902 - Schwarzghans, figs. 103-107.
 1998 *Umbrina cirrosa* (Linnaeus, 1758) - Reichenbacher, pl. 3, fig. 2.
 2007 *Umbrina* cf. *cirrosa* (Linnaeus, 1758) - Brzobohaty et al., pl. 7, fig. 6.
 2008 *Umbrina* aff. *cirrosa* (Linnaeus, 1758) - Cziczter et al., fig. 12.
 2013 *Umbrina subcirrhosa* Schubert, 1902 - Schultz, pl. 90, fig. 6.

Studied Material: A single specimen from the collection of Gorjanović-Kramberger, CNHM 109.5. Although the specimen was kept with four others that were obtained from the Porteferrian of

Okrugljak, it cannot be excluded that it could actually come from a different and stratigraphically older locality.

Discussion. *Umbrina subcirrhosa* is characterized by a relatively wide ostial - caudal interspace reaching 25 to 30% of the sulcus length. It resembles the extant *U. cirrosa* from which differs in the slightly more elongate shape (otolith length to height ratio 1.4-1.6 vs 1.3-1.45) and the absence of a postcentral umbo on the outer face (vs present). *Umbrina subcirrhosa* is a long ranging species of the Central Paratethys occurring from the Karpatian to the Pannonian. The youngest unambiguous record was documented by Lörenthey (1906) [described as *Ot. (Sciaenidarum) schuberti*, here synonymized with *U. subcirrhosa*] from the Transdanubian (Pannonian H) of Hungary; according to a recent stratigraphic review of the locality formerly investigated by Lörenthey (1906), the fossiliferous strata can be referred to a time interval between 8.3 to 8.1 Ma (Sztano et al. 2013). *Umbrina subcirrhosa* is one of the few fish species that survived both the middle Badenian crisis and the Badenian/Sarmatian extinction event.

DISCUSSION

The emergence of a vanished sciaenid bioprovince

Today, sciaenid species exhibit a peculiar pattern of species richness with a comparable high diversity in the Indo-West Pacific, Eastern Pacific and Western Atlantic regions and less diverse communities living along the coasts of the Eastern Atlantic (see Trewavas 1977; Chao 1978; Sasaki 1989; Lo et al. 2015). The richest sciaenid assemblages are found along the shores and in the rivers of the tropical Americas (Chao 1978; Lo et al. 2015). Most extant genera are confined to just one of those bioprovinces with a few ranging across two bioprovinces and two genera distributed across all three areas (*Atractoscion* and *Umbrina*). The warm waters of southern Europe are home to a much impoverished sciaenid association with three species of *Umbrina* and one each of *Argyrosomus* and *Sciaena* (Chao 1986).

The family Sciaenidae appears to be of relatively young origin from a deep time perspective. The earliest unambiguous records are otoliths from the middle Eocene of the Gulf Coast area (Frizzell

& Dante 1965; Nolf 1995; Müller 1999; Nolf & Stringer 2003). These forms exhibit a very plesiomorphic morphology, some of which have been identified as extinct genera (*Eokokenia* Frizzell & Dante 1965, *Jefitchia* Frizzell & Dante 1965) but most have been referred to as sciaenids of uncertain relationships or as representatives of extant genera with plesiomorphic otolith patterns such as *Umbrina*. The age and origin of the present distributional pattern is inadequately known. The most extensive fossil otolith-based sciaenid fauna known is that from the tropical America, which revealed that many endemic American genera and lineages date back to the middle Miocene or even early Miocene times (Aguilera et al. 2016).

The earliest European records are also based on isolated otoliths and date back to the early Oligocene (Koken 1884, 1891; Schwarzhans 1993). These records are morphologically similar to the early sciaenid otolith morphologies found in the Eocene of the Atlantic Coastal Plain and Gulf Coast area. The earliest skeleton-based sciaenid is *Caucasisciaena* Bannikov, Carnevale & Landini, 2009 from the early Miocene of the Eastern Paratethys. Like its otolith counterparts, the phylogenetic relationships of *Caucasisciaena* are difficult to determine. Many other fossil records from the Neogene of Europe match up well with extant genera characteristic of this region, i.e. *Argyrosomus* with three otolith-based and one skeleton-based species, *Umbrina* with several otolith-based species, *Sciaena* with possibly two otolith-based species and an extinct genus close to *Atractoscion*, namely *Landinisciaena* with a skeleton- and an otolith-based species each. *Landinisciaena popovi* is also the only fossil sciaenid from Europe known to date with otoliths found *in situ*. In addition, there are indications of an occasional faunal exchange with North America as witnessed by the occurrence of American sciaenid genera in the early to middle Miocene of Europe, primarily the North Sea Basin, e.g. otoliths of *Cynoscion* and *Sciaenops* (Schwarzhans 2010).

However, as documented in the present paper, there is also a number of both skeleton- and otolith-based sciaenid taxa suggesting the existence of a Neogene endemic sciaenid stock in the Paratethys, which has now totally vanished. It comprises the fossil skeleton-based genera *Croatosciaena* n. gen. (middle Miocene), *Carnevalella* Bannikov, 2013 (late Miocene to early Pliocene) and the otolith-based

genera *Trewasciaena* Schwarzhans, 1993 (early Miocene to early Pleistocene as proposed in this study), *Chaoia* n. gen. (late Miocene to early Pliocene), *Leptosciaena* n. gen. (middle Miocene to early Pliocene) and *Pontosciaena* n. gen. (late Miocene). They all are interpreted as representing part of an endemic Paratethyan fish assemblage that originated and evolved after the Mid-Miocene Karaganian crisis, with the sole exception of *Trewasciaena moguntina* (Weiler, 1942). *Trewasciaena moguntina* occurred in the early Miocene of the Upper Rhine Graben in freshwater and brackish paleobiotopes. Moreover, it is possible that future finds of skeletal remains with otoliths *in situ* will reduce the number of taxa through the synonymization of some of them. This would be particularly interesting in the case of *Carnevalella*, which is so much apart phylogenetically from all extant sciaenid groups that it was placed in an extinct subfamily of its own, the Carnevalellinae (Bannikov 2013).

The following is a chronological account of the endemic evolution of Paratethyan sciaenids as currently understood based on the fossils documented herein, and their hypothesized occupation of the Paratethyan subregions and exchanges with the Mediterranean Sea (Figs 10, 11).

During the early and early middle Miocene (Langhian), prior to the Karaganian/middle Badenian crisis, the Paratethyan sciaenid contingent reflected a dominance of marine taxa that are in many cases related to extant European or tropical Atlantic genera. These were probably dominantly euryhaline and are mostly otolith-based (except *Landinisciaena popovi* and *Caucasicaena ignota*): *Argyrosomus similis*, *A. corii*, *Landinisciaena elongatissima*, *Miracorvina? compacta*, *Pogonias? styriacus*, *Sciaena? kirchbergensis*, *Umbrina polonica* and *U. subcirrhosa*. All the otolith-based data are from the Western and Central Paratethys while the two skeleton-based records (one with otoliths *in situ*) are from the Eastern Paratethys. This complicates correlation across the Paratethys, and, in any case, there is no or only little evidence of a nucleus for a subsequent endemic Paratethyan sciaenid stock during that time. However, only a much detailed knowledge of the early Miocene sciaenid assemblages of the Eastern Paratethys will allow an adequate interpretation of the faunal composition before the Karaganian crisis.

The northern region of the Upper Rhine Graben and adjacent smaller basins were the scene

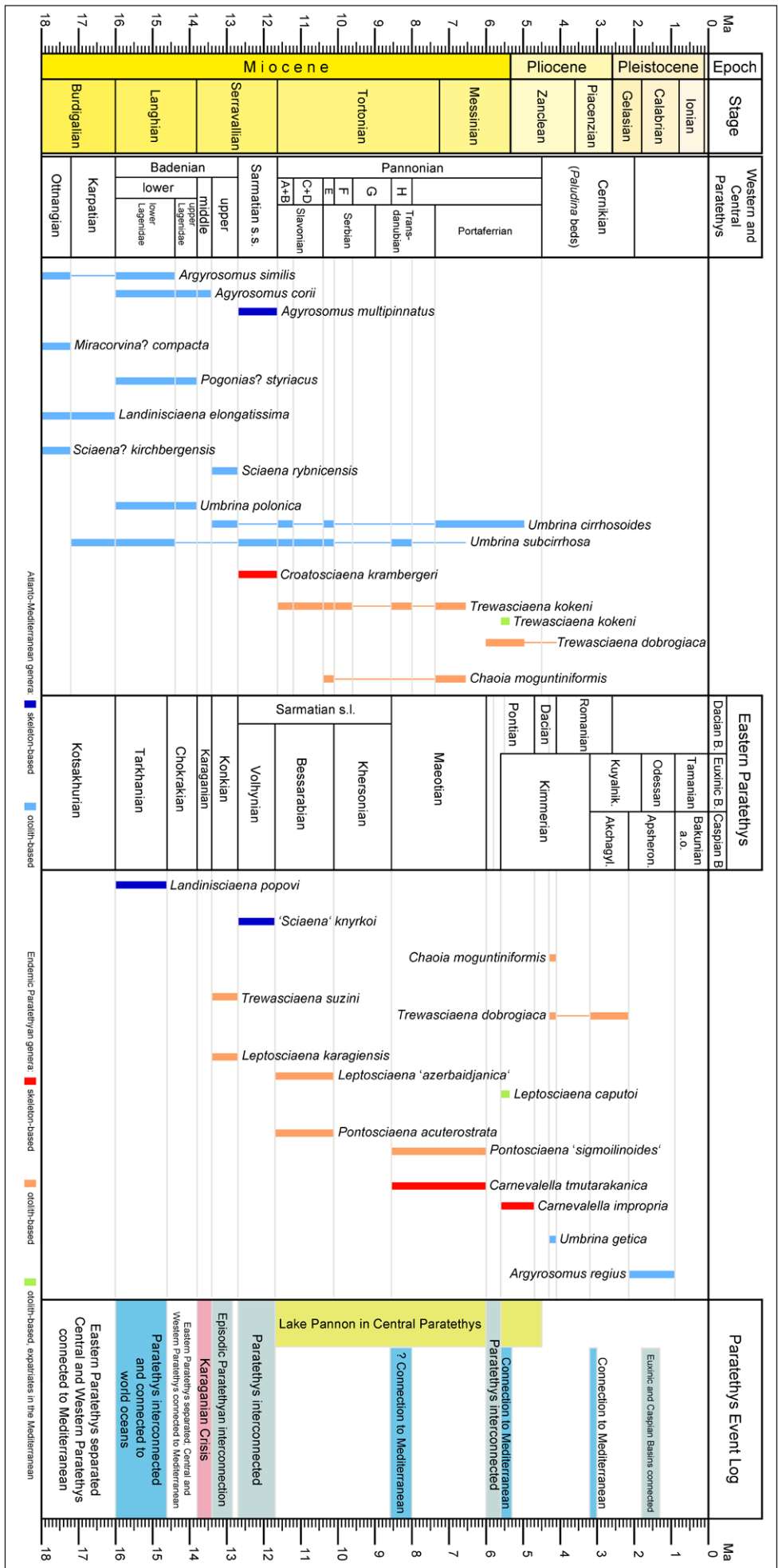


Fig. 10 - Stratigraphic range chart of sciencid remains, skeletons and otoliths, in the Neogene (late Burdigalian and younger) of the Paratethys. Thin lines represent ghost ranges or uncertain references. Chronostratigraphy after Gradstein et al. (2012); Central Paratethys stratigraphy after Hartzhauser et al. (2018); Pannonian subdivision after Hartzhauser et al. (2004) and Neubauer et al. (2015); Eastern Paratethys stratigraphy to Sarmatian s.l. after Gózdzyk et al. (2015); Eastern Paratethys from Mioctian combined from Ter Borgh et al. (2014), Forte & Cowgill (2013), Neubauer et al. (2015) and Andreescu et al. (2013).

