Available online at www.sciencedirect.com
ScienceDirect
C. R. Palevol 8 (2009) 535–544
COMPTES RENDUS PALEVOL

Systematic palaeontology (vertebrate palaeontology)

A new Early Miocene genus of the family Sciaenidae (Teleostei, Perciformes) from the eastern Paratethys

Alexandre Fedorovich Bannikov [a], Giorgio Carnevale [b,*,c], Walter Landini [b,c]

[a] *Borisyak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, Moscow 117997, Russia*
[b] *Dipartimento di Scienze della Terra, Università di Pisa, via Santa Maria, 53, 56126 Pisa, Italy*
[c] *Museo di Storia Naturale e del Territorio, Università di Pisa, via Roma, 79, 56011 Calci (PI), Italy*

Received 31 October 2008; accepted after revision 23 February 2009
Available online 16 April 2009

Presented by Phillipe Taquet

Abstract

A new genus of sciaenid fish *Caucasisciaena* is erected to accommodate the Early Miocene eastern Paratethys species *Perca ignota* Smirnov, 1936, which, subsequently, was variously attributed to the modern genera, either *Larimus* or *Otolithoides*. The materials examined include 32 specimens from four Caucasian and Crimean localities of Sakaraulian age (Lower Burdigalian). The new genus is based on a unique combination of features, including: parasphenoid with a dorsal rounded bony flange; basisphenoid present; premaxilla with short ascending process forming obtuse angle with alveolar process and ascending/alveolar process ratio about 0.17; anterior premaxillary teeth enlarged; posttemporal with few robust spines along its posterior margin; presence of 25 vertebrae; presence of three tiny supraneurals; dorsal fin with 11 spines plus 22–24 soft rays; anal fin with two spines and 7–8 soft rays; second anal-fin spine long and massive; pectoral fin elongate; scales ctenoid on body and cycloid on head (except for one or two rows of ctenoid scales on the cheek). Paleoecological considerations suggest that *Caucasisciaena* probably was a predatory fish that inhabited the coastal waters of the eastern sector of the Paratethyan basin. ***To cite this article: A.F. Bannikov et al., C. R. Palevol 8 (2009).***

Résumé

Un nouveau genre de la famille des Sciaenidae (Téléostéens, Perciformes) du début du Miocène de la Parathéthys orientale. Un nouveau genre de poisson sciaenidé *Caucasisciaena* apparaît pour prendre la place de l'espèce Miocène précoce de la Parathéthys orientale *Perca ignota* (Smirnov 1936), qui a été, par la suite, attribuée tour à tour aux genres modernes *Larimus* ou *Otolithoides*. Le matériel examiné comporte 32 spécimens en provenance de localités du Caucase ou d'Ukraine, d'âge Sakaraulien (Burdigalien inférieur). Le nouveau genre est fondé sur une unique combinaison de carctéristiques incluant : parasphénoïde avec un bourrelet osseux arrondi dorsal ; basisphénoïde présent ; prémaxillaire avec un court processus ascendant formant un angle obtus avec le processus alvéolaire et un rapport processus ascendant/processus alvéolaire d'environ 0,17 ; dents du prémaxillaire antérieur élargies ; post-temporal avec quelques épines robustes le long de la marge postérieure ; présence de 25 vertèbres ; présence de trois minuscules supraneuraux ; nageoire dorsale avec 11 épines et 22–24 rayons mous ; nageoire anale avec 2 épines et 7–8 rayons mous ; seconde épine de la nageoire anale longue et massive ; nageoire pectorale allongée ; écailles cténoïdes sur le corps et cycloïdes sur la tête (excepté une ou deux rangées d'écailles cténoïdes sur la joue). Des considérations paléoécologiques suggèrent que *Caucasisciaena*

* Corresponding author.
E-mail address: carnevale@dst.unipi.it (G. Carnevale).

1631-0683/$ – see front matter © 2009 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.crpv.2009.03.001

était vraisemblablement un poisson prédateur qui habitait les eaux côtières du secteur oriental du bassin de la Parathéthys. ***Pour citer cet article : A.F. Bannikov et al., C. R. Palevol 8 (2009).***

Keywords: Teleostei; Sciaenidae; *Caucasisciaena* gen. nov.; Miocene; Sakaraulian; Caucasus; Crimea; eastern Paratethys

Mots clés : Téléostéens ; Sciaenidae ; *Caucasisciaena* gen. nov. ; Miocène ; Sakaraulien ; Caucase ; Crimée ; Paratéthys orientale

1. Introduction

Fishes of the family Sciaenidae are widespread in tropical and subtropical coastal and estuarine waters throughout the world. A number of species of this family also inhabit rivers, in south-eastern Asia, India, and North and South America. The family Sciaenidae is one of the largest within the perciforms, with approximately 270 species in about 70 genera [19]. Many of these fishes are of commercial or sport-fishery relevance. The sciaenids are commonly called croakers or drums because of their ability to produce a variety of sounds by means of muscles attached to the swimbladder. The history of the sciaenids is relatively well documented in the stratigraphic record, primarily by their large and thick otoliths, whereas articulated skeletal remains are rare. Sciaenid otoliths are rather abundant in Oligocene and Neogene terrigenous deposits of Europe and America [22,27]. The oldest representative of the family was reported by Nolf [21] from the Ypresian Bashi Marls, Mississippi.

In the Early Miocene, sciaenids appeared in the epicontinental basin of eastern Paratethys. Smirnov [28] first described croakers from the Chernaya Rechka locality in North Ossetia (northern Caucasus) as a new species of perch, *Perca ignota*. He regarded the Upper Maikopian deposits as the Oligocene in age. Danilchenko [8] corrected both the systematic position of Smirnov's species and the age of the rocks of the Chernaya Rechka locality. He assigned *Perca ignota* Smirnov to the sciaenid genus *Larimus*, and dated the Upper Maikopian deposits by the Lower Miocene: "Zuramakent Horizon" [8,9] or "Voskovaya Gora Horizon" [10]. Up to date, *Larimus ignotus* is recorded from at least four localities of the eastern Paratethys, in Azerbaijan (Apsheron peninsula), Russia (Apsheronsk district, North Ossetia) and Ukraine (Kerch peninsula) (Fig. 1). Certain differences in the composition of the Late Maikopian fish assemblages of different localities in the Caucasus and Crimea led to suppositions about their different age. These localities have been tentatively assigned to the Upper Caucasian [2] (or Aquitanian [23,29]) or the Sakaraulian [2] (or Burdigalian [23,29]). However, it seems more correct to suppose the same (Sakaraulian) age for these localities and the compositional structure of the fish assemblages of Late Maikopian localities are probably related to different depositional environments. The Sakaraulian of the eastern Paratethys is correlated with the Lower Burdigalian [20].

Fig. 1. Sketch map of southern portion of European Russia and adjacent countries (modified from [4]). The fish skeletons indicate the location of the fossiliferous localities of *Caucasisciaena ignota* (Smirnov).

Fig. 1. Carte schématique de la portion méridionale de la Russie d'Europe et régions adjacentes (modifié selon [4]). Les squelettes de poisson indiquent la localisation des sites fossilifères de *Caucasisciaena ignota*. (Smirnov).

Recently, Bannikov [3] noted that the Early Miocene sciaenid species lacks the autapomorphies of the amphi-American genus *Larimus* Cuvier [25], and referred it as *Otolithoides* (?) *ignotus*. Indeed, the fossil Paratethyan species strongly resembles the Recent species of the Indo-Pacific genus *Otolithoides* by identical jaw dentition, a slender and cylindrical body, a relatively small orbit, and similar meristic counts. However, a detailed morphological revision of this Early Miocene croaker clearly shows that it does not fit the diagnosis of *Otolithoides* in many characters; therefore a new genus *Caucasisciaena* is erected here to accommodate it.

2. Methods

The specimens were examined using a Leica MS5 stereomicroscope equipped with a camera lucida drawing tube. Measurements were taken with a dial caliper, to the nearest 0.1 mm. Comparative data were derived mainly from the literature.

2.1. Abbreviations

ach: anterior ceratohyal; **ar**: articular; **bah**: basihyal; **br**: branchiostegal rays; **bsp**: basisphenoid; **cl**: cleithrum; **co**: coracoid; **d**: dentary; **f**: frontal; **h**: hyomandibula; **hyh**: hypohyals; **mx**: maxilla; **op**: opercle; **pas**: parasphenoid; **pch**: posterior ceratohyal; **pcl**: postcleithrum; **PIN**: Borisyak Paleontological Institute of the Russian Academy of Sciences, Moscow; **pmx**: premaxilla; **pop**: preopercle; **ptt**: posttemporal; **q**: quadrate; **ra**: pectoral-fin radial; **sca**: scapula; **scl**: supracleithrum; **SL**: standard length; **sop**: subopercle; **uh**: urohyal.

3. Systematic paleontology

Subdivision Teleostei *sensu* Patterson & Rosen, 1977.

Order Perciformes *sensu* Johnson & Patterson, 1993.

Family Sciaenidae Cuvier, 1829.

Genus *Caucasisciaena* gen. nov.

Etymology: generic epithet is after the Caucasus and the genus *Sciaena*; gender feminine.

Type species: *Perca ignota* Smirnov, 1936; Lower Miocene of the Caucasus and Crimea.

Diagnosis: body elongate, with slender caudal peduncle. Maximum body depth slightly more that 1/4 of SL. Head large, reaching at least 1/3 of SL. Orbit moderate. Parasphenoid with a dorsal rounded bony flange. Basisphenoid present. Mouth gape wide and terminal. Premaxilla with short ascending process forming obtuse angle with alveolar process. Ascending/alveolar process ratio about 0.17. Jaw teeth small, those of the outer series longer. Anterior premaxillary teeth slightly enlarged, but not canine-like. Preopercular serrations moderately developed and not numerous. Suspensorium not depressed dorso-ventrally. Posteriormost branchiostegal ray only moderately thickened. Posttemporal with few robust spines along posterior margin. Twenty-five vertebrae (11 + 14). Epineurals very slender. Three tiny supraneurals. Dorsal fin deeply notched, with 11 spines (two supernumerary) and 22 to 24 soft rays. Anal fin with two spines and 7 to 8 soft rays. Second anal-fin spine long and massive. Pectoral fin relatively long. Caudal fin truncate. Scales ctenoid on body and cycloid on head (except for one or two rows of ctenoid scales on cheek).

Species composition: type species only.

Caucasisciaena ignota (Smirnov, 1936) Figs. 2 and 3.

Perca ignota: Smirnov, 1936: 70, pl. IX, figs. 40, 42, pl. X, fig. 47b, pl. XI, figs. 3–6.

Larimus ignotus: Danilchenko, 1960: 125, pl. X, fig. 2, text-fig. 24; 1964, pl. XII, fig. 3; 1980: 134.

Lectotype: PIN 485/61, imprint of the skeleton (counterpart figured by Smirnov, 1936, pl. X, fig. 47b); Upper Maikopian, Lower Miocene of the Chernaya Rechka locality, North Ossetia, SW Russia.

Referred material: Upper Maikopian, Lower Miocene (all in PIN collection): type locality (1 specimen); left cliff of canyon 1 km southwest from Shirvanskaya village, Apsheronsk district, SW Russia (26 specimens); cape Tarkhan, Kerch peninsula, Crimea, Ukraine (3 specimens); bank of Sumgait River, Apsheron peninsula, Azerbaijan (1 specimen).

Diagnosis: as for the genus.

Measurements: SL of the lectotype 75 mm. SL of the referred specimens up to 100 mm. Other measurements (of the lectotype) as percentage of SL: head length from tip of snout to posterior border of opercle 37; maximum body depth 23; depth of caudal peduncle 9; distance between tip of snout and spiny dorsal fin 35; distance between tip of snout and soft dorsal fin 56; distance between tip of snout and anal fin 72; distance between pelvic fin and anal fin 33; length of base of spiny dorsal fin 20; length of base of soft dorsal fin 27; length of base of entire dorsal fin 48; length of base of anal fin 9; length of longest spine of dorsal fin 15; length of longest soft ray of dorsal fin 15; length of second spine of anal fin 17; length of pelvic-fin spine 13; preorbital distance 9; horizontal diameter of orbit 9; length of lower jaw 21.

Description: the body is relatively elongate, with a slender caudal peduncle (Fig. 3A). The caudal peduncle depth is 26–32% of the body depth. The head is relatively large, its length (tip of snout to posterior edge of opercle) 1.2–1.3 times larger than the body depth. The head length is contained 2.8–3.0 times in SL. The orbit is moderate, its diameter is 22–30% of the head length. The snout is short; its length is 23–25% of the head length. The dorsal and ventral profiles of the body are almost equally convex.

The neurocranial structures are difficult to interpret because of inadequate preservation (Fig. 3B). The neurocranium is relatively low, with the supraoccipital crest evidently poorly developed. The frontals are the largest bones of the skull roof. These bones are moderately cavernous. The ventral projection of the frontals appear to be absent. The ethmoid block is relatively short. The parasphenoid is rather robust and almost straight; it bears a broad dorsal flange characterized by rounded profile. The basisphenoid appears to be present.

No infraorbital bones are recognizable except for the remains of the elongate lachrymal.

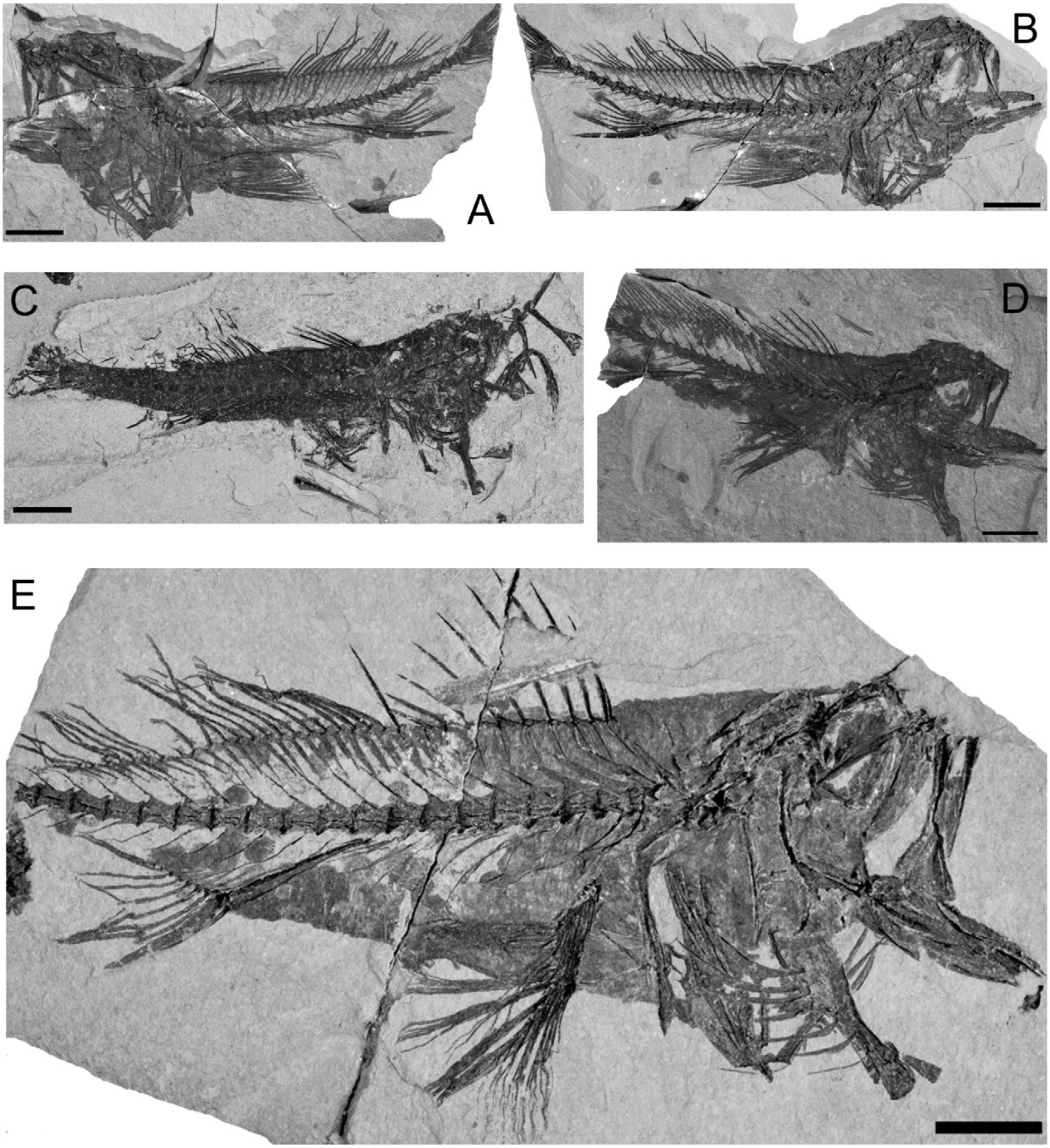

Fig. 2. *Caucasisciaena ignota* (Smirnov) from the Lower Miocene, Upper Maikopian. A. PIN 1413/820a. B. PIN 1413/820b. C. PIN 3974/12. D. PIN 1413/821. E. PIN 1413/819. A–B and D–E. Left cliff of ravine 1 km southwest from Shirvanskaya village, Apsheronsk district, SW Russia. C. Cape Tarkhan, Kerch peninsula, Crimea, Ukraine. Scale bars: 10 mm.

