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KRUMVIRICHTHYS BRZOBOHATYI GEN. ET SP. NOV. – THE OLDEST RECORD OF THE DEEP-SEA SMELTS (BATHYLAGIDAE, ARGENTINIFORMES)

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Abstract. The family Bathylagidae (deep-sea smelts) is a group of marine meso- and bathypelagic argentiniform fish with relatively poor fossil record. The described specimens from the Egerian deposits of the Krumvíř locality, named *Krumvirichthys brzobohatyi* gen. et sp. nov. represent oldest verifiable record of the bathylagid fishes known up to date. The new genus and species is characterized by semicircular orbitosphenoid at the dorsal section of the orbit, basisphenoid developed, opercle bearing posterodorsally developed large process, opercle and subopercle posteroventrally radially grooved, preopercle with triangle-shaped process at the posteroventral margin of the bone, cleithrum with enlarged triangle-shaped posterior lamina, no postcleithra, pectoral fin with eight or nine rays and elongated up to the level of the insertion of the dorsal fin, pelvic fin with nine rays inserted just below the middle of the dorsal fin, dorsal fin with ten or eleven rays, up to eight supraneurals presented in front of dorsal fin, vertebral column consists by at least 23 + 21 vertebrae, body covered by thin and large cycloid scales, and lateral line scales reinforced around tubular part. The combined presence of the orbitosphenoid and basisphenoid in new species particularly reminds the Recent bathylagid genera *Lipolagus*, *Melanolagus*, and *Bathylagichthys*.

Introduction

The family Bathylagidae (deep-sea smelts) is a small group of argentinifrom fish with slightly more than twenty contemporary species arranged in eight living genera with Subarctic to Antarctