C. R. Palevol 13 (2014) 691–700

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

General palaeontology, systematics and evolution (Vertebrate palaeontology)

Revision of the family Propercarinidae (Perciformes, Stromateoidei) with description of a new species from the Oligocene of the Carpathians

Révision de la famille des Propercarinidae (Perciformes, Stromateoidei), avec la description d'une nouvelle espèce de l'Oligocène des Carpates

Tomáš Přikryl[a,*], Alexandre F. Bannikov[b], Ionuţ Grădianu[c], Iwona Kania[d], Wiesław Krzemiński[e]

[a] *Institute of Geology, Academy of Sciences of the Czech Republic, v.v.i., Rozvojová 269, CZ-165 00 Prague 6, Czech Republic*
[b] *Borisyak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow 117997, Russia*
[c] *Natural Science Museum, Petru Rares No. 26, 610119 Piatra Neamt, Romania*
[d] *Department of Environmental Biology, Faculty of Biology and Agriculture, University of Rzeszow, Zelwerowicza 4, 35-959 Rzeszow, Poland*
[e] *Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, ul. Św. Sebastiana 9, 31-049 Kraków, Poland*

ARTICLE INFO

Article history:
Received 26 May 2014
Accepted after revision 15 July 2014
Available online 16 September 2014

Handled by Danièle Grosheny

Keywords:
Perciformes
Stromateoidei
Propercarinidae
Bony fish
Oligocene

ABSTRACT

The monotypic fish family Propercarinidae (Perciformes, Stromateoidei) was found in the Paratethys area only; it is represented by the genus *Propercarina* Paucă, 1929, whose two species were originally described from the Oligocene deposits of Romania. The material of these species was revised, and new Oligocene specimens from the Polish and Romanian Carpathians allowed the description of a new species, *P. problematica* sp. nov. The morphology of Propercarinidae was compared with that of extant stromateoids revealing a mixture of primitive and relatively advanced features in the family Propercarinidae.

Mots clés :
Perciformes
Stromateoidei
Propercarinidae
Poissons osseux
Oligocène

RÉSUMÉ

La famille de poissons monotypes des Propercarinidae (Perciformes, Stromateoidei) a été trouvée uniquement dans le domaine de la Paratéthys ; elle est représentée par le genre *Propercarina* Paucă, 1929, dont deux espèces ont été initialement décrites dans les formations oligocènes de Roumanie. Le matériel fourni par ces deux espèces a été révisé et de nouveaux spécimens oligocènes des Carpates roumaines et polonaises a permis la

* Corresponding author.
E-mail addresses: prikryl@gli.cas.cz (T. Přikryl), aban@paleo.ru (A.F. Bannikov), igradianu@hotmail.com (I. Grădianu), iwonakania@onet.eu (I. Kania), wieslawk4@gmail.com (W. Krzemiński).

http://dx.doi.org/10.1016/j.crpv.2014.07.001
1631-0683/

description d'une nouvelle espèce, *P. problematica* sp. nov. La morphologie des Propercarinidae a été comparée à celle de stromatéoïdés vivants, révélant un mélange de traits primitifs et relativement avancés dans la famille des Propercarinidae.

1. Introduction

The isolation of the Paratethys realm from the Mediterranean area began during the Eocene/Oligocene transition. During the early Oligocene (Rupelian or the equivalent lower Kiscellian Paratethys stage of central and eastern Europe), the Paratethys was connected to the Mediterranean just in its western region (and maybe also one more small communication space in the eastern part; for details and references see Schultz et al., 2005). This process led to the origin of highly specific and sometimes anoxic environments inhabited by the fish assemblages characterized by many endemic fish forms. One such case is represented by the fish genus *Propercarina* Paucă, 1929, described based on several specimens from the Romanian lower Oligocene deposits. In the original description (Paucă, 1929), two species of this genus were described but not illustrated. The emended diagnosis of the genus and both species were published soon after with the photos and a schematic reconstruction (Paucă, 1934). In both publications, a relation was suggested between *Propercarina* and the Recent percid genus *Percarina* Nordmann, 1840 from the Black Sea basin based on their superficial similarity. Now *Propercarina* is considered as a putative stromateoid fish (mostly due to the numerous characteristics similar to those of the Recent family Amarsipidae; Bannikov, 1995). According to Nelson (2006: 434), the suborder Stromateoidei is characterized by a toothed saccular outgrowth in the gullet (except in the amarsipids); a lachrymal bone covering most of the maxilla; scales usually cycloid, weakly ctenoid in some; 5–7 branchiostegal rays; 2–5 hypural plates; caudal fin with 15 branched rays; and 24–61 vertebrae. The suborder is traditionally restricted to the six Recent families (Doiuchi et al., 2004; Horn, 1984; Nelson, 2006); however, the fossil family Propercarinidae was also tentatively regarded as a stromateoid (Bannikov, 1995).

The fossils of the genus *Propercarina* were only collected in the Paratethys area, and for a relatively long period of time *Propercarina* was regarded as a problematic taxon, which was not accepted by some authors at all (see discussion below). Here, we present a revision of the family together with the description of a new species from the Polish and Romanian Carpathians, comparison with similar forms and notes that should clarify relationships of this taxon.

2. Material and methods

The specimens were mechanically prepared by small scalpels and needles or left unprepared. The fossil specimens are listed in the systematic part. The comparative X-ray figure of *Amarsipus carlsbergi* Haedrich, 1969 was provided by Prof. N.V. Parin from the material used by Konovalenko and Piotrovskiy (1988). Other data regarding this specimen including its size, sex and locality are missing.

Anatomical abbreviations: A – anal fin; ang – angulo-articular; BD – body depth; br – branchiostegal rays; C – caudal fin; ce – ceratohyal; cl – cleithrum; CPD – caudal peduncle depth; CPL – caudal peduncle length; D1 – first dorsal fin; D2 – second dorsal fin; d – dentary; ect – ectopterygoid; en – epineurals; epu – epuralia; fr – frontal; HD – head depth; hm – hyomandibular; HL – head length; hs – haemal spine; hyp – hypural; mx – maxilla; na – nasal; ns – neural spine; op – opercle; orb – orbit; P – pectoral fin; pal – palatine; pd – predorsals; pel – pelvis; pcl – postcleithrum; php – parhypural; pop – preopercle; pmx – premaxilla; preA – preanal length; preD1 – length anterior to first dorsal fin; preD2 – length anterior to second dorsal fin; preO – preorbital length; psph – parasphenoid; pst – posttemporal; pu – preural vertebra; r – rib; q – quadrate; scl – supracleithrum; SL – standard length; TL – total length; uh – urohyal; un – uroneural; us – urostyle; V – pelvic fin.

Institutional abbreviations: GA (Grigore Antipa Museum, Bucharest, Romania), NMB (National Museum of Geology in Bucharest, Romania), PAS (Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland), PNM (Piatra Neamţ Museum of Natural History, Romania).

The arrangement of the dorsal- and anal-fin pterygiophores to the neural and haemal spines, respectively, follows Ahlstrom et al. (1976); therefore, each slash represents a neural or haemal spine and inserted numbers are numbers of spines or rays associated with the appropriate pterygiophore housed in the interneural (interhaemal) space. The number zero is used for predorsals (i.e., supraneurals) and for ray-less interneurals (between the first and second dorsal fins). The urostyle is included in the vertebral count.

Not all of the original specimens published by Paucă were identified and located. Although at least seven specimens of this genus were mentioned by Paucă (1934), we were able to find only four original specimens from the Suslaneşti-Muscel locality (one specimen is identifiable only to the generic level and it is not included). The specimen from Gura Humorului (PNM 864) was discovered in 2009 in the Lower Dysodilic Shale Formation (Tarcău Nappe) and was described earlier in an unpublished thesis by one of us (I.G. 2010).

3. Systematic part

Order: Perciformes Bleeker, 1859
Suborder: STROMATEOIDEI *sensu* Haedrich, 1967
Family: Propercarinidae Bannikov, 1995

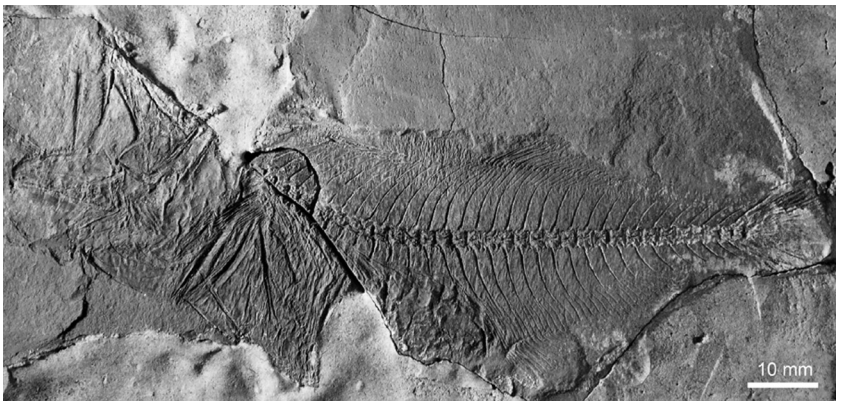

Fig. 1. *Propercarina rebeli* Paucă, 1929. Holotype specimen NMB P50119.
Fig. 1. *Propercarina rebeli* Paucă, 1929. Spécimen holotype NMB P50119.

Type genus: *Propercarina* Paucă, 1929
Diagnosis: As for the genus.

Genus: *Propercarina* Paucă, 1929
Type species: *Propercarina rebeli* Paucă, 1929 (designated by Bannikov, 2010).

Emended diagnosis (according to Paucă, 1929, 1934 and Bannikov, 1995, 2010, modified): Body elongated. Dorsal and ventral edges of body are almost parallel and they run alongside the axis of the vertebral column; the body is covered by small cycloid scales; the lateral line is parallel to the dorsal edge of the body and runs just dorsal to the vertebral column; massive but short preorbital area (snout); mouth gap is moderate; jaws possess teeth; ventral edge of the preopercle smooth; the postcleithrum is massive and long (almost reaching the ventral profile of body); three predorsals; two separated dorsal fins (first with six to nine spines; second with one spine and numerous posteriorly shortened soft rays); the dorsal fins are separated by about 5 or 6 ray-less interneurals; anal fin with two short spines and numerous soft rays; anal-fin rays more numerous than soft dorsal-fin rays; pectoral fins are relatively short and situated just under the level of the vertebral column; pelvic fins with a spine and 5 rays, located under pectoral fins, present in adults; caudal fin is moderately long and forked; 35–36 rectangular vertebrae with the posterior abdominal ones bearing long parapophyses with associated thin and long ribs.

Propercarina rebeli Paucă, 1929 (Fig. 1)

1929 *Propercarina rebeli*; Paucă: 3.
1934 *Propercarina rebeli* Paucă; Paucă: 622, pl. IV, fig. 7.
1961 *Palimphyes brevis* Agassiz; Gorbatch: 135, pl. II, figs 2, 3.
1995 *Propercarina* cf. *P. rebeli* Paucă; Bannikov: 179, fig. 2.
1996 *Palimphyes* cf. *P. chadumicus* Danilchenko; Micklich and Parin: 139, fig. 16.
1999 *Palimphyes rebeli* (Paucă); Constantin: 127.
2010 *Propercarina* cf. *P. rebeli* Paucă; Bannikov: 152.

Holotype: specimen NMB P50119; Rupelian of Suslaneşti-Muscel, Romania.

Emended diagnosis (according to Paucă, 1934, modified): The species differs from other species in lower number of spines in the first dorsal fin (VI vs. VII in *P. pietschmanni* and VIII or IX in *P. problematica* sp. nov.); lower number of rays in the second dorsal fin (I + 23 vs I + 27 in *P. pietschmanni* and 25 probably with first spinous in *P. problematica* sp. nov.); and lower number of rays in anal fin (II + 32) than in *P. pietschmanni* (II + 40), but more than in *P. problematica* sp. nov. (28 rays–spines are not recognizable).

Localities: The species was described from Romania (Paucă, 1929, 1934) and the Ukraine (Gorbatch, 1961), and figured from the Mainz basin (Micklich and Parin, 1996) and Poland (Bannikov, 1995).

Remarks: The species is relatively bulky (the proportions are not influenced by the fossilization process) with maximum body depth between the dorsal fins; head is probably deeper (or equally deep) than long; body depth is about ¼ of SL. The lower jaw articulation seems to be under the posterior part of the orbit. The teeth are

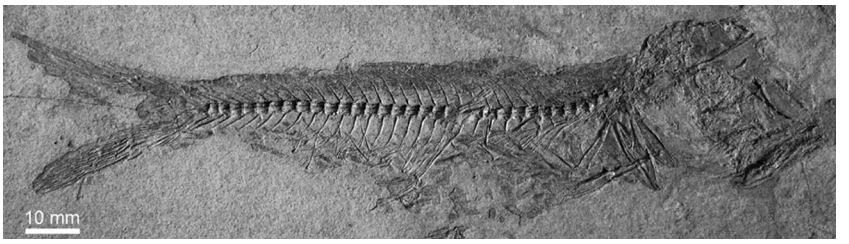

Fig. 2. *Propercarina pietschmanni* Paucă, 1929. Specimen NMB P50067.
Fig. 2. *Propercarina pieschmanni* Paucă, 1929. Spécimen NMB P50067.

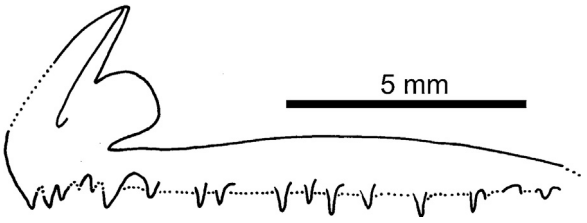

Fig. 3. *Propercarina pietschmanni* Paucă, 1929. Premaxilla of specimen NMB P50067.
Fig. 3. *Propercarina pietschmanni* Paucă, 1929. Premaxilla du spécimen NMB P50067.

strong and well developed in upper and lower jaws. The opercle has one "spine" in the postero-dorsal edge of the bone. The second spine of the first dorsal fin is the longest one. Although specimen NMB P50119 is not complete, it is possible to recognize the interneural formula as follows/0/0 + 1?/1 + 1/1/1/1/0/0/0/0/0/1/1/1/1 + 1 + 1/1 + 1/1 + 1/1 + 1/1 + 1 + 1/1 + 1/1 + 1 + 1/1 + 1 + 1/1. Only two supraneurals are recognizable due to the state of preservation. The fifth rayless interneural bone is in contact with the neural spine of the twelfth preserved abdominal vertebra. The interhaemal formula is probably 2/1 + 1 + 1 + 1/1 + 1 + 1/1 + 1/1 + 1 + 1/1 + 1 + 1/1 + 1/1 + 1 + 1/1 + 1 + 1 + 1/1 + 1/1 + 1 + 1/1 + 1, but the anterior part of the fin and its supportive skeleton is compressed and, therefore, hardly recognizable.

Propercarina pietschmanni Paucă, 1929 (Figs. 2, 3)

1929 *Propercarina pietschmanni*; Paucă: 3.

1934 *Propercarina pietschmanni* Paucă; Paucă: 623, text fig. 19, pl. IV, fig. 6.

1999 *Palimphyes pietschmanni* (Paucă); Constantin: 127.

Holotype: location unknown; Rupelian of Suslaneşti-Muscel, Romania.

Referred specimens: specimens NMB P50067, GA 11007/62.

Emended diagnosis: The species differs from other species by the presence of VII spines in the first dorsal fin vs. VI in *P. rebeli* and VIII or IX in *P. problematica* sp. nov.; higher number of second dorsal-fin rays (I + 27 vs. I + 23 in *P. rebeli* and 25 probably with first spinous in *P. problematica* sp. nov.); and greater number of rays in the anal fin (II + 40 vs. II + 32 in *P. rebeli* and 28 with unrecognizable spines in *P. problematica* sp. nov.).

Localities: The species was described only from Romania (Paucă, 1929, 1934).

Remarks: In comparison with *P. rebeli, P. pietschmanni* seems to be a more elongated species. Body depth is about 1/5 of the SL. The premaxilla (Fig. 3) bears strongly postero-dorsally oriented ascending and articular processes (they are divided by a small notch on the lingual side) and with no postmaxillary process. The alveolar process of the premaxilla bears numerous relatively large teeth on the ventral edge. Similar teeth are also developed in the lower jaw. The opercle has one "spine" in the postero-dorsal edge of the bone. The anterior part of D1 is not preserved sufficiently in GA 11007/62 (only one supraneural is visible). The last interneural bone (i.e., fifth) is in contact with the neural spine of the twelfth preserved abdominal vertebra. The second dorsal fin originates about seven vertebrae behind the end of the D1. The interneural formula is/0 + 1/1/1 + 1/1/1/1/0/0/0/0/0/1/1/1 + 1/1 + 1/1 + 1 /1 + 1 + 1/1 + 1/1 + 1/1 + 1/1 + 1/1 + 1/1 + 1/1. The interhaemal formula is 2/1 + 1/1 + 1 + 1/1 + 1/1 + 1 + 1/1 + 1 + 1/1 + 1/1 + 1 + 1/1 + 1/1 + 1 + 1/1 + 1/1 + 1 + 1/1 + 1 + 1, but posteriorly only fin rays are visible (with no preserved pterygiophores).

Propercarina problematica sp. nov. (Figs. 4–8)

Holotype: specimen PAS, part Pi-F/MP/170a/1626/14 and counterpart Pi-F/MP/170b/1626/14.

Diagnosis: This species differ from the other species in the greater number of spines in the first dorsal fin (VIII or IX vs. VI in *P. rebeli* and VII in *P. pietschmanni*); by presence of 25 rays (first is probably spinous) in the second dorsal fin vs. I + 23 in *P. rebeli* and I + 27 in *P. pietschmanni*; lower number of rays in anal fin (28 rays with unrecognizable spines vs. II + 32 in *P. rebeli* and II + 40 in *P. pietschmanni*); and by presence of small teeth on the premaxilla (vs. relatively large teeth in the other species).

Derivation of name: the species name refers to some enigmatic characters of this propercarinid species.

Horizon and locality: Oligocene diatomites, Hermanowa locality, Poland (IPM2 zone according to Kotlarczyk and Jerzmańska, 1976; Kotlarczyk et al., 2006). The specimen was collected from the "R" layer (manuscript in preparation). Associated fish fauna of the appropriate layer is represented by *Anenchelum glarisianum*, *Glossanodon muscelli*, *"Clupea" sardinites*, *Palaeogadus simionescui*, *Eophycis* cf. *E. jamnensis*, *Centriscus* sp., *Trachinus minutus*, *Holosteus* sp., *Ammodytes* cf. *A. antipai*, Gadidae and Perciformes (scales and unidentified fragments of skeletons).

Referred specimens: specimens PNM 864 (part and counterpart), Tarcău Nappe, Lower Dysodilic Shale Formation, Oligocene (Gura Humorului, northern Romania).

Description and remarks: The holotype is represented by a complete fish skeleton with large head and elongated body (the elongation of the body is similar to that of *P. pietschmanni*). The measurements and their percentage of HL and SL are displayed in Table 1.

The head is approximately as long as deep. The neurocranium is moderately deep. The frontals are wider in their posterior part and border the upper edge of the orbit. The bones of the ethmoid region are hardly distinguishable except for the nasal bones. The parasphenoid seems to be strong and running through the lower third of the orbit. The orbit is large, somewhat bigger than the preorbital distance, but smaller than the postorbital distance. The circumorbitals are not discernable. The otic part of the skull is crushed and unclear. The viscerocranium is moderately well preserved. The mouth is oblique. The premaxilla bears teeth but other details are not observable. The maxilla seems to be strong with a bulky maxillary head. The supramaxilla seems to be absent. In the anterior part of the palato-quadrate complex (probably on the ventral surface of the palatine) teeth are developed. The vomer is not observable. The quadrato-articular joint is situated

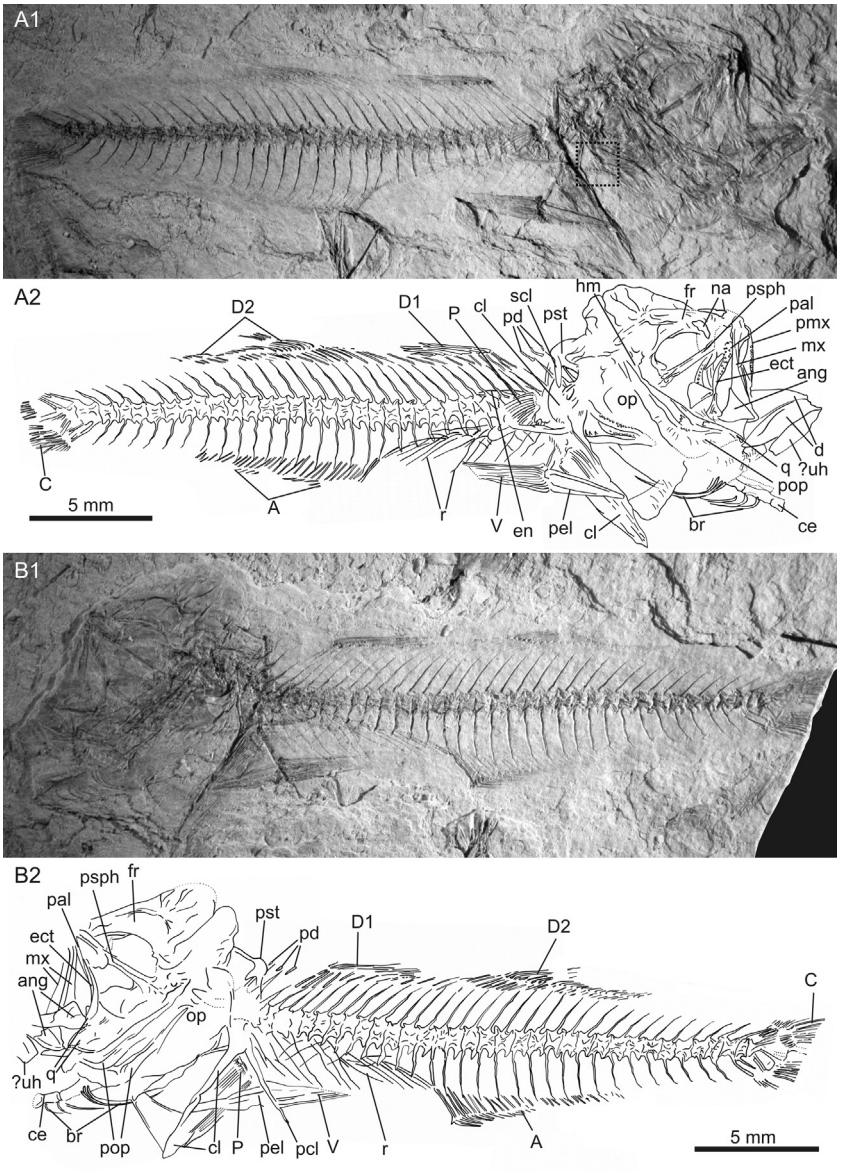

Fig. 4. *Propercarina problematica* sp. nov., holotype. A1 – specimen PAS Pi-F/MP/170a/1626/14; A2 – its interpretation; B1 – counterpart specimen PAS Pi-F/MP/170b/1626/14; B2 – its interpretation. Marked area figured in Fig. 5.
Fig. 4. *Propercarpina problematica* sp. nov., holotype. A1 – Spécimen PAS Pi-F/MP/170a/1626/14 ; A2 – son interpretation ; B1 – contre-empreinte du spécimen PAS Pi-F/MP/170b/1626/14 ; B2 – son interprétation. La zone concernée est représentée sur la Fig. 5.

vertically at the level of the middle of the orbit or slightly posteriorly. The dentary seems to be toothless in the holotype, but teeth are present on the dentary of specimen PNM 864.

The hyomandibula is not recognizable completely, but its articular head is more or less distinguishable in the postorbital area. The preopercular vertical limb is about twice as long as the horizontal one. The posterior edge of the preopercle is smooth. The other bones of the opercular series are not recognizable, but it is possible to tentatively determine the position of the opercle with no traces of a spine. The ceratohyal and epihyal are thin. The presence of a beryciform foramen is not known. There are six branchiostegal rays. An imprint of the toothed last branchial arch is present between the opercular region and pectoral girdle of the holotype (see Fig. 5). The preserved teeth are about 0.2 mm length, these are straight or slightly curved. Their original arrangement is not known.

The vertebral column consists of 36 (14 or 15 abdominal and 21 or 22 postabdominal) vertebrae – for discussion see below. There are well-developed, elongated parapophyses in the posterior part of the abdominal portion of the vertebral column. There are nine to ten pairs of ribs; the last rib is associated with the 15th vertebra. Epineurals are present and they are distributed at the lateral side of the neural arches in the anterior part of the vertebral column and

Table 1
Measurements of the holotype *Propercarina problematica* sp. nov.
Tableau 1
Mensurations de l'holotype *Propercarina problematica* sp. nov.

	mm	% of SL	% of HL
SL	33		
TL	ca 35		
HL	10	30.3	
HD	8		80
preO	1.6		16
orb	2.2		22
BD	8.5	25.8	
preD1	13.3	40.3	
preD2	20.4	61.8	
preA	18.9	57.3	
CPL	6.5	19.7	
CPD	2.3	7	

SL: standard length; TL: total length; HL: head length; HD: head depth; preO: preorbital length; orb: orbit; BD: body depth; preD1: length anterior to first dorsal fin; preD2: length anterior to second dorsal fin; preA: preanal length; CPL: caudal peduncle length; CPD: caudal peduncle depth.

at the lateral side of the ribs in the posterior part of the abdominal portion (the series show a gradual displacement ventrally).

The pectoral fin is relatively short and it is composed of 16 to 18 rays. The posttemporal is V-shaped. The supracleithrum is short. The cleithrum is not well preserved, but its ventral part seems to be more robust than the dorsal part. The lamina posteroventralis cleithri is well developed. The postcleithrum is massive and long.

The pelvic fin is represented by one spine and probably five soft rays as expected for most of perciforms. The pelvic bone has the shape of an elongated triangle, with no posterior projections.

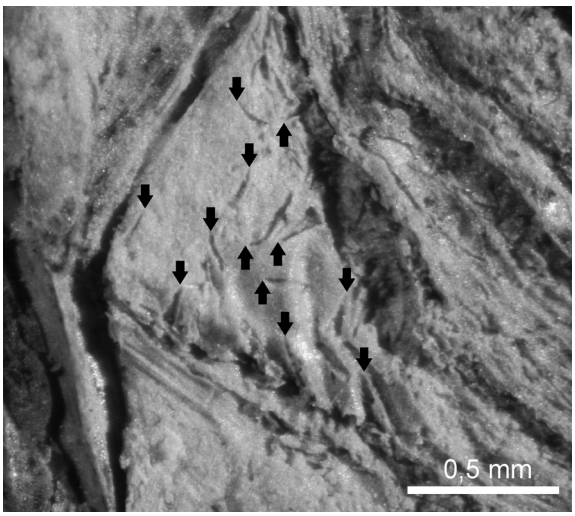

Fig. 5. *Propercarina problematica* sp. nov., holotype (PAS Pi-F/MP/170a/1626/14). Detail of the area between the opercular region and pectoral girdle with well-discernible pharyngeal teeth (their tips marked by arrows). Anterior to right.
Fig. 5. *Propercarina problematica* sp. nov., holotype (PAS Pi-F/MP/170a/1626/14). Détail de la zone entre la région operculaire et la ceinture pectorale, avec les dents pharyngiennes bien discernables (leurs pointes sont marquées par des flèches). Partie avant sur la droite.