Fig. 2. *Caucasisciaena ignota* (Smirnov) du Miocène inférieur, Maikopien supérieur. A. PIN 1413/820a. B. PIN 1413/820b. C. PIN 3974/12. D. PIN 1413/821. E. PIN 1413/819. A–B et D–E. Escarpement gauche du ravin, 1 km au sud-ouest du village de Shirvanskaya, district d'Apsheronsk, Sud-Ouest de la Russie. C. Cap Tarkhan, péninsule de Kerch, Crimée, Ukraine. Barres d'échelle : 10 mm.

The mouth is wide and terminal (Fig. 3B). The lower jaw articulation is situated approximately under the posterior border of the orbit. The premaxilla has long and narrow alveolar process; its ascending process is distinct from articular process and relatively short. The ascending/alveolar process ratio is about 0.17, the ascending process forming obtuse angle with alveolar process. The postmaxillary process is broad but very low. The upper

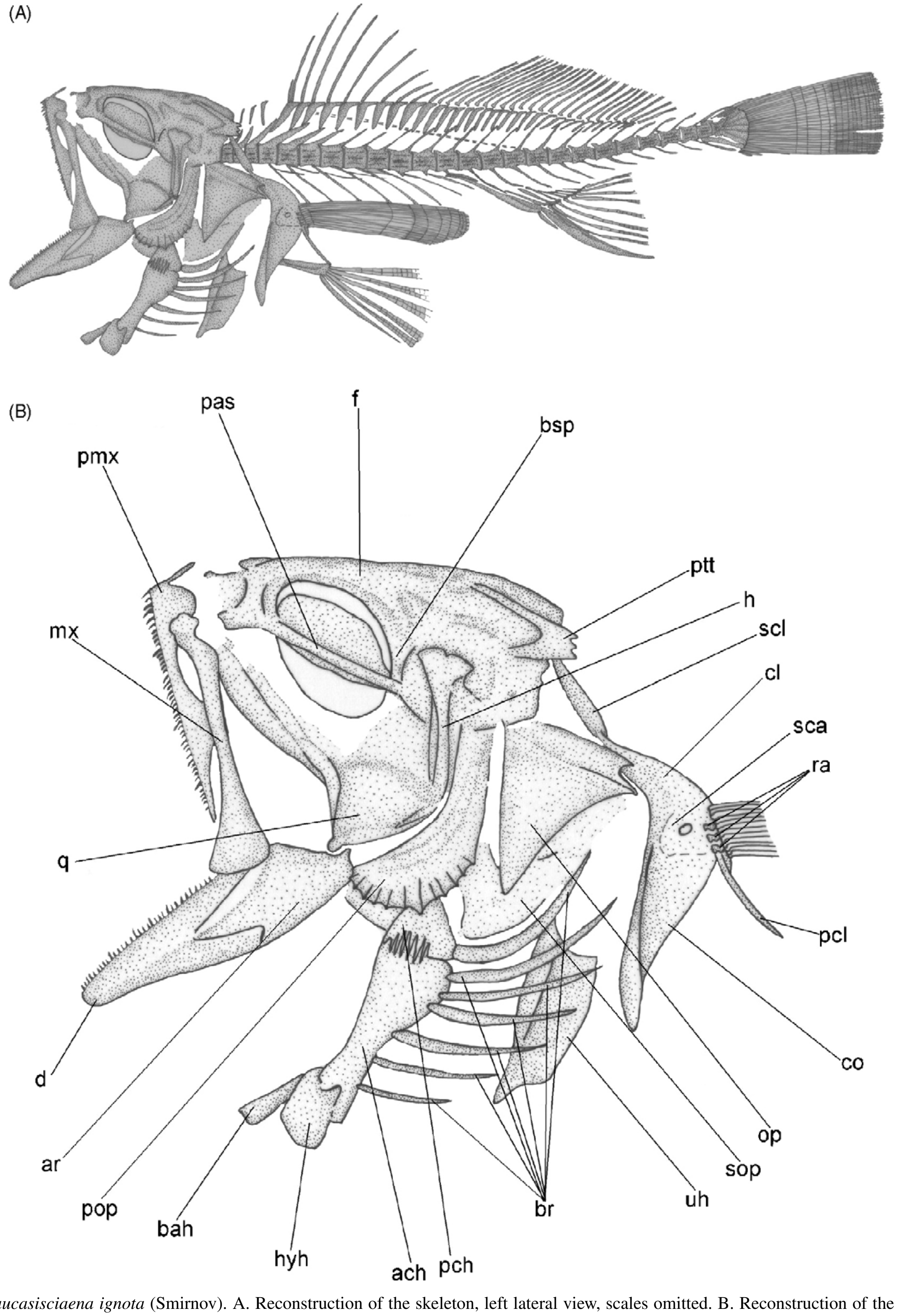

Fig. 3. *Caucasisciaena ignota* (Smirnov). A. Reconstruction of the skeleton, left lateral view, scales omitted. B. Reconstruction of the head, left lateral view.

Fig. 3. *Caucasisciaena ignota* (Smirnov). A. Reconstitution du squelette, vue latérale gauche, sans échelle. B. Reconstitution de la tête, vue latérale gauche.

jaw teeth are small, those of the outer series are longer than inner teeth. The anterior premaxillary teeth are slightly enlarged, but not canine-like. The maxilla is a long narrow bony shaft expanded distally; its posteroventral corner is slightly tapered. The lower jaw is relatively low; its length is 50–57% of head length. The dentary symphysis is low, without downward projection. The oral border of the dentary bears numerous small conical teeth, some of outer teeth are stronger.

The hyomandibula is rather robust, with two large articular heads; its shaft is slightly inclined posteroventrally. The quadrate is moderately large and triangular; its dorsal margin is difficult to interpret due to inadequate preservation. The symplectic, pterygoid bones and palatine are only partially preserved.

The opercular region is relatively narrow and not depressed dorso-ventrally. The preopercle is moderately curved. Preopercular serrations are moderately developed and not numerous. The opercle is roughly triangular, with two pungent spines, the lower of which is strengthened by bony ridge. The anterior margin of this bone is thickened while the posterior one is slightly concave. The subopercle is partially preserved in the lectotype.