of a brackish to freshwater inland sea in the late Oligocene and early Miocene, which harbored a very specific teleost fauna dominated by Gonorhynchidae, Cyprinodontidae, non-marine Gobiidae and even Channidae (Reichenbacher 2000). This fauna also contained two sciaenid species, which obviously were tolerant to brackish waters. One is the late Oligocene, *Sciaena? irregularis* Koken, 1884, which is known also from the North Sea Basin, thereby suggesting that it migrated into the northern Upper Rhine Graben area through an ephemeral connection (Reichenbacher 2000). The second species from the early Miocene, *Trewasciaena moguntina*, the type species of *Trewasciaena*, is not known from outside the brackish water inland sea (Schwarzahns 1993; Reichenbacher 2000). This observation indicates that the earliest species of this particular group of sciaenid fishes which later-on showed a dynamic endemic evolution in the Paratethys had an early origin outside of the Paratethys, but were already adapted to marginal marine and possibly non-marine environments.

The Konkian in the Eastern Paratethys and the late Badenian and Sarmatian s.s. in the Central Paratethys were characterized by a rapid decrease of those earlier putative euryhaline sciaenids and the advent of new lineages, a pattern already suggested by Bratishko et al. (2015). Among the few persistent lineages are *Argyrosomus* with the skeleton-based *A. multipinnatus* in the Sarmatian s.s. and *Umbrina subcirrhosa*, which were associated to taxa of more recent appearance, including the skeleton-based *Croatosciaena krambergeri* and the otolith-based *Umbrina cirrhosoides* in the Central Paratethys. In the Eastern Paratethys it is possible to trace the first Paratethyan occurrences of the otolith-based genera *Trewasciaena* and *Leptosciaena*. The coeval Sarmatian s.s. skeleton-based species *Croatosciaena krambergeri* and '*Sciaena? knyrkoi*' differ greatly from each other and have unknown relationships. Interestingly, we do not see interaction of the Eastern Paratethyan sciaenids with those of the Central Paratethys, while other Eastern Paratethyan fish groups are known to have migrated into the Central Paratethys during the late Badenian (Bratishko et al. 2015).

The onset of the brackish Lake Pannon in the Central Paratethyan region is remarkable for an increase of sciaenid diversity documented by the persistence of both *Umbrina* species and the concurrent appearance of *Trewasciaena kokeni* and

Chaoia moguntiniiformis. Obviously, the *Umbrina* species were very tolerant to reduced salinity and both experienced a long lasting presence in the Central Paratethys. The occurrence of *Trewasciaena kokeni* may have been fostered by the reduced salinity as well, considering the earliest record of the genus from the brackish water Upper Rhine Graben. Our knowledge of sciaenids from the equivalent time interval in the Eastern Paratethys is rather poor, and mainly depending on an otolith-based fauna from the Bessarabian of the Crimea (which is currently being studied by Bratishko and Schwarzahns) and Azerbaijan (Djafarova 2006), which contain two endemic Eastern Paratethyan species, *Pontosciaena acuterostrata* and *Leptosciaena 'azerbaidjanica'*. Both genera are characterized by a relatively small otolith size and by a trend in simplification of their otolith morphology, i.e. by reduction of the otolith width and postotolith lobe as well as the length of the downturned rear part of the cauda. In the Maeotian, there is a further record of the genus *Pontosciaena* based on otoliths and the first record of the skeleton-based Carnevalellinae (*Carnevalella tmutarakanica*). Like the Gobiidae, the Sciaenidae apparently benefited from the restricted marine environment in the Eastern Paratethys (Bratishko et al. 2015; Schwarzahns et al. 2017). It was the time of an accelerated endemic radiation in both groups, although gobies outnumbered sciaenids by far in abundance and species richness. Interestingly, there is no indication of faunal exchange then between the Central and the Eastern Paratethys in sciaenids. This may be due to the different ecological conditions that existed between the brackish-lacustrine Lake Pannon as compared to the restricted marine Eastern Paratethys, as well as to a presumed lack of geographical interconnection (Müller et al. 1999).