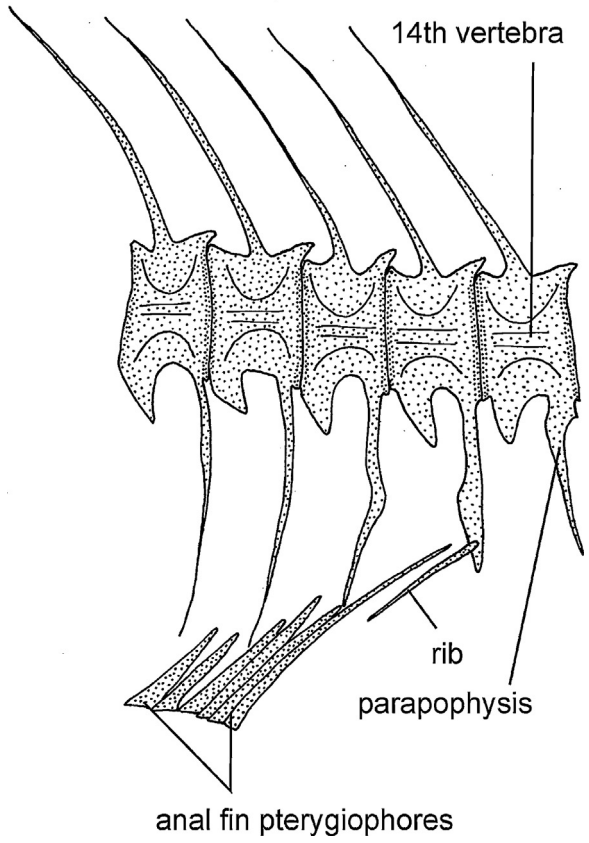

Fig. 6. *Propercarina problematica* sp. nov. Vertebrae in the transition from the abdominal to the caudal part of the vertebral column, based on the holotype. The rib on the 14th abdominal vertebra with epineurals and interneurals omitted.
Fig. 6. *Propercarina problematica* sp. nov. Vertèbres à la transition des parties abdominale et caudale de la colonne vertébrale dessinées à partir de l'holotype. La nervure sur la 14e vertèbre abdominale, les épineuraux et interneuraux n'ont pas été représentés.

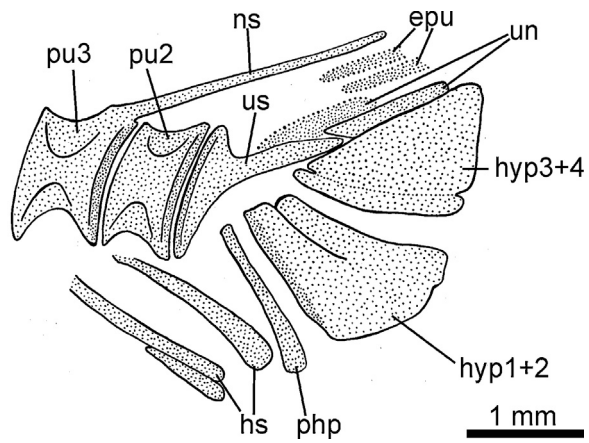

Fig. 7. *Propercarina problematica* sp. nov. Caudal skeleton based on the holotype.
Fig. 7. *Propercarpina problematica* sp. nov. Squelette caudal dessiné à partir de l'holotype.

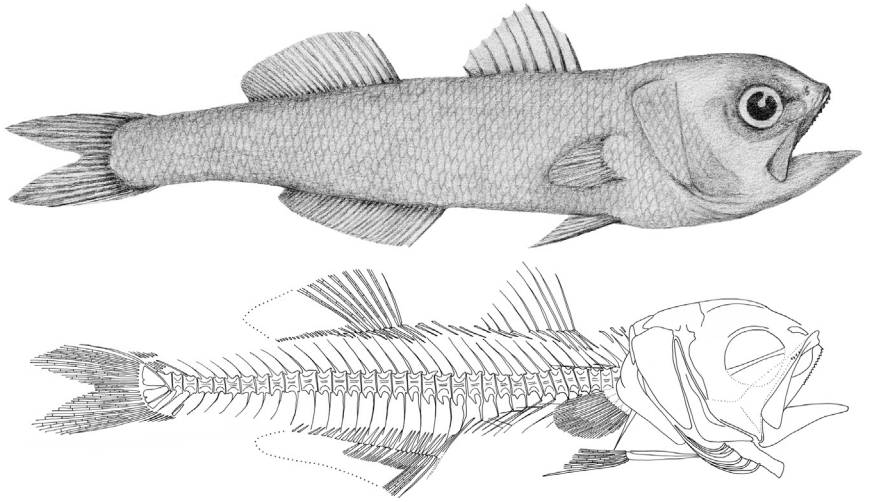

Fig. 8. *Propercarina problematica* sp. nov. Reconstruction of the fish and skeleton. Lateral line is omitted.
Fig. 8. *Propoercarina problematica* sp. nov. Reconstitution du poisson et de son squelette. La ligne latérale n'a pas été représentée.

Three supraneurals (predorsals) are present. The first dorsal fin consists of 8 or 9 spines – we are not able to determine if the last spine is not overlaid by the previous one in the holotype. The length of each spine increases posteriorly to the third one that is the longest, and then the rest becomes shorter posteriorly in the series. There are about six interneurals between the first and second dorsal fins not associated with the fin rays. The second dorsal fin is formed by about 25 rays (it is not possible to differentiate its spines from the soft rays) with 20 preserved pterygiophores in the holotype. One spine is visible in D2 of specimen PNM 864. The arrangement of the predorsals and pterygiophores to the neural spines shows the following formula: 0/0/0/1/1/1/1 + 1/1/1/1/1/0/0/0/0/0 + 0/1 + 1/1 + 1/1 + 1/1/1/ and the remaining part is not discernable.

Only 16 fin rays (the possible spines are not discernable) and about 28 pterygiophores are preserved in the anal fin of the holotype; 2 small spines (associated with first pterygiophore of the anal fin) and 28 rays are visible in specimen PNM 864. The arrangement of the pterygiophores to the haemal spines in the holotype is 1?/1 + 1 + 1/1 + 1/1 + 1 + 1/1 + 1 + 1/1 + 1 + 1/1/1 + 1 + 1/1 + 1?/1 + 1?/1 + 1?/and the remaining part is not discernable.

The caudal skeleton is poorly preserved; it seems to be composed of the fused hypurals 1 + 2 and 3 + 4 (probably together with 5), parhypural, two uroneurals, and two epurals. The caudal fin formula is probably 7 + I,8-7,I + 6.

The scales are very small and thin, cycloid, with borders hardly discernable. Scales are developed on the body and in the opercular region. The position of the lateral line is not discernable.

4. Discussion and results

Propercarinid fishes are known from the Oligocene deposits of Romania (Paucă, 1929, 1934; Gradianu–unpublished data), Poland (Bannikov, 1995; Kotlarczyk et al., 2006; data herein), Ukraine (Gorbatch, 1961), Caucasus (Bannikov, 1995, 2010), and probably also from the Mainz Basin (Bannikov, 1995). The studied fossil specimens reach up to 120 mm in SL. Due to the fossilization process we are not able, of course, to determine the maturity of the specimens. However, Ahlstrom et al. (1976) outlined the morphological limits between the stromateoid larva and juvenile on the basis of:

- completion of fin rays in all fins;
- initiated scalation process.

Horn (1984) correctly pointed out that both processes are connected and the scalation process in stromateoids generally began after the development of the fin rays. Due to the presence of scales in all studied specimens, these are considered to be juveniles, sub-adults or adults, but not larvae. The maximum size of adult fish is unknown.

Three propercarinid species can be distinguished based on meristic data (related to the dorsal and anal fins; Table 2). On the other hand, the body of *P. problematica* sp. nov. is elongated similarly as in *P. pietschmanni*.

Table 2
Selected meristic features of the *Propercarina* species.
Tableau 2
Traits méristiques sélectionnés de l'espèce *Propercarina*.

	Vertebrae	D1	D2	A
Propercarina rebeli Paucă, 1929	15 + 21	VI	I + 23	II + 32
Propercarina pietschmanni Paucă, 1929	15 + 21	VII	I + 27	II + 40
Propercarina problematica sp. nov.	15 + 21 or 14 + 22	VIII or IX	25 (first probably spine)	28 rays (spines are not recognizable on holotype)

D1: first dorsal fin; D2: second dorsal fin; A: anal fin.

Fig. 9. *Amarsipus carlsbergi* Haedrich, 1969. X-ray figure of the specimen in lateral view.
Fig. 9. *Amarsipus carlsbergi* Haedrich, 1969. Figure obtenue aux rayons X du spécimen en vue latérale.

Unfortunately, the holotype of *P. pietschmanni* is probably lost, and none of the unpaired fins in the referred specimens of this species was preserved well enough; therefore, we are dependent on the original description (Paucă, 1929, 1934), with no possibility of its verification.

As was mentioned earlier (Bannikov, 1995), propercarinids share many similarities with the Recent monotypic stromateoid family Amarsipidae. The species *Amarsipus carlsbergi* Haedrich, 1969 (Fig. 9) was originally described on the basis of non-mature specimens (Haedrich, 1969), but about two decades later adults were also described (Konovalenko and Piotrovskiy, 1988). Although the species lacks the toothed pharyngeal sack, it is linked with other stromateoids by a unique well-developed sub-dermal canal system (Haedrich, 1969; Konovalenko and Piotrovskiy, 1988).

Nevertheless, the position of *Amarsipus* within the Stromateoidei based on the cladistic analysis is not consistent (compare Horn, 1984 and Doiuchi et al., 2004), and on the basis of some features its grouping with other stromateoids is even questionable (see Springer and Johnson, 2004). The latest work that largely discussed the phylogeny of stromateoids (molecular phylogenetic analysis based on mitochondrial DNA sequences) by Doiuchi and Nakabo (2006) unfortunately lacks data about amarsipids. The comparison of propercarinids with *Amarsipus* (and marginally with other stromateoids) led to the results described below.

The skull of propercarinids, similarly as in *Amarsipus*, is moderately long, with a terminal mouth. Jaws in all stromateoids bear teeth (Horn, 1984), similarly as in *P. rebeli* and *P. pietschmanni* (in both species the teeth are relatively large). In *P. problematica* sp. nov., teeth were observed on the premaxilla (small teeth, but their shape and organization is not discernable), but the preserved dentary of the holotype seems to be toothless. This condition is very unusual and the question is if it is a natural state, or is it more probable that it is an artifact caused by preservation? Specimen PNM 864 with the toothed dentary is tentatively classified with the new species. However, if future discoveries confirm an edentulous dentary in *P. problematica* sp. nov., then specimen PNM 864 will be regarded as belonging to another species. Therefore, until other specimens are discovered we are not able to address this issue.

In the anterior region of the palato-quadrate complex (probably palatine) of *P. problematica* sp. nov., fine teeth seem to have developed. Similar to the premaxillary teeth, their shape and organization are unclear. The state of preservation of the available specimens of *P. pietschmanni* and *P. rebeli* does not allow a verification of the presence of this character. Ahlstrom et al. (1976) did not identify palatine teeth in the studied specimens of *Amarsipus* and Doiuchi et al. (2004) coded them as absent in their analysis. On the other hand, palatal teeth in *Amarsipus* were described by Konovalenko and Piotrovskiy (1988). This discrepancy can be due to the larger specimens studied by Konovalenko and Piotrovskiy (1988: 21 specimens with SL 162–216 mm), whereas the biggest specimen studied by Ahlstrom et al. (1976) reached 124 mm and the only one studied by Doiuchi et al. (2004) reached SL 57 mm. According to Doiuchi et al. (2004), the palatal teeth are developed in the genera *Cubiceps*, *Nomeus*, *Psenes* and *Tetragonurus* in a single row. Thus, it seems that:

- palatine teeth in *Amarsipus* develop in the bigger adults (i.e., later in post-larval development);
- in *Propercarina problematica* sp. nov. (and maybe in all propercarinids), palatal teeth developed much earlier in post-larval development than in *Amarsipus*;
- this feature of Propercarinidae is similar to the families Nomeidae and Tetragonuridae.

The postero-ventral margin of the preopercle is serrated in *P. pietschmanni* and *P. rebeli* according to Paucă (1934), but we were not able to confirm this. In *P. problematica* sp. nov., the ventral preopercular margin is smooth. Specimen PNM 864 possesses a preopercle with very fine serrations on its ventral edge, and an undescribed specimen of *Propercarina* sp. from the Oligocene of the Caucasus also bears very fine serrations on the ventral margin of the preopercle. This feature in Recent stromateoids has not been systematically commented on by any author. Horn (1984) mentioned the spines on the preopercle of the genus *Schedophilus*; Doiuchi et al. (2004) – who did not include the feature of the investigated characters figured serrations of the preopercle also in *Hyperoglyphe japonica* (fig. 4A). It is necessary to say that the character mentioned here does not represent a complete list and its importance in the Propercarinidae is not clear; however, its presence in some specimens can perhaps be suggested as a character at the specific level.

Six branchiostegal rays are present in *P. problematica* sp. nov., but we are not able to determine if there are six or seven of them in the other species. According to Doiuchi et al. (2004), this character state is the same in *Amarsipus*,

Ariomma, *Cubiceps*, *Nomeus*, *Peprilus*, *Psenes*, *Stromateus* and some specimens of *Tetragonurus* [with possible variability described by Haedrich (1967) and Ahlstrom et al. (1976)], whereas *Pambus* has five branchiostegal rays and other members are characterized by seven rays.