The hyoid bar is well exposed in many specimens. The anterior ceratohyal is elongate, it is concave both dorsally and ventrally; the beryciform foramen is absent. The posterior ceratohyal is triangular; this bone contacts the anterior ceratohyal through a strongly interdigitating suture. Distinction between the hypohyals is obscured. The urohyal is a flattened laminar bone, with a thickened dorsal ridge characterized by an anteriorly directed process. There are seven sabre-like branchiostegal rays, six on the anterior ceratohyal plus one on the posterior one. Posteriormost branchiostegal ray is only moderately thickened. The basihyal is narrow and wedge-shaped. The bones of the branchial skeleton are indistinct.

There are 25 vertebrae, including the urostyle: 11 abdominal and 14 caudal. The axis of the vertebral column is almost straight. The vertebral centra are rectangular, longer than high and constricted in the middle. The length of the abdominal portion of the vertebral column is about 68–69% of the length of the caudal portion. The vertebral spines are relatively short, slightly curved, and very slender. The neural spines of the six anterior vertebrae are moderately expanded anteroposteriorly. The haemal spines of the anterior caudal vertebrae are strongly inclined. Short neural prezygapophyses can be easily observed, except in the anterior and posteriormost vertebrae. Parapophyses are scarcely recognizable in the abdominal vertebrae. The pleural ribs are slender and moderately elongate; these are strongly inclined posteroventrally. Few slender epineurals are recognizable in the abdominal cavity below the vertebral column.

The terminal centrum consists of fused first preural centrum plus two ural centra. The parhypural, two uroneurals, five hypurals, haemal spines of second and (perhaps) third preural centra are autogenous. A hypural diastema between the epaxial and hypaxial hypural plates 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 evidently a short crest. There are three slender epurals; the first is longest. The caudal fin is moderately long and truncated to slightly convex. There are 17 principal rays in the caudal fin (I,8–7,I); precise number of procurrent rays is unknown.

Two short and slender supraneurals are recognizable in some specimens; however, the existence of a third supraneural is evident in the remaining specimens. The dorsal fin is relatively long-based; it originates over the fifth vertebra and ends over the ninth or tenth caudal vertebra. There is a deep notch between the spiny and soft portions of the dorsal fin. There are 11 dorsal-fin spines and 22–24 soft segmented rays. The dorsal-fin spines are slender, the longest (fourth) spine 3.75–4.6 times longer than the shortest (first) spine. The last spine is 1.77–1.79 times longer than the penultimate spine. The first two dorsal-fin spines are supernumerary on the first dorsal-fin pterygiophore; these are closely spaced. The first two soft dorsal-fin rays are segmented but unbranched, whereas all the others are branched. The longest soft ray of the dorsal fin is almost as long as the longest dorsal-fin spine. The length of the base of the soft portion of the dorsal fin is 1.38–1.42 times longer than the base length of the spiny portion of the dorsal fin. The anterior dorsal-fin pterygiophores are expanded anteroposteriorly, and bear a longitudinal strengthening ridge; the succeeding pterygiophores gradually become narrower. Posteriorly in the series the pterygiophores become more strongly inclined and of decreased length.

The anal fin originates under the fifth caudal vertebra. The length of the base of the anal fin is rather short, approximately corresponding to the length of 2.5 vertebrae. There are two spines and seven or eight soft segmented rays in the anal fin; all of these are branched. The second anal-fin spine is about 4.5 times longer than the first spine; it is thick and bears tiny longitudinal grooves along the posterior margin. Both spines are supernumerary. The longest anal-fin soft ray almost equals in length to the longest dorsal-fin soft ray. The first anal-fin pterygiophore is long and sturdy, but relatively narrow; it is strongly inclined to the body axis. The succeeding anal-fin pterygiophores are slender and also strongly inclined; these quickly decrease in length posteriorly in the series. The posterior pterygiophore is almost horizontally oriented.

The posttemporal is forked and bears three or four robust spines along the posterior margin. The supracleithrum is an elongate bone. The cleithrum is large, crescent-shaped; its upper part is curved anteriorly and placed just under the third vertebra. The dorsal postcleithrum is hardly recognizable, whereas the posteroventrally directed ventral postcleithrum is rib-like and slender. The coracoid is definitely narrow. Both the scapula and pectoral radials are scarcely recognizable. The base of the pectoral fin is situated approximately under the sixth vertebra, near the midpoint between the vertebral column and the ventral profile of the body. The pectoral fin consists of about 14 rays and is relatively long. The pectoral-fin length is 24–28% of SL.

The pelvic bones usually are preserved as a single unit in dorso-ventral view. The pelvic fin contains a spine and five soft branched rays; it is inserted just behind the pectoral-fin base. The pelvic fin is rather long; the pelvic-fin spine is slender and only slightly shorter than the longest (second) anal-fin spine.

Moderately large scales cover the entire body and the head. Each body scale bears 6 to 8 radii in the basal field. Scales are ctenoid on the body and cycloid on the head (except for one or two rows of ctenoid scales on the cheek). The lateral line is in close proximity to the dorsal profile of the body below the third and fourth dorsal-fin spines; it descends to the level of the vertebral column near the fifth caudal vertebra.

4. Taxonomic placement and comparison

Because of their abundance, diversity and commercial value, fishes of the family Sciaenidae have been widely investigated from a taxonomical point of view. Many regional studies have been realized during the last five decades [5,7,17,31,32] and a comprehensive phylogenetic study has been published by Sasaki [25], who defined several synapomorphic features of this family. The morphological analysis of the material available has revealed a number of features that unquestionably support their assignment within the family Sciaenidae, including: frontals moderately cavernous, base of the soft dorsal fin greatly elongate (and much longer than anal-fin base), presence of two anal-fin spines, endoskeletal elements of the median fins not trisegmental, supramaxilla absent, a single branchiostegal ray on the posterior ceratohyal.

