General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

Skeletal anatomy of the early morid fish *Eophycis* (Gadiformes, Moridae) from an Oligocene deposit in Poland

Anatomie du squelette d'un ancien poisson moridé Eophycis *(Gadiformes, Moridae) issu d'un dépôt oligocène de Pologne*

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ABSTRACT

The family Moridae (Gadiformes) is diagnosed by an otophysic connection, a horizontal gas bladder septum, unique otoliths and a specific architecture of the caudal skeleton. Their skeletal fossil record is rather scarce and uncertain: the oldest proven representatives (from Oligocene sites of the Paratethys area) are classified in the genus *Eophycis*. Newly collected specimens from the Hermanowa locality (Poland) allow the description of and commentary on previously unknown characters. The species *Eophycis jamnensis* was a typical morid fish with an elongated body, a triangular head, and single dorsal and anal fins that are not coalesced with the caudal fin. This species was most similar to the Recent species *Guttigadus nana* that differs from it (as from other *Eophycis* species) in meristic features, having two dorsal fins but lacking a vomer. A brief review of the fossil skeletal record of morid fish is presented.

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RÉSUMÉ

La famille des Moridae (Gadiformes) est clairement définie par une connexion autophysaire, un septum horizontal de la vessie gazeuse, des otolithes d'un type unique et une architecture spécifique du squelette caudal. Leur registre fossile est assez pauvre et incertain, leurs plus anciens représentants démontrés (des gisements oligocènes du domaine paratéthysien) étant attribués au genre *Eophycis*. Des spécimens nouvellement récoltés dans la localité de Hermanowa (Pologne) permettent la description et l'analyse de caractères jusqu'alors inconnus. L'espèce *Eophycis jamnensis* est un moridé typique, au corps allongé, avec une tête triangulaire et des nageoires dorsale et anale uniques ; qui ne sont pas coalescentes avec la nageoire caudale. Cette espèce est très semblable à l'espèce actuelle *Guttigadus nana*, qui n'en diffère (de même que des autres espèces de *Eophycis*) que par des caractères méristiques, ayant deux nageoires dorsales et étant dépourvue de vomer. Une brève revue des moridés fossiles est présentée.

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1. Introduction

Living representatives of the family Moridae Goode and Bean, 1896 are marine, deep-water fish, rarely occurring in brackish environments, with about 18 genera and 105 species (Nelson, 2006). The group is diagnosed by the contact of the anteriorly enlarged horns of the gas bladder and otic capsules (i.e., otophysic connection), the horizontal septum of the gas bladder, the specific morphology of otoliths and the unique architecture of the caudal skeleton (e.g. Fitch and Barker, 1972; Paulin, 1983, 1988, 1989; Svetovidov, 1967). Howes (1991) used another character to diagnose the family (i.e., presence of a parasphenoid with a transversely aligned ascending process) but this feature is neglected by most authors. The fossil record (articulated or semi-articulated skeletons) of this group is relatively poor (see below for details) and often hardly distinguishable from superficially similar groups (see Section 4). However, otoliths are easily recognisable, and show a well-documented stratigraphic range from the Eocene up to Recent (for details see Schwarzhans, 1980, 1985; Nolf, 2013).

The species *Eophycis jamnensis* Jerzmańska, 1968 was described from a Lower Oligocene site in central Paratethys (Polish Carpathians) by Jerzmańska (1968), who considered it the most primitive gadid fish of the Paleogene and compared her specimens with the living phycids *Phycis* Walbaum, 1792 and *Urophycis* Gill, 1863. Later, the new species *Eophycis froidefontainensis* Pharisat, 1991 was described from the southern part of western Paratethys (locality Froidefontaine; Rhine Valley Rift System) by Pharisat (1991), who generally shared earlier ideas about this genus, including its placement in the family Gadidae Rafinesque, 1810. Finally, Rozenberg and Prokofiev (2004) described a third species, *Eophycis pshekhiensis* Rozenberg and Prokofiev, 2004, from the eastern Paratethys (Lower Oligocene of northern Caucasus). Their specimens possessed otoliths *in situ*, with distinctive morid morphology and thus, after more than thirty years, the genus was transferred to the family Moridae.

Eophycis represents the oldest known fossil record of the family Moridae. Newly collected specimens of *E. jamnensis* from the locality Hermanowa (Lower Oligocene of Polish Carpathians) display numerous previously undescribed features. The species is compared here with selected Recent morid species and a brief commentary is made on the fossil record of other morids.

2. Materials and methods

The specimens were left unprepared, except the larger specimens, which were prepared using small scalpels or needles. The photos were taken using a Canon EOS 1000D camera attached to a Leica MZ6 stereomicroscope. The drawings were prepared with help of a camera lucida drawing tube. The measurements of the specimens were taken from the photos.

The specimens were collected at a single locality (Hermanowa) which has previously provided fossils from various groups of teleosts (Přikryl et al., 2011, 2014, 2015). This locality was classified in the IPM2 zone (*sensu* Kotlarczyk et al., 2006).

The studied specimens are housed in the collection of the National Museum in Prague (NMP); the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow (PAS); the University of Rzeszów (UR/KBŚ); and Wroclaw University (ZPALWR).

Abbreviations: A – anal fin; art – angulo-articular; ax – axonost; BD – body depth; br – branchiostegal rays; C – caudal fin; chm – corpus hyomandibulae; chy – ceratohyal; cl – cleithrum; D – dorsal fin; den – dentary; ect – ectopterygoid; ehy – epihyal; end – endopterygoid; epp – epipleural; fr – frontal; HD – head depth; HL – head length; hph – hypohyal; hsp – haemal spine; hy – hyomandibula; io – interopercle; lpr – lower process of hyomandibula; mtp – metapterygoid; mx – maxilla; ncr – neurocranium; ns – neural spine; O – orbit length; occ – occipital; op – opercle; P – pectoral fin; pa – palatine; pcl – postcleithrum; pmx – premaxilla; pop – preopercle; prar – articular process of premaxilla; prart – articular process of hyomanibula; pras – ascending process of premaxilla; preA – preanal length; preD – predorsal length; preO – preorbital length; presL – preserved length of the specimen; preV – preventral length; prf – prefrontal; prop – opercular process of hyomanibula; prpm – postmaxillar process of premaxilla; prpo – preopercular process of hyomanibula; psph – parasphenoid; pst – posttemporal; pter – pterotic; q – quadrate; r – ribs; ra – fin rays; scl – supracleithrum; SL – standard length; soc – supraoccipital; sph – sphenotic; sy – symplectic; TL – total length; V – ventral fin; v – vomer; vert - vertebrae.

3. Systematic part and description

Subdivision Teleostei *sensu* Patterson and Rosen, 1977
Order Gadiformes *sensu* Endo, 2002
Family Moridae Goode and Bean, 1896
Genus *E*ophycis Jerzmańska, 1968
Diagnosis (according to Jerzmańska, 1968; and Rozenberg and Prokofiev, 2004; emended):
Anterior part of the skull (preorbital length + length of orbit) is bigger than its postorbital portion; 37 to 50 vertebrae (with 9–11 of them abdominal); small uniform teeth present on the premaxilla and dentary; pelvic fins in jugular position with two long and at least one short rays; dorsal fin single with 48–55 rays; anal fin with 42–50 rays; neither dorsal nor anal fins confluent with the caudal fin. Morid type of otolith with flat inner side; external side is plane and strongly convex; height of otolith is approximately the same as its width; ventral field forms a long furrow restricted at the top, comb shaped projections at the ventral edge.

Type species: *Eophycis jamnensis* Jerzmańska, 1968

Species *Eophycis jamnensis* Jerzmańska, 1968
(Figs. 1–10)
Diagnosis (according to Jerzmańska, 1968; emended):
Lower jaw is not prominent; 37–40 vertebrae (9–11 abdominal ones); dorsal fin with ca 50 rays; anal fin with ca 45 rays; caudal fin is composed by ca 20 rays.
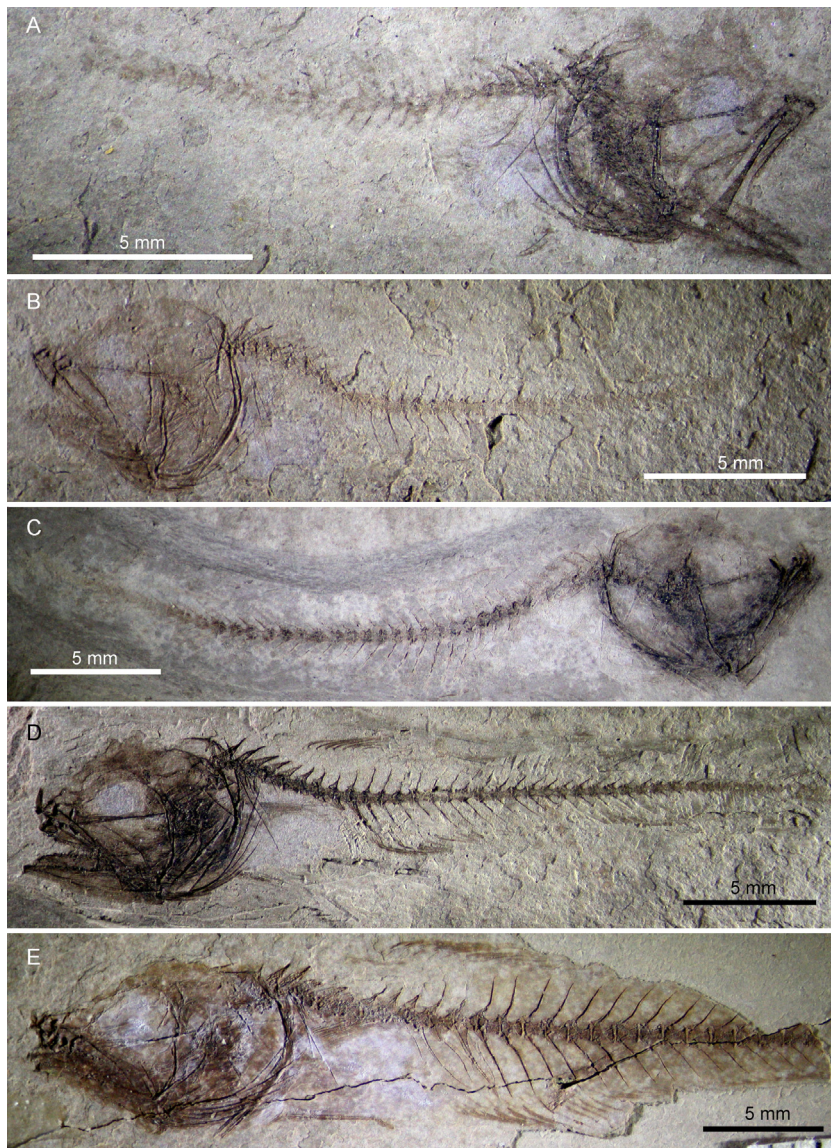
Fig. 1. (Color online.) *Eophycis jamnensis* Jerzmańska, 1968. Specimens from the Hermanowa locality show size and variability of preservation. A. Specimen UR/KBŚ/414a. B. Specimen NMP Tv1002a. C. Specimen UR/KBŚ/309. D. Specimen NMP Tv1003. E. Specimen UR/KBŚ/180.
Fig. 1. (Couleur en ligne.) *Eophycis jamnensis* Jerzmańska, 1968. Les échantillons de la localité d'Hermanowa montrent taille et variabilité de préservation. A. Éch. UR/KBŚ/414a. B. Éch. NMP Tv002a. C. Éch. UR/KBŚ/309. D. Éch. NMP Tv1003. E. Éch. UR/KBŚ/180.

Holotype: ZPALWR A/839 (Jerzmańska, 1968: 413; fig. 8, pl III fig. 3)

Referred specimens: NMP: Tv1002 (part and counterpart), TV1003; PAS: MP/7/1592/11 (part and counterpart), MP/9/1592/11, MP/11/1592/11, MP/13/1592/11 (part and counterpart); UR/KBŚ: 97, 180, 183 (part and counterpart), 201 (part and counterpart), 204 (part and counterpart), 285, 286, 294, 296, 308, 309, 414 (part and counterpart), 419, 523 (part and counterpart); ZPALWR: A/839, A/898.

Description of newly collected specimens: The fish is elongated with sub-triangular head, head length representing about 30% of SL, head depth is about 80% of head length, body depth is about 20% of SL, predorsal length is about 35%

of SL, preanal length is about 43% of SL, preventral length is about 25% of SL (Figs. 1–2, Table 1).

The neurocranium is obviously hypo-ossified. It is possible to recognise the frontal part without skull ridges and a very weak crest in the midline. Paired elements located anteriorly were identified as prefrontals (Fig. 3). The ethmoid area is not well preserved in any of the studied specimens. The parasphenoid extends through the lower third of the orbit and it is anteriorly articulated with the vomer. The head of the vomer does not show the presence of any teeth. The otic part of the neurocranium is crushed; in one slightly bigger specimen (KBŚ/523) the imprint of a sphenotic and pterotic is identifiable (Fig. 4). Contact of the lateral shelves of these bones is not clear (mainly due to the
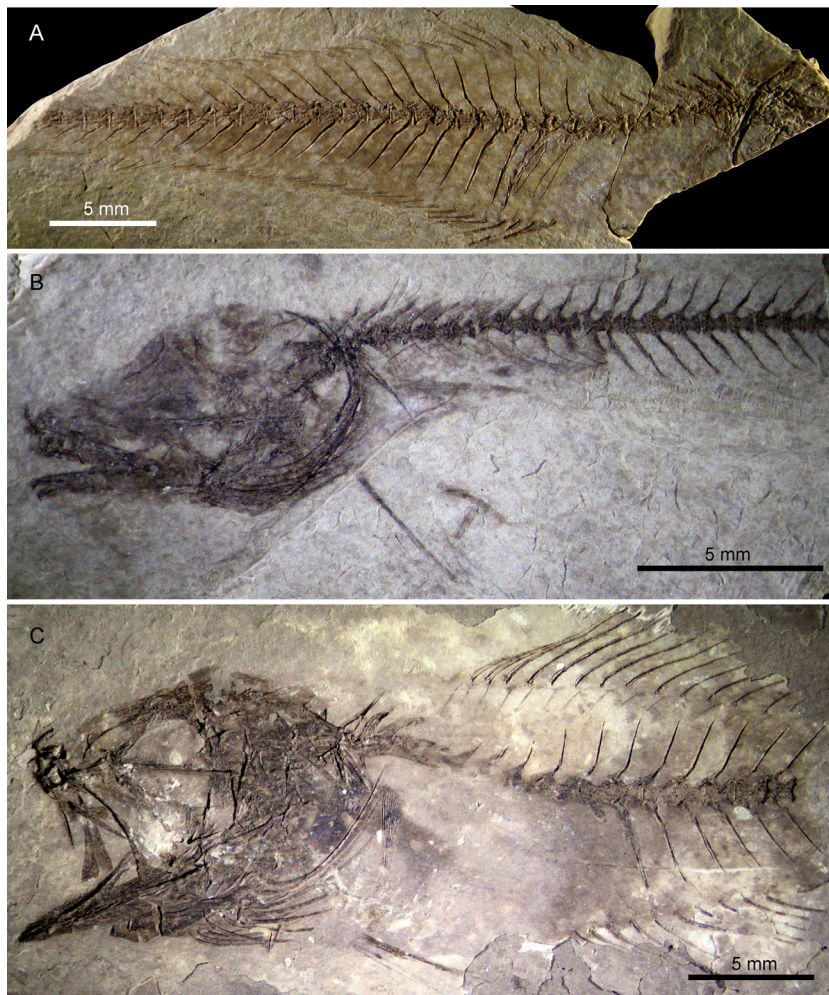
Table 1
Morphometric features of selected specimens of *Eophycis jamnensis* Jerzmańska, 1968.
Tableau 1
Caractéristiques morphométriques d'échantillons sélectionnés d'*Eophycis jamnensis* Jerzmańska, 1968.

	TL (mm)	SL (mm)	presL (mm)	HL (mm)	% of SL	preO (mm)	% of HL	O (mm)	% of HL	HD (mm)	% of SL	% of HL	BD (mm)	% of SL	% of HL	preD (mm)	% of SL	preA (mm)	% of SL	preV (mm)	% of SL
Tv1002a	24.84	23.06		6.53	28.32	1.87	28.64	1.55	23.74	5.94	25.76	90.96	5.32	23.07	81.47					6.20	26.89
Tv1003	29.25	27.74		7.65	27.58	1.69	22.09	2.16	28.24	6.10	21.99	79.74	5.06	18.24	66.14	9.87	35.58	12.15	43.80	7.42	26.75
KBŚ-183b			24.99	10.01		2.80	27.97	2.37	23.68	8.04		80.32	6.91		69.03	8.42					
KBŚ-204a	22.18	21.22		6.73	31.72															6.13	28.89
KBŚ-286			21.96	10.21		2.46	24.09	2.74	26.84	7.98		78.16						16.08		9.50	
KBŚ-296			16.90	4.80		1.20	25.00	1.16	24.17	4.40		91.67	3.15		65.63						
KBŚ-309		29.54		8.28	28.03	2.17	26.21	2.11	25.48	6.65	22.51	80.31	5.10	17.26	61.59						
KBŚ-414a			17.10	6.08		1.49	24.51	1.43	23.52	5.05		83.06	3.48		57.24					6.31	

Fig. 2. (Color online.) *Eophycis jamnensis* Jerzmańska, 1968. Specimens from the Hermanowa locality show size and variability of preservation. A. Specimen Pi-F/MP/7a/1592/11. B. Specimen Pi-F/MP/11/1592/11. C. Specimen UR/KBŚ/97.
Fig. 2. (Couleur en ligne.) *Eophycis jamnensis* Jerzmańska, 1968. Les échantillons de la localité d'Hermanowa montrent taille et variabilité de conservation. A. Éch. Pi-F/MP/7a/1592/11. B. Éch. Pi-F/MP/11/1592/11. C. Éch. UR/KBŚ/97.

fact that the specimen is represented by imprint), but they seem not to be in contact each with other. The supraoccipital crest is moderately developed and it is articulated with the neural spine of the first abdominal vertebra.

The maxilla has a small articular head (with no recognisable details), is elongated and posteriorly slightly ventrally enlarged. The premaxilla is relatively subtle with a well-developed processus ascendens and articularis (both of them diverged dorsally) and postmaxillaris (situated in the posterior third of the bone; Fig. 5A). At the ventral margin of the bone small conical teeth are developed in two or three rows. The dentary bears similarly arranged teeth and it is firmly connected with the anguloarticular.

The jaw joint is situated at the level of the posterior border of the orbit. The quadrate is triangularly shaped with well-developed fossa symplectica (Fig. 5D). The vertical ramus of the ectopterygoid is attached to the anterior margin of the quadrate. The horizontal ramus of the ectopterygoid is approximately the same length and mass as the vertical ramus, but its preservation is limited in all studied specimens. The endopterygoid is developed, as a thin membranous bone, but its precise shape is hardly recognisable. A palatine is not discernable. The metapterygoid is triangular in shape, with a well-delimited dorsal process that is in contact with the hyomandibula. The symplectic is rod-like, its length being approximately the same as the depth of the quadrate. The hyomandibula (Fig. 5C) has conspicuous articular, opercular and preopercular processes, and a ventrally located shaft. Dorsally, the hyomandibula is attached to the neurocranium by a single contact via an articular process. Posteriorly, a thin dorsal lamina is developed with a strong opercular process that is in contact with the articular head of the opercle. Ventrally to the opercular process, the preopercular process is developed with a ventrally oriented distal part. The tip and posterior margin of this process are attached to the antero-dorsal part of the preopercle. In some specimens, a small elevation at the anterior margin of the
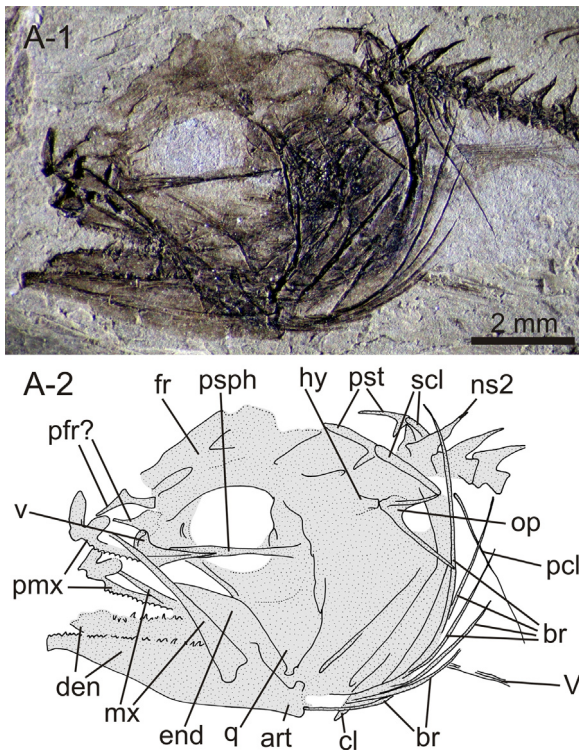
Fig. 3. (Color online.) *Eophycis jamnensis* Jerzmańska, 1968. A-1. Head of specimen NMP Tv1003. A-2. Interpretation of the "A-1". For abbreviations see Section 2.

Fig. 3. (Couleur en ligne.) *Eophycis jamnensis* Jerzmańska, 1968. A-1. Tête de l'échantillon NMP Tv1003. A-2. Interprétation de l'A-1. Pour les abréviations, voir la section 2.

Fig. 4. (Color online.) *Eophycis jamnensis* Jerzmańska, 1968. A-1. Head of specimen UR/KBŚ/523. A-2. Interpretation of the "A-1". B. Detail of the sphenotic-pterotic part of the skull. For abbreviations see Section 2.

Fig. 4. (Couleur en ligne.) *Eophycis jamnensis* Jerzmańska, 1968. A-1. Tête de l'échantillon UR/KBŚ/523. A-2. Interprétation de l'A-1. B. Détail de la partie sphénotique-ptéritique du crâne. Pour les abréviations, voir la section 2.

hyomandibula (here tentatively interpreted as a lower process of the hyomandibula) is visible (Fig. 5C: lpr). The shaft of the hyomandibula is ventrally attached to the metapterygoid and symplectic. The preopercle seems to be large, sickle shaped, and with a canal in the centre of the bone. Its posterior margin is smooth; it is in contact with preopercular process of the hyomandibula, the postero-ventral tip of the corpus hyomandibulae and the quadrate (via the preopercular process). Two interosseous openings are recognisable (Fig. 4), one dorsal (between the hyomandibula and preopercle) and one ventral (between the preopercle, quadrate and symplectic). The opercle is V shaped, with well-delimited horizontal and vertical rami (both of them are connected at an angle of about 80°). A small lamina is developed at the dorsal margin of the horizontal ramus.

The hyoid bar (Fig. 5B) is elongated; the length of the hypohyal is about one fifth of the length of the ceratohyal which is dorso-ventrally compressed in its posterior part. There is no 'beryciform foramen'. The epihyal is incompletely preserved, but seems to be short (about the same length as the hypohyal). The ventral border of the ceratohyal is in contact with the branchiostegal rays, only four of which are recognisable in situ. The branchiostegal rays are long and thin, and about seven or eight in number. The other parts of the branchial skeleton are not recognisable
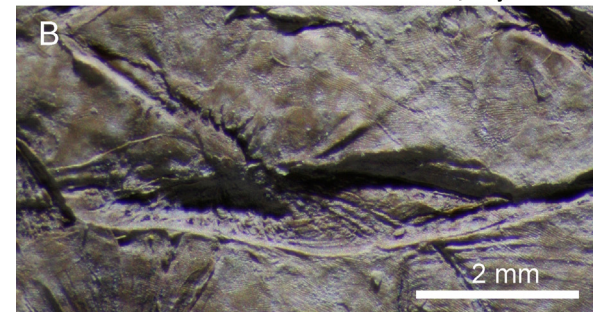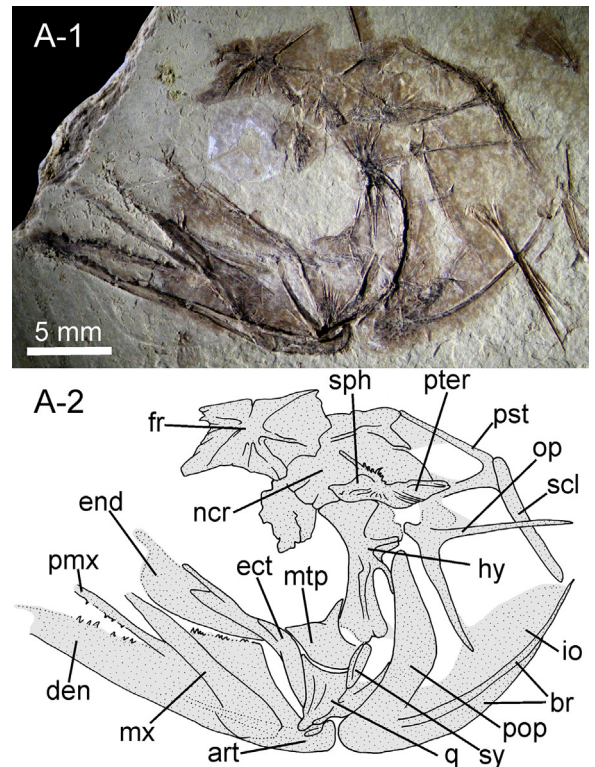
in detail in any of the studied specimens, but some parts were obviously associated with strongly toothed patches.

The vertebral column is composed of 39 or 40 vertebrae; 9 to 11 of them are abdominal, 29 to 30 are caudal ones (including the urostyle). The four most posterior abdominal vertebrae bear well-developed parapophyses on their ventral margins. Dorsal and ventral prezygapophyses are well developed at the abdominal vertebrae and the anterior part of the caudal region of the spine. The neural spine of the first vertebra is enlarged and attached to the occipital part of the skull (Fig. 6). The neural spines of other abdominal vertebrae are large and strongly inclined posteriorly. The neural spines of more posteriorly set vertebrae are thin and long. The ribs at the last three abdominal vertebrae
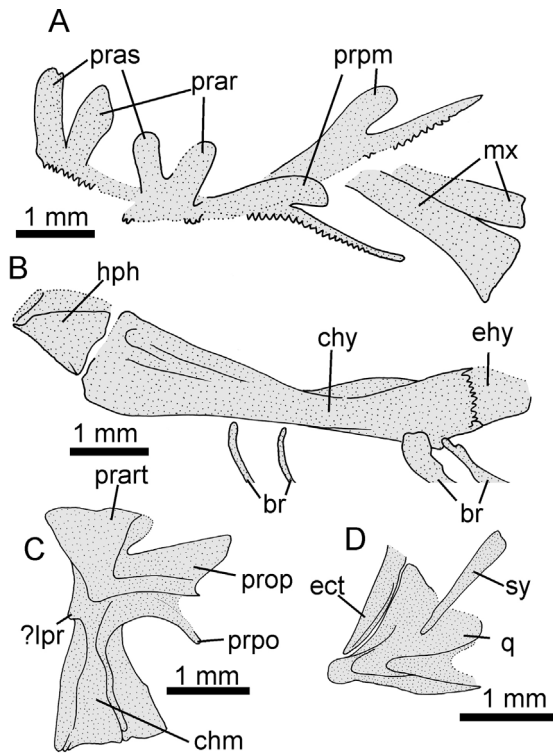
Fig. 5. *Eophycis jamnensis* Jerzmańska, 1968. Skull bones (based on the specimen UR/KBŚ/97). A. Premaxillae. B. Hyoid bar. C. Hyomandibula. D. Quadrate, symplectic and associated vertical part of the ectopterygoid. For abbreviations see Section 2.

Fig. 5. *Eophycis jamnensis* Jerzmańska, 1968. Os du crâne (basés sur l'éch. UR/KBŚ/97). A. Prémaxillaires. B. Barre hyoïdde. C. Hyomandibule. D. Carré, symplectique et partie verticale associée de l'ectoptérygoïde. Pour les abréviations, voir la section 2.

Fig. 6. *Eophycis jamnensis* Jerzmańska, 1968. Occipital part of the skull, anterior abdominal vertebrae and associated bones (based on specimen Pi-F/MP/7b/1592/11). For abbreviations see Section 2.

Fig. 6. *Eophycis jamnensis* Jerzmańska, 1968. Partie occipitale du crâne, vertèbres abdominales antérieures et os associées (basés sur l'échantillon Pi-F/MP/7b/1592/11). Pour les abréviations, voir la Section 2.
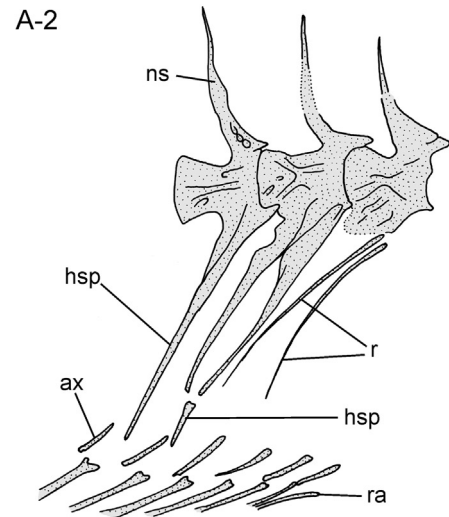

Fig. 7. (Color online.) *Eophycis jamnensis* Jerzmańska, 1968. Vertebral column and its transition from abdominal to caudal area with associated skeletal elements (based on specimen UR/KBŚ/308). For abbreviations see Section 2.

Fig. 7. (Couleur en ligne.) *Eophycis jamnensis* Jerzmańska, 1968. Colonne vertébrale et sa transition entre partie abdominale et partie caudale, avec les éléments associés du squelette (basés sur l'échantillon UR/KBŚ/308). Pour les abréviations, voir la section 2.

are long and slender; ribs at the more anterior vertebrae are shorter and more bulky. The first and second vertebrae are not associated with ribs. In the anterior part of abdomen epipleural bones are developed, but the precise arrangement is not clear. The first caudal vertebra bears enlarged haemal arches (these are widely open) and the haemal spine is not completely fused with them in some specimens (Fig. 7). The caudal skeleton is not recognisable in any of the specimens.
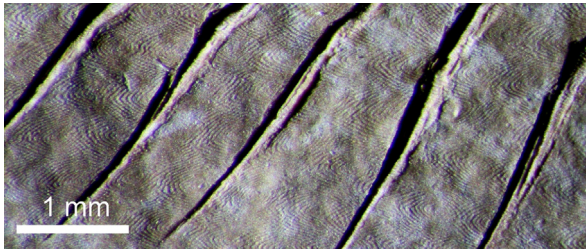
The cleithrum is slightly bent and moderately enlarged in the ventral portion. The supracleithrum is rodlike and relatively short. The posttemporal is V shaped with the rami meeting at an angle of about 40°. The postcleithrum is thin and long. Neither a scapula nor a coracoid is recognisable, similar to the case for the radials of the pectoral fin. The pectoral fin is composed by about 13 to 14 relatively long rays. Their posteriormost tips can reach up to the level of the eighth abdominal vertebra.

The ventral fins are filamentous and their distal tips can reach up to the origin of the anal fin. The fins are composed by two strongly elongated rays, segmented in their distal half, while in the proximal part at least one short fin ray is presented (the preservation of some specimens suggests
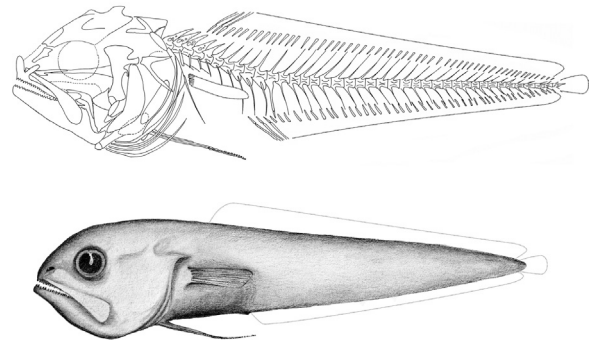

Fig. 9. Original specimens. A. Interpretative drawing of the head and part of vertebral column of the *Eophycis jamnensis* Jerzmańska, 1968 holotype (ZPALWR A/839). B. Fragment of the skull of specimen ZPALWR A/898.
Fig. 9. Échantillons originaux. A. Dessin interprétatif de la tête et d'une partie de la colonne vertébrale de l'holotype d'*Eophycis jamnensis* Jerzmańska, 1968 (ZPALWR A/839). B. Fragment du crâne de ZPALWR A/898.

Fig. 10. *Eophycis jamnensis* Jerzmańska, 1968. Reconstruction.
Fig. 10. *Eophycis jamnensis* Jerzmańska, 1968. Reconstitution.

that there are more fin rays or the single one is split to its basis). The ventral fins are attached to the body anteriorly to the pectoral fins. A pelvic girdle is not recognisable.

The dorsal fin is single and elongated. Predorsal elements are not developed. The precise number of fin rays (more than 40) is not recognisable in the newly collected specimens, similarly with the case of the anal fin. Axonosts of both fins are distributed to the neural (or haemal) spines in a ratio of about 1.5:1.

About four to six anteriormost anal fin axonosts are located in front of the first haemal spine.

The caudal fin is rounded, with about 20 rays.

The body is covered by cycloid scales (Fig. 8), including the head. Their shape is rounded in the abdominal part while in the other parts of the body the scales are oval shaped. Their counts and lateral line position are not determinable.

4. Discussion

Although the genus *Eophycis* was originally classified as a member of the family Gadidae, the possible affinity of this genus with morids was considered earlier by Patterson (1993) but final proof was published by Rozenberg and Prokofiev (2004) on the basis of the specific architecture of the otolith, one of very few unquestionable features that can be used for the determination of fossil morids (Fitch and Barker, 1972; Paulin, 1989).

The original description of the species was based on 13 specimens from two localities of central Paratethys (11 from Jamna Dolna and two from Lesczawa; Jerzmańska, 1968). During examination of part of the original collection (at Wroclaw University during 2013), the available specimens revealed general condition in accordance with published data, with two important aspects: (1) the opercular and hyomandibular parts of the skull are not well preserved at the holotype (ZPALWR A/839; see interpretation in the Fig. 9A) and original reconstruction by Jerzmańska (1968) was completed on the basis of specimen ZPALWR A/898 (Fig. 9B); (2) neither the dorsal nor the anal fins are coalesced with the caudal fin in the holotype, whereas both fins are coalesced (or have an extremely short interval) between the caudal and dorsal or anal fins in specimen ZPALWR A/898 (the same specimen that was
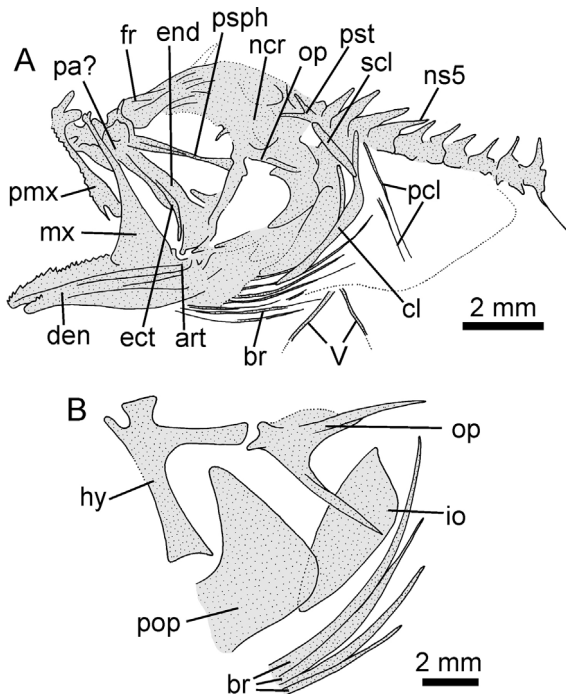
used as the source of information for the reconstruction of the hyomandibula and opercular area).

Articulation of the hyomandibula with the neurocranium in the single articulation facet was considered one of the synapomorphic features of the Gadiformes (Endo, 2002; but seems also to be present in at least some Zeiformes – see Grande et al., 2013: 396); therefore, such a state can be expected also for *Eophycis* (this state was evidenced in newly collected specimens). Nevertheless, specimen ZPALWR A/898 shows two articulation facets on the hyomandibula (if preserved appropriately) and thus cannot be considered conspecific with the holotype. Consequently, the coalescence of the dorsal and anal fins with the caudal fin is not a character of the genus *Eophycis* (i.e., the genus has a separate caudal fin).

The lower process of the gadiform hyomandibula represents a derived condition and it is present in *Muraenolepis*, gadines, lotines, phycines, and gaidropsarines but other gadiforms and outgroup lack it (Endo, 2002). On the other hand, the figures (Endo, 2002: figs. 13D, E) show a small elevation at the anterior margin of the hyomandibula of two morids (*Lotella phycis* and *Laemonema longipes*) comparable to the state observed in *E. jamnensis*. This elevation is obviously not of the same degree as the typical pronounced lower process of the above-mentioned selected gadiforms. It is also possible that this minor structure is in fact the termination of the lateral shelf of the hyomandibula. The significance of this character is not clear.

Two relatively wide interosseous openings are recognisable anteriorly from the hyomandibula and quadrate. The upper interosseous opening was considered to be a derived character and varies from narrow to wide in morids, *Merluccius*, *Raniceps*, *Bregmaceros*, *Muraenolepis*, gadines, lotines, phycines and gaidropsarines (Endo, 2002). This feature was also considered one of the two synapomorphies supporting branch F (Moridae + branch G) in the published strict consensus tree (Endo, 2002: fig. 27) and its presence allowed the placement of eophycids in this branch.

According to Rosen and Patterson (1969) and Markle (1989), there is a trend of paracanthopterygian fishes to increasing posterior extension of the body cavity. Markle (1989) mentioned that the ancestral condition seems to be represented by a state with less than 15 abdominal vertebrae and with the posterior margin of the body cavity bordered by the first haemal spine and first anal radial. The state described in *Eophycis* is practically the same as that described by Markle (1989: 76, fig. 14) for the family Moridae, but the number of abdominal vertebrae is even lower (11). It suggests a relatively short abdominal part of the body in early morids (represented by *Eophycis*) and its

consequent elongation by increasing numbers of abdominal vertebrae.