The pharyngeal toothed sac is absent in *Amarsipus*, whereas it is present in all other members of the suborder Stromateoidei (Ahlstrom et al., 1976; Horn, 1984) – instead of a pharyngeal sac, well-developed pharyngeal teeth (3–4 mm long) are present in *Amarsipus* (Konovalenko and Piotrovskiy, 1988). Similarly, pharyngeal teeth were also developed in *Propercarina problematica* sp. nov. (Fig. 5), although these are significantly smaller (size of the preserved ones is less than 0.25 mm), and the pattern of their original arrangement is unclear.

The vertebral column of propercarinids is constructed of 35–36 subrectangular (deeper than long) vertebrae with well-developed slender parapophyses in the posterior portion of the abdominal part of the vertebral column. Compared to *Amarsipus*, the number of vertebrae in propercarinids is distinctly less (35–36 vs. 45–48; Ahlstrom et al., 1976). As was mentioned by Ahlstrom et al. (1976), the division of the precaudal and caudal vertebrae in stromateoid fishes is complicated, since:

- ribs often are associated with the haemal spine (or spines) of some caudal vertebrae
- there is a backward protrusion of the abdominal cavity into the area normally occupied by the haemal spines of the anterior caudal vertebrae.

The latter fact does not complicate the situation in propercarinids, because the fossils show posteroventral orientation of the anal-fin pterygiophores; therefore, we do not suppose any significant protrusion of the abdominal cavity to the caudal region. Contrary to this, the presence of rib (-s) on the caudal vertebra (-e) was observed in *Amarsipus*, *Ariomma*, *Cubiceps*, *Nomeus*, *Pampus*, *Peprilus*, *Psenes*, *Stromateus* and *Tetragonurus* (Doiuchi et al., 2004), and this may cause interpretative problems in propercarinids. In any case, the last rib is associated with the 15th vertebra (see Fig. 6), and therefore we do interpret this as an abdominal one according to the traditional usage.

Epineurals are well developed in *P. problematica* sp. nov. They are associated with neural spines of the anteriormost vertebrae, and posteriorly they shifted ventrally and are associated with the ribs. Epineurals in *Amarsipus* were figured by Doiuchi et al. (2004: fig. 8A), but these seem to be distributed in a different way (along the ventral border of the vertebral centra).

The caudal skeleton of the propercarinids was characterized by Bannikov (1995) as non-oligomerized. *P. problematica* sp. nov. seems to have a derived condition with the hypurals fused into two plates (hyp 1 + 2 and 3 + 4+ probably 5), but the state of preservation does not allow confirmation of this. On the other hand, it is possible to recognize two uroneurals, two epurals and an easily discernable parhypural. Two epurals were found only in the stromateoid genera *Icichthys*, *Pampus*, *Peprilus*, *Stromateus* and *Tetragonurus*, while other members of the suborder were identified as having three (Doiuchi et al., 2004).

The dorsal fins are well separated in all *Propercarina* species, with ca. 5 or 6 rayless pterygiophores developed between them, whereas the dorsal fins are divided, but closely spaced in *Amarsipus*. The interneural formulas of propercarinids show some species variability and the significance is currently unknown, due to limitations in the number of specimens. The anal-fin rays are more numerous than the second dorsal fin rays in propercarinids, exactly as in *Amarsipus*. The first proximal pterygiophore of the anal fin in propercarinids is noticeably elongated and approaches the parapophysis of the 15th vertebra. This situation is generally similar to that in most stromateoids, where the first pterygiophore is also elongated (in *Pampus*, *Peprilus*, *Psenes* and *Stromateus* the first and second proximal anal-fin pterygiophores are elongated and oriented postero-dorsally), but in *Amarsipus* the first proximal pterygiophore is not elongated, and its shape is completely different from that of *Propercarina* (see Doiuchi et al., 2004: fig. 8A). Similarly as with the interneural formula, interhaemal formulas of propercarinids show some variability.

Scales are very thin and relatively small in all propercarinids. Originally these were described as ctenoid, but we identified cycloid scales in all species. These are distributed over the whole body and are also well recognizable in the opercular area (probably also on the dorsal ramus of the preopercle). The opercle is scaled in most stromateoids [not in *Ariomma* and *Psenes*, according to Doiuchi et al. (2004); it is naked also in *Amarsipus*, according to Horn (1984)], and the preopercle is also scaled in most of the stromateoids, except for *Amarsipus*, *Ariomma*, *Centrolophus*, *Hyperoglyphe*, *Psenopsis*, *Schedophilus* and *Seriolella* (Doiuchi et al., 2004). Ctenoid scales were observed in *Psenes* and *Tetragonurus*, while the other stromateoids studied by Doiuchi et al. (2004) have cycloid scales.

The data presented above clearly show a mixture of primitive and relatively advanced stromateoid features in the genus *Propercarina*. Bannikov (1995) suggested the probable origin of the amarsipids and propercarinids from a pre-centrolophid form, which is considered to be the most basal one (according to Haedrich, 1967).

According to the original description (Paucă, 1929, 1934), the genus *Propercarina* is similar to the Recent genus *Percarina*, but its affinity to the family Percidae is groundless. *Propercarina* was also sometimes confused with the genus *Palimphyes* (family Euzaphlegidae of the suborder Scombroidei) (Gorbatch, 1961; Micklich and Parin, 1996). An attempt (Sychevskaya and Prokofiev, 2005) to synonymize *Propercarina* under the genus *Palimphyes* is groundless (Bannikov, 2010, 2012): it lacks any of the diagnostic features of *Palimphyes* (see Monsch and Bannikov, 2011).

The propercarinids also share several important features with the family Sillaginidae Richardson, 1846 [this similarity of meristic features was mentioned also by Bannikov (1995)], such as an elongated body, two separated dorsal fins, second dorsal and anal fins with numerous rays, and three predorsals. The detailed osteological description of the family Sillaginidae provided by Kaga (2013) allows a more careful comparison of both groups. The two differ mostly in:

- the first dorsal fin is composed of X to XIII spines in sillaginids (vs. VI to IX in propercarinids);
- long preorbital distance (vs. short in propercarinids);
- horizontal limb of the preopercle is elongated (vs. short horizontal limb of the preopercle in propercarinids)–this feature is obviously connected to the elongation of the sillaginid head (especially in the preorbital area);
- teeth on palatine are absent (they seem to be present in propercarinids, but it is difficult to confirm this feature in all species).

Therefore, the two families most probably are not related.