Being undoubtedly a sciaenid fish, *Caucasisciaena* possesses a unique combination of diagnostic features which strongly justifies its separation as a new genus. Many characters of relevant phylogenetic value [25] cannot be observed in *Caucasisciaena*, and some of characters diagnostic for the new genus are regarded as having limited phylogenetic value. Therefore, it is difficult to ascertain exact phylogenetic position of *Caucasisciaena* within the Sciaenidae. Many features diagnostic for the sciaenids at both generic and specific level refer to swimbladder, saccular otolith and musculature. All of these structures are evidently absent in the fossil sciaenid under consideration, mostly because they are not prone to the fossilization process. Moreover, some of the osteological characters (chiefly of the neurocranium) are also unknown in *Caucasisciaena ignota* because of inadequate preservation of the fossil material. Nevertheless, a comparative analysis of the detected diagnostic structures is very useful to establish the distribution of such features within the sciaenids.

The frontal of certain sciaenids, such as *Johnius*, *Kathala*, *Pseudotolithus*, and *Argyrosomus japonicus*, projects ventrally forming a bony interorbital septum, in association with the lateral ethmoid and parasphenoid [25]. This ventral projection has not been observed in the frontal of *Caucasisciaena*.

As reported above, *Caucasisciaena* possesses a basisphenoid; this bone is absent in some sciaenid genera, as *Lonchurus*, *Ophioscion*, *Panna*, *Otolithoides*, and *Stellifer* [25].

Most of the sciaenid genera have either inferior or oblique mouth. Unlike these, *Caucasisciaena* has terminal and unusually wide mouth similar to that of the certain species of the genera *Atractoscion*, *Otolithoides*, *Panna*, *Pennahia*, *Johnius*, *Cynoscion* [6,32]. Among the various types of the sciaenid jaw dentition figured by Sasaki [25] and Taniguchi [30], the new genus possesses that of *Otolithoides* and *Collichthys*. *Caucasisciaena ignota* has an exceptionally short ascending process of the premaxilla in relation to the other sciaenid genera: the ascending/alveolar process ratio is about 0.17 vs. 0.28 to more than 1.0 in other sciaenids [25,30].

The new genus lacks such synapomorphy of *Pachyurus* and *Pachypops* as the strongly depressed suspensorium [25].

The branchiostegal rays of *Caucasisciaena* have typical sciaenid number and distribution (six on the anterior ceratohyal and one on the posterior one), however, the last ray of *Caucasisciaena ignota* seems to be narrower than that of the recent sciaenids. The posterior margin of the posttemporal of sciaenids is fimbriated or finely serrated [25,32]. Posttemporal spines of the new genus are evidently stronger than in extant sciaenid genera.

Even though the number of vertebrae ranges between 24 and 30, the basic vertebrae complement of the family Sciaenidae is 25 [25,32]. As documented above, the vertebral column of *Caucasisciaena* contains 25 vertebrae; therefore, *Caucasisciaena* differs from the genera *Lonchurus*, *Paralonchurus*, *Pogonias* and certain species of the genus *Johnius* that possess a different vertebral number [5,32].

Caucasisciaena possesses an enormously developed second anal-fin spine, similarly to the extant genera *Bahaba*, *Bairdiella*, *Boesemania*, *Larimus*, *Macrospinosa*, *Pseudotolithes*, *Ophioscion* and certain species of *Nibea*.

Like in most of the extant genera, in front of the dorsal fin of *Caucasisciaena* there are three weak supraneurals. Such a condition is not shared by the genera *Otolithes*, *Otolithoides* and *Pterotolithus*, in which they may be absent [32], *Cynoscion*, *Macrodon*, and *Isopisthus* which possess only two elements, and *Equetus*, in which these are definitely absent [25].

Most sciaenids have short pectoral fins, whereas *Lonchurus* and *Paralonchurus elegans* are characterized by extremely elongate pectoral fins, which extend well beyond the anal-fin origin. The pectoral fins of *Caucasisciaena* are relatively elongate, intermediate between those of *Lonchurus* and *Paralonchurus* and those of the remaining genera, except *Atrobucca*, *Larimus*, *Micropogonias*, *Sonorolux* and some species of the genera *Johnius*, *Panna*, and *Stellifer* that closely resemble the Miocene genus [6,26,32].

The squamation pattern of *Caucasisciaena* seems to be unique within the sciaenids. This Miocene genus shows a peculiar distribution of ctenoid scales on the head, which are present on the cheek only; extant sciaenids display different pattern of ctenoid scales on the head, where they are usually present on the opercular region and top of head, or elsewhere behind the snout and subocular region [26].

As discussed in the Introduction section, the fossil record of the family Sciaenidae is primarily represented by otoliths, while articulated skeletal remains are rather rare. According to Bannikov [3], there are two Miocene skeleton-based genera of the Sciaenidae from California, *Lompoquia* and *Ioscion*. One more genus, *Pseudoumbrina* from the Pliocene of the Crimea, is hardly recognizable because of the imperfect preservation of the material. Nevertheless, based on the description of Menner [16], *Pseudoumbrina* differs from *Caucasisciaena* by larger number of dorsal-fin rays (29 vs. 22–24 in *Caucasisciaena*), smaller number of anal-fin rays (6 vs. 7–8 in *Caucasisciaena*) and larger number of radii in the basal scale field (9–10 vs. 6–8 in *Caucasisciaena*).

Ioscion morgani from the Californian Miocene is described based on a single incomplete specimen without the skull and anterior part of the body [12]. We wonder why David [11] refused its attribution to the Sciaenidae and suggested a carangid relationship. *Ioscion* shows the typical sciaenid configuration of unpaired fins (a combination of extended soft dorsal fin and short-based anal fin). Despite its incompleteness, *Ioscion* differs significantly from *Caucasisciaena* by its especially elongate body and shorter caudal portion of the vertebral column which consists of 12 rather than 14 vertebrae.

According to David [11], the other Miocene Californian sciaenid genus, *Lompoquia*, consists of two species: *Lompoquia retropes* and *Lompoquia culveri* [13,14]. Both have more vertebrae (12 + 14 = 26), much less numerous dorsal-fin rays (11–14), more numerous anal-fin rays (9–12) and lunate caudal fin, being therefore easily recognizable from *Caucasisciaena*.