A number of events during the terminal Miocene and the early Pliocene seems to have resulted in remarkable shifts in the composition of the sciaenid stocks in both regions (Fig. 11). The transformation of the brackish-lacustrine Lake Pannon to the remnant Lake Slavonia freshwater lake in the Central Paratethyan region (Mandic et al. 2015) has been poorly studied for teleosts. There is a single indication for sciaenid otoliths in an old publication by Gorjanović-Kramberger (1891), who figured a relatively small sciaenid otolith from the 'Paludina layer' of Sibinj, which appears to be a representative of the genus *Trewasciaena*, possibly *T. dobrogiaca*. *Trewas-*

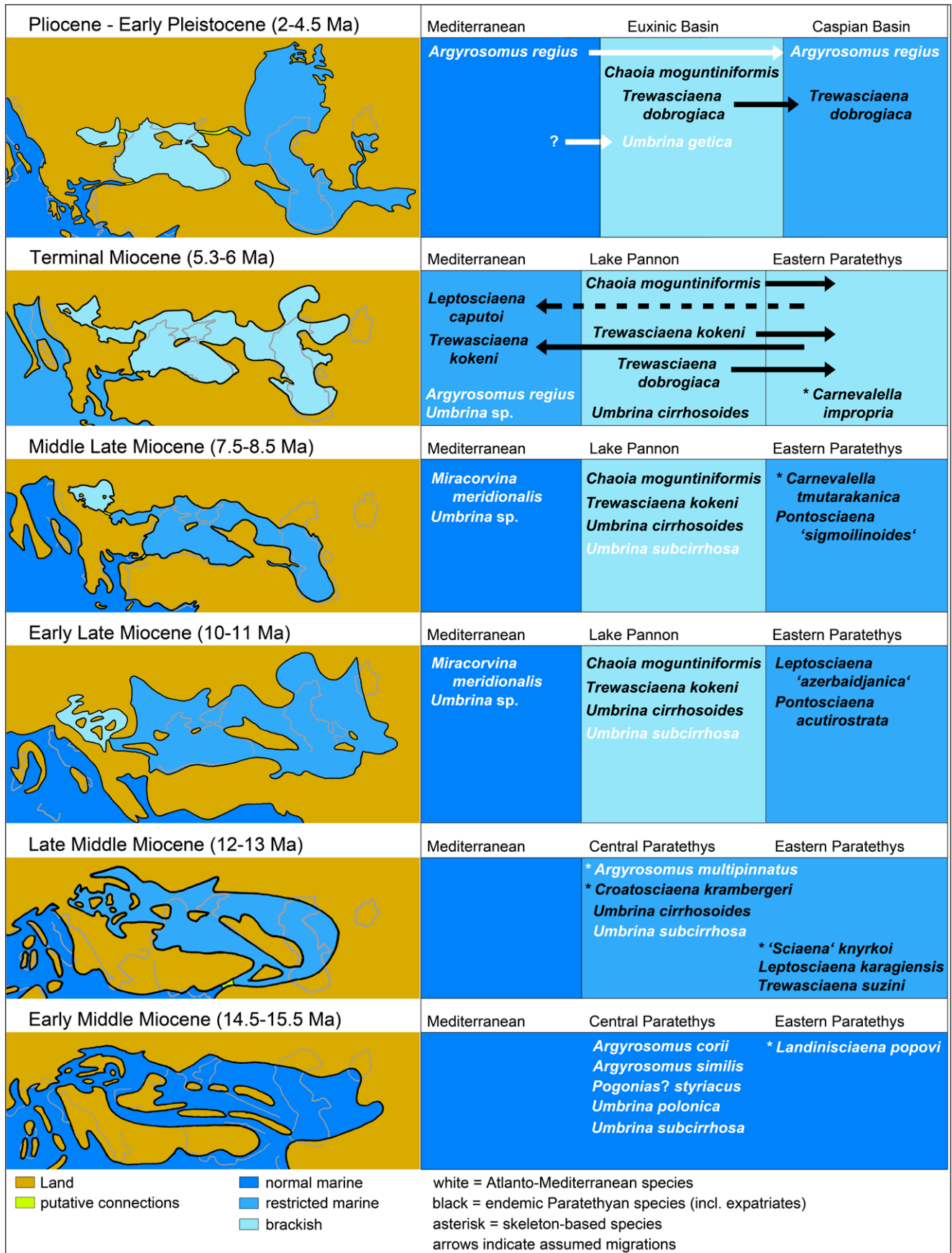


Fig. 11 - Middle Miocene to Pliocene paleobiogeographic distribution of Sciaenidae in the Paratethys and adjacent seas. Paleogeographic maps are based on Popov et al. (2004, 2006). Environmental interpretation is based on Müller et al. (1999).