Fins are badly preserved in the newly collected specimens, but the general observation provided by Jerzmańska (1968) is probably sufficient, at least for the general distribution and numbers of fins. A surprising observation is the single dorsal fin of *Eophycis*, which is atypical for morids (most of them possess two dorsal fins). Nevertheless, numerous juvenile stages of different morid species were figured with both dorsal fins clearly closely associated (and sometimes divided only by a "shallow" dorsal notch), such as *Antimora microlepis* Bean, 1890 (Okamoto et al., 2007: fig. 2; Okamoto et al., 2009: fig. 2b), *Physiculus japonicus* Hilgendorf, 1879 (Okamoto et al., 2007: fig. 3; Okamoto et al., 2009: fig. 2c), *Lepidion inosimae* (Günther, 1887) (Okamoto et al., 2009: figs. 1, 2a), *Gadella jordani* (Böhlke and Mead, 1951) (Okamoto et al., 2010: fig. 2).

Pectoral rays are present at a higher number than in the original description, but not by many (12 vs. 13–14) and so the hypothesis by Rozenberg and Prokofiev (2004) that the low number of pectoral fin rays of *E. jamnensis* is a taphonomic artifact cannot be confirmed.

All the species of the genus *Eophycis* are generally similar, with very few meristic differences (see Table 2). Furthermore, the postmaxillary process of the premaxilla in *E. pshekhiensis* is moved remarkably anteriorly (see Rozenberg and Prokofiev, 2004: fig. 2d) and the posterior edge of the lower jaw does not bear a postarticular process (Rozenberg and Prokofiev, 2004).

Rozenberg and Prokofiev (2004) classified *Eophycis* in the "Physiculus group" (containing *Physiculus* Kaup, 1858, *Gadella* Lowe, 1843, *Laemonema* Günther, 1862, *Salilota* Günther, 1887, and *Tripterophycis* Boulenger, 1902; for details see Schwarzhanz, 1980; and Paulin, 1989) judging by the otolith shape and considered it (on the basis of several anatomical features) to be most similar to the Recent species *Guttigadus nana* (Taki, 1953).

According to Meléndez and Markle (1997), *G. nana* lacks a vomer. This state is relatively unusual and completely different from the genus *Eophycis*. In all species of this extinct genus a vomer was identified (large and subtriangular) and the specimens described herein furthermore show a lack of teeth. Although some authors (e.g., Daniltshenko, 1953) considered the presence or absence of vomerine teeth a taxonomically usable feature in morid fish, Paulin (1983) mentioned that this feature is ontogenetically conditioned. Accordingly, small specimens of *Eophycis* show no vomerine teeth and if they are developed at all, they are developed in much bigger specimens. Another important difference between eophicids and *G. nana* is the single dorsal fin in eophycids, whereas two are present in *G. nana*.

Table 2
Comparison of meristic features of *Eophycis* species.
Tableau 2
Caractéristiques méristiques d'espèces d'*Eophycis*.

Species	Vert	D	A	C	P	V	Reference
Eophycis jamnensis	9–11 + 29–30	ca 50	ca 45	ca 20	13–14	3 + ?	Data herein, Jerzmańska, 1968
E. froidefontainensis	9–10 + 40	55	50	16–20		3	Pharisat, 1991
E. pshekhiensis	9–10 + 32–33	48–50	42–45	17–18	ca 20	?	Rozenberg and Prokofiev, 2004

Eophycids are similar to *G. nana* in: (1) the construction of the ventral fins (two elongated rays with few additional short rays in the proximal part of the fin); (2) low number of the abdominal (9–11 vs. 10–12) and caudal (29–30 vs. 27–30; 40 in *E. froidefontainensis*) vertebrae (numbers of *G. nana* follow Meléndez and Markle, 1997); (3) general body shapes (Fig. 10); (4) subtle scales; and (5) dwarf size.

The dwarf size of *Eophycis* was considered by Rozenberg and Prokofiev (2004) a paedomorphic character, similarly as in *G. nana* (Meléndez and Markle, 1997). Unfortunately, the presence of mature sexual organs cannot be evidenced in fossils and remains thus a hypothesis with no direct evidence. Furthermore, numerous fossil fish specimens are of small size and bigger (adult) specimens are not known, simply for the reason that they lived in different environments (e.g., *Trachinus minutus*, for details see Přikryl, 2015).

Skeletal fossils earlier classified within the Moridae, such as *Strinsia alata* Steindachner, 1859, *S. sobievi* Daniltshenko, 1953, *Onobrosmius elongatus* (Kramberger-Gorjanowic, 1883), *O. oligocenicus* Bogatshev, 1938, *Eclipes veternus* Jordan and Gilbert, 1919, *E. manni* Jordan, 1921, *E. extensus* Jordan, 1921, *E. santamonicae* David, 1943, *Merriamina ectenes* Jordan and Gilbert, 1919, *Lotella andrusovi* (Bogatshev, 1933) and *L. smirnovi* Daniltshenko, 1953 cannot be classified in this group with certainty (see Fitch and Barker, 1972; and Swidnicki et al., 1990).

Clearer fossil evidence of this family is represented by *Lepidion miocenica* Sato, 1962 from the Miocene of Japan (Sato, 1962); undescribed morid specimens from the Miocene of California (Huddleston and Takeuchi, 2006); a *Physiculus-Salilota* like specimen from the Late Oligocene/Early Miocene of Argentina (Bogan and Agnolin, 2011); *Fanteichthys torricellensis* Carnevale, 2007 from the Middle Miocene (Serravalian) of central Italy (Carnevale, 2007); *Gadella* Lowe, 1843 from the Messinian of Sierra Columbares (Gaudant, 1995b), the Messinian of Lorca (Gaudant, 1995a: pl. II, fig. 7), the Pliocene of the Marecchia River (Sorbini, 1988: pl. 16: fig. 2), and the Pliocene of the Crete (Gaudant, 2001). A similar morphotype to *Eophycis* was mentioned also from the Moler formation (Bonde, 1987: 36), but with no description, and therefore no further comment is possible.

Acknowledgement

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