In summary, the survey of the distribution of the main diagnostic features of the fossil sciaenid documented herein clearly indicates that it shows a unique combination of characters that unequivocally justify its attribution in a new separate genus. Unfortunately, such a survey did reveal neither the phylogenetic nor the possible phenetic relatives of *Caucasisciaena*. The incompleteness of the fossil material makes it extremely difficult the evaluation of the phylogenetic affinities of this new genus. The analysis of certain phylogenetically relevant features of the swimbladder and muscles [25] represents an insurmountable barrier for the study of fossil sciaenids, for which a well-supported integrated comparative study is evidently problematic because of the extremely reduced chances of preservation of these structures during the fossilization process.

5. Conclusions

Despite diversity and abundance of the fishes of the family Sciaenidae in tropical and subtropical coastal and estuarine waters all over the world, their articulated skeletal remains are rather rare in the fossil record. On the contrary, the sciaenid otolith record is extremely rich, particularly in the Neogene deposits [27]. This differential abundance is primarily related to the life habits of these fishes, since these bottom-dwelling carnivores are common in nearshore marine and brackish environments with oxygenated coarse-grained, sandy or soft grounds, where they feed on fishes or benthic invertebrates; these fishes are therefore absent or extremely rare in the depositional environments characterized by ecological or sedimentary features that allow the preservation of articulated skeletal remains (anoxic bottoms, microbial mats, etc.), whereas their preferred clastic depositional environments evidently favour the preservation of their large and massive otoliths. Therefore, given the rarity of sciaenid skeletal remains in the record, the description of a new sciaenid genus from the Sakaraulian deposits of the Caucasus and Crimea provides new significant information about the evolutionary history of a poorly known component of the Early Miocene ichthyological communities of Eastern Paratethys.

However, *Caucasisciaena ignota* does not represent the only Neogene Paratethyan representative of the family Sciaenidae. Three skeleton-based taxa from the Sarmatian deposits of the Caucasus and Ukraine and from the Pliocene of the Caucasus have been species assigned to genus *Sciaena* [10]. Moreover, the material referred to *Labrax multipinnatus* from the Sarmatian deposits of Croatia [15], subsequently assigned to the genus *Morone* by Anđelković [1], evidently belongs to the family Sciaenidae [3]; such a Sarmatian sciaenid clearly differs from *Caucasisciaena* by having 24 (rather than 25) vertebrae, a shorter premaxilla and a smaller second anal-fin spine [15]. Finally, the existence of several Paratethyan representatives of the genera *Argyrosomus*, *Atractoscion*, *Sciaena* and *Umbrina* was also testified by otoliths [24,27].

The genus *Caucasisciaena* apparently was endemic of the Paratethyan realm. A cursory survey of the Early Miocene assemblage of eastern Paratethys reveals the presence of some endemic genera (*Bestiolablennius*, *Bregmacerina*, *Lednevia*, *Onobrosmius*, *Palaeomolva*), within communities characterized by a mixture of widely distributed (*Alosa*, *Aulostomus*, *Caranx*, *Echeneis*, *Glossanodon*, *Merluccius*, *Priacanthus*, *Sardinella*, *Sarda*, *Scomber*, *Selar*, *Seriola*, *Syngnathus*), Atlantic-Mediterranean (*Buglossidium*, *Nerophis*, *Spicara*), Indo-Pacific (*Aeoliscus*, *Alepes*, *Scomberoides*) and Oligocene relict (*Anenchelum*, *Caprovesposus*, *Pinichthys*, *Leiognathoides*) taxa.

Like other sciaenids, *Caucasisciaena* probably inhabited the shallow water biotopes close to the coasts of the Paratethyan basin; such hypothesis seems to be consistent with the taxonomic composition of the associated biota, even if the presence of epipelagic and outershelf taxa indicates also the existence of deeper waters in the vicinity of the depositional environments.

As reported above, the dentition of *Caucasisciaena* greatly resembles that characteristic of the genus *Otolithoides*, thereby suggesting a similar diet; fishes belonging to the genus *Otolithoides* primarily feed on small fishes, prawns and invertebrates [18].

Acknowledgements

The visit of the senior author to Pisa was made possible by grant of the CNR-Russian Academy of Sciences exchange program, thanks to its Russian coordinator S.V. Popov. We are particularly obliged to Pierluigi Scaramozzino (Museo di Storia Naturale e del Territorio, Università di Pisa) for the photographs. Sandra Raredon (National Museum of Natural History, Smithsonian Institution, Washington) kindly provided radiographs of extant sciaenids. We thank two anonymous reviewers whose criticism and suggestions allowed the improvement of the manuscript. Thanks also are due to Federica Giudice for improvement of the English. The research of the senior author was supported by the Russian foundation for basic research, grant No. 08-05-00654.