Recent stromateoids are marine fishes of the temperate and tropical zones (Horn, 1984) and their juveniles are commonly associated with floating objects (Haedrich, 1967; Horn, 1984). A similar way of life is expected for the propercarinids. In the case of *P. problematica* sp. nov., the possible floating objects could be represented by the sea grass clusters that are found occasionally at the Hermanowa locality. Such clusters could serve as a "substrate" also for other fauna at the locality, such as *Hipposyngnathus* (Přikryl et al., 2011), *Syngnathus*, and swimming crabs *Portunus*. This suggestion is in accordance with the deliminated idea of the "quasi-Sargasso" assemblages (sensu Jerzmańska and Kotlarczyk, 1975, 1976). Similar associated fauna was also described from the other localities characterized by the propercarinid remains.

Acknowledgements

We are much grateful to the late Prof. N.V. Parin for the X-ray of the extant *Amarsipus carlsbergi*. Many thanks to Dr. Călin Ricman, Dr. Dan Grigore (National Museum of Geology) and Dr. Melanya Stan (National Museum of Natural History "Grigore Antipa") for the permission to examine the material. We would like to also acknowledge both anonymous reviewers for their valuable comments. The research of T.P. was financially supported by Czech science foundation (GAČR) project no. GP13-19250P. The research of A.F.B. was supported by the Russian Foundation for Basic Research, grant no. 14-04-00005. The research of I.G. was supported by the National University Research Council (CNCSIS), grant no. 74GR/2008.

References

Ahlstrom, E.H., Butler, J.L., Sumida, B.Y., 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the Northwest Atlantic. Bull. Mar. Sci. 26, 285–402.

Bannikov, A.F., 1995. Morphology and phylogeny of fossil stromateoid fishes (Perciformes). Geobios 19, 177–181.

Bannikov, A.F., 2010. Fossil Acanthopterygian fishes (Teleostei, Acanthopterygii). GEOS, Moscow (244 p., in Russian).

Bannikov, A.F., 2012. The first record of the genus *Isurichthys* (Perciformes, Ariommatidae) in the Lower Oligocene of the northern Caucasus. Paleontol. J. 46, 171–176.

Bleeker, P., 1859. Enumeratio specierum piscium hucusque in Archipelago indico observatarum. Acta Soc. Sci. Indo-Neerl. 6, 1–276.

Constantin, P., 1999. Oligocene–Lowermost Miocene fossil fish-fauna (Teleostei) from Romanian Eastern Carpathians. GEO ECO Marina 4, 119–134.

Doiuchi, R., Nakabo, T., 2006. Molecular phylogeny of the stromateoid fishes (Teleostei: Perciformes) inferred from mitochondrial DNA sequences and compared with morphology-based hypotheses. Mol. Phylogenet. Evol. 39, 111–123.

Doiuchi, R., Sato, T., Nakabo, T., 2004. Phylogenetic relationships of the stromateoid fishes (Perciformes). Ichthyol. Res. 51, 202–212.

Gorbatch, L.P., 1961. On some pelagic fishes from the Carpathian Oligocene. Paleontol. Sb. (L'vov) 1, 131–136 (in Russian).

Haedrich, R.L., 1967. The Stromateoid fishes: systematics and a classification. Bull. Mus. Comp. Zool. 135, 31–139.

Haedrich, R.L., 1969. A new family of aberrant stromateoid fishes from the equatorial Indo-Pacific. Dana Rep. 76, 1–14.

Horn, M.H., 1984. Stromateoidei: development and relationships. In: Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall Jr., A.W., Richardson, S.L. (Eds.), Ontogeny and systematics of fishes. Allen Press, Lawrence, KS, USA, pp. 620–628.

Jerzmańska, A., Kotlarczyk, J., 1975. Fossils of the quasi-Sargasso assemblage in the menilite beds of the Skole Unit, Polish Carpathian mountains. Kwartalnik Geol. 19, 875–886 (in Polish).

Jerzmańska, A., Kotlarczyk, J., 1976. The beginnings of the Sargasso assemblage in the Tethys? Palaeogeogr. Palaeocimatol. Palaeoecol. 20, 297–306.

Kaga, T., 2013. Phylogenetic systematics of the family Sillaginidae (Percomorpha: order Perciformes). Zootaxa 3642, 1–105.

Konovalenko, I.I., Piotrovskiy, A.S., 1988. First description of adult amarsipid *Amarsipus carlsbergi*. Vopr. Ihtiol. 28, 683–686 (in Russian).

Kotlarczyk, J., Jerzmańska, A., 1976. Biostratigraphy of Menilite Beds of Skole Unit from the Polish Flysch Carpathians. B. Pol. Acad. Sci. Earth 24, 55–62.

Kotlarczyk, J., Jezmańska, A., Świdnicka, E., Wiszniowska, T., 2006. A framework of ichthyofaunal ecostratigraphy of the Oligocene-Early Miocene strata of the Polish Outer Carpathian basin. Ann. Soc. Geol. Pol. 76, 1–111.

Micklich, N., Parin, N., 1996. The fishfauna of Frauenweiler (Middle Oligocene, Rupelian; Germany): first results of a review. Publ. Espec. Inst. Esp. Oceanogr. 21, 129–148.

Monsch, K.A., Bannikov, A.F., 2011. New taxonomic synopses and revision of the scombroid fishes (Scombroidei, Perciformes), including billfishes, from the Cenozoic of territories of the former USSR. Earth Env. Sci. Trans. Roy. Soc. Edinb. 102, 253–300.

Nelson, J.S., 2006. Fishes of the World, Fourth ed. John Wiley & Sons, Inc, Hoboken (624 p.).

Nordmann, A., 1840. Observations sur la faune pontique. In: Démidoff, A. (Ed.), Voyage dans la Russie méridionale et la Crimée, Vol. III. Ernest Bourdin et Cie éditeurs, Paris, pp. 355–635.

Paucă, M., 1929. Fossile Fische aus dem Rumänischen Alttertiär. Bull. Sec. Sci. Acad. Roumaine 12, 206–212.

Paucă, M., 1934. Die fossile Fauna und Flora aus dem Oligozän von Suslänesti-Muscel in Rumänien. Eine systematische und paläobiologische Studie. Ann. Inst. Geol. Roumaine 16, 575–668.

Přikryl, T., Krzemiński, W., Kania, I., 2011. New information about the anatomy of a peculiar fish of the genus *Hipposyngnathus* Daniltshenko, 1960. C. R. Palevol 10, 559–566.

Richardson, J., 1846. Report on the ichthyology of the seas of China and Japan. Rep. Br. Ass. Advmt. Sci. 1845, 187–320.

Schultz, H.-M., Bechtel, A., Sachsenhofer, R.F., 2005. The birth of the Paratethys during the Early Oligocene: From Tethys to an ancient Black Sea analogue? Global Planet. Change 49, 163–176.

Springer, V.G., Johnson, G.D., 2004. Study of the dorsal gill-arch musculature of teleostome fishes, with special reference to the Actinopterygii. Bull. Biol. Soc. Wash. 11, 1–236.

Sychevskaya, E.K., Prokofiev, A.M., 2005. The first occurrence of fishes of the family Centrolophidae (Perciformes, Sromateoidei) in the Late Paleocene of Turkmenistan. J. Ichthyol. 45, 141–144.