ciaena dobrogiaca was also documented by Jovanović et al. (2010) (as *Trewasciaena kokeni*) from sediments of the latest stage of the Lake Pannon. In the Eastern Paratethys there is a second species of the enigmatic genus *Carnevalella* (*C. impropria*) in the brackish Pontian and a rich sciaenid otolith assemblage from the late Dacian (Parskovian) of the Dacian Basin in Romania described by Pana (1977, 1995) and reviewed herein. The Romanian otolith assemblage contains *Trewasciaena dobrogiaca* and *Chaoia moguntiniformis* plus the uncommon and poorly understood *Umbrina getica*. *Trewasciaena dobrogiaca* and *Chaoia moguntiniformis* are also known from the late stage of the Lake Pannon during the Portaferrian, which precedes the Dacian in Romania. The presence of both these species in the Lake Pannon and the Eastern Paratethys postdates a short phase of interconnection during the Pontian that apparently favored an eastward migration (Müller et al. 1999). Probably, the change from a restricted marine to brackish lacustrine paleobiotopes in the Eastern Paratethys allowed the immigration of sciaenids already adapted to the low salinity conditions typical of the Lake Pannon. However, the late Miocene is also the time of intermittent connection of the Eastern Paratethys with the Mediterranean. Faunal immigration from the Eastern Paratethys during the Lago Mare phase of the Messinian salinity crisis in the Mediterranean has been postulated by a number of authors (see, e.g., Roveri et al. 2014; Carnevale et al. 2018). In our assessment, the occurrence of *Trewasciaena kokeni* in Lago Mare sediments of Italy may have been facilitated by such a short-lived connection. There is, however, another occurrence of a putative endemic Paratethyan sciaenid in the Lago Mare interval, that of the genus *Leptosciaena*, represented during the Lago Mare phase by the species *L. caputoi*. This species possibly represents the last member of the *Leptosciaena* lineage and was characterized by an advanced stage of reduction of the morphological features of the otoliths. *Leptosciaena* is not known from this time interval in the Eastern Paratethys, but there are also no records of the genus for a long time interval spanning the Khersonian and Maeotian. Therefore, the exact origin of *Leptosciaena caputoi* remains obscure and it is not possible to conclusively determine whether it migrated into the Mediterranean during the Lago Mare event and the lacking knowledge in this time interval of the Eastern Paratethys is purely ar-

bitrary and related to missing otolith research, or the ancestors of *L. caputoi* migrated earlier into the Mediterranean, and adapted to the marginal marine paleobiotope abundant along the coasts. An earlier migration may have been facilitated by the paleogeographical configuration and connectivity that characterized the early Maeotian (Popov et al. 2006; Forte & Cowgill 2013). The occurrence of a poorly defined *Umbrina* species in the Dacian of Romania (*U. getica*) might indicate that the exchange of faunal elements during the Lago Mare phase may have not been strictly unidirectional. *Umbrina getica* might provide evidence for a migration of a sciaenid taxon from the Mediterranean into the Eastern Paratethys.

The youngest record of any endemic sciaenid in the Eastern Paratethys is from the Akchagylian of Azerbaijan and Turkmenistan (the exact timing of the latter is rather uncertain) represented by *Trewasciaena dobrogiaca*. Thus, we must assume that the Paratethyan sciaenid “bioprovince” finally vanished during the early to middle Pleistocene after a gradual decrease of diversity that occurred during the Pliocene. The latest record of a sciaenid (otolith) from the Eastern Paratethys is from the Apsheronian (middle Pleistocene) of the Caspian Sea and represents an extant species - *Argyrosomus regius*. The immigration of *A. regius* into the Caspian Sea may be related to the Akchagylian transgression, which probably for the last time facilitated limited faunal exchange of the Ponto-Caspian Basin with the Mediterranean (Forte & Cowgill 2013). Nowadays, there are no sciaenids in the Caspian Sea, and a few euryhaline species migrated from the Mediterranean into the Black Sea after that the Black Sea was occupied by fully marine waters (e.g., Forte & Cowgill 2013).

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