References

[1] J.S. Anđelković, Tertiary fishes of Yugoslavia. A stratigraphic-paleontologic-paleoecological study, Paleont. Jugosl. 38 (1989) 1–121.
[2] A.F. Bannikov, Fossil scombrids of the USSR, Trudy Paleontol. Inst. Acad. Sci. USSR 210 (1985) 1–111 (in Russian).
[3] A.F. Bannikov, Fossil vertebrates of Russia and adjacent countries. Fossil Acanthopterygian fishes (Teleostei, Acanthopterygii), GEOS, Moscow, in press (in Russian).
[4] G. Carnevale, A.F. Bannikov, W. Landini, C. Sorbini, Volhynian (Early Sarmatian sensu lato) fishes from Tsurevsky, North Caucasus, Russia, J. Paleont. 80 (2006) 684–699.
[5] N.L. Chao, A basis for classifying western Atlantic Sciaenidae (Teleostei: Perciformes), NOAA Tech. Rep. Circ. 415 (1978) 1–64.
[6] N.L. Chao, Sciaenidae, in: W. Fisher, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter, V.H. Niem (Eds.), Guia FAO para la identificación para los fines de la pesca, 2, Pacifico centro-oriental, 1995, pp. 1427–1518.
[7] Y.T. Chu, Y.L. Lo, H.L. Wu, A study on the classification of the sciaenoid fishes of China, with description of new genera and species, in: Sci. Tech, Press Shangai, Shangai, 1963, pp. 1–100 (in Chinese).
[8] P.G. Danilchenko, Bony fishes of the Maikop deposits of the Caucasus, Trudy Paleontol. Inst. Acad. Sci. USSR 78 (1960) 1–208 (in Russian).
[9] P.G. Danilchenko, Superorder Teleostei. Bony fishes, in: D.V. Obruchev (Ed.), Fundamentals of Paleontology, Agnathans, Fishes, Nauka, Moscow, 1964, pp. 396–472 (in Russian).
[10] P.G. Danilchenko, Orders Lampridiformes, Beryciformes, Zeiformes, Perciformes, Echeneiformes, Tetraodontiformes, Trudy Paleontol. Inst. Acad. Sci. USSR 178 (1980) 91–96, 99–104, 115–169, 173–174 (in Russian).
[11] L.R. David, Miocene fishes of southern California, Spec. Pap. Geol. Soc. Am. 43 (1943) 1–193.
[12] D.S. Jordan, The fish fauna of the California Tertiary, Stanford Univ. Publ. Univ. Ser. Biol. Sci. 1 (1921) 235–300.
[13] D.S. Jordan, The fossil fishes of the Miocene of Southern California. Contribution no. VIII, Stanford Univ. Publ. Univ. Ser. Biol. Sci. 4 (1925) 1–51.

[14] D.S. Jordan, J.Z. Gilbert, Fossil fishes of Southern California, Stanford Univ. Publ. (1919) 1–98.
[15] D. Kramberger-Gorjanovic, Die jungtertiäre Fishfauna Croatiens, Beitr. Paläont. Österreich-Ungarns Orients 2 (1882) 86–135.
[16] V.V. Menner, Sciaena from the Kimmeridgan deposits of the Kerch Peninsula, Probl. Theor. Pract. Geol. 5 (1948) 23–31 (in Russian).
[17] R.S.L. Mohan, A synopsis of the Indian genera of the fishes of the family Sciaenidae, Indian J. Fish. 16 (1972) 82–98.
[18] R.S.L. Mohan, Sciaenidae, in: W. Fischer, G. Bianchi (Eds.), FAO species identification sheets for fishery purposes, western Indian Ocean (Fishing Area 51) 4 (1984) 1–34.
[19] J.S. Nelson, Fishes of the world, fourth edition, John Wiley & Sons Inc, Hoboken, 2006, 601 p.
[20] L.A. Nevesskaya, E.I. Kovalenko, E.V. Beluzhenko, S.V. Popov, I.A. Goncharova, G.A. Danukalova, I.Y. Zhidovinov, A.V. Zaitsev, A.S. Zastrozhnov, L.B. Iljina, N.P. Paramonova, T.N. Pinchuk, N.S. Pis'mennaya, A.K. Agadjanian, A.V. Lopatin, V.M. Trubikhin, Explanatory Note to the unified regional stratigraphical scheme of the Neogene deposits of the Southern regions of the European part of Russia. Paleontol. Inst. Russ. Acad. Sci., Moscow, 2004, 83 pp. (in Russian).
[21] D. Nolf, Studies on fossil otoliths – The state of the art, in: D.H. Secor, J.M. Dean, S.E. Campana (Eds.), Recent developments in fish otolith research, University of South Carolina Press, 1995, pp. 513–544.
[22] D. Nolf, O. Aguilera, Fish otoliths from the Cantaure Formation, Bull. Inst. R. Sci. Nat. Belgique 68 (1998) 237–262.
[23] S.V. Popov, E.M. Bugrova, O.V. Amitrov, A.S. Andreyeva-Grigorovich, M.A. Akhmetiev, N.I. Zaporozhets, I.A. Nikolaeva, E.K. Sychevskaja, I.G. Shcherba, Biogeography of the northern Peri-Tethys from the Late Eocene to the Early Miocene. Pt 3. Late Oligocene – Early Miocene. Marine basins, Paleontol. J. (Suppl.) 38 (2004) 653–716.
[24] U. Radwańska, Fish otoliths in the Middle Miocene (Badenian) deposits of southern Poland, Acta Geol. Pol. 42 (1992) 141–328.
[25] K. Sasaki, Phylogeny of the family Sciaenidae, with notes on its zoogeography (Teleostei, Perciformes), Mem. Fac. Fish. Hokkaido Univ. 36 (1989) 1–137.
[26] K. Sasaki, Family Sciaenidae, in: K.E. Carpenter, V. Niem (Eds.), FAO species identification for fishery purpose. 5 (2001) 3117–3174, The living marine resources of the western Central Pacific.
[27] W. Schwarzhans, A comparative morphological treatise of recent and fossil otoliths of the family Sciaenidae (Perciformes), Piscium Catalogus: Part Otolithi piscium 1 (1993) 1–245.
[28] V.P. Smirnov, Fishes of the North Caucasian Oligocene (Chernaya Rechka District), Trudy Uzb. State Univ. 1 (1936) 1–92 (in Russian).
[29] E.K. Sytchevskaya, Late Oligocene – Early Miocene history of the ichthyofauna of Eastern Paratethys, Kaupia, Darmst. Beitr. Naturges. 14 (2005) 65–67.
[30] N. Taniguchi, Comparative osteology of the sciaenid fishes from Japan and its adjacent waters-III. Premaxillary and dentary, Japan, J. Ichthyol. 17 (1970) 135–140.
[31] E. Trewavas, A basis for classifying the sciaenid fishes of tropical West Africa, Ann. Mag. Nat. Hist. 13 (1962) 167–176.
[32] E. Trewavas, The sciaenid fishes (croakers or drums) of the Indo-West-Pacific, Trans. Zool. Soc. London 33 (1977) 253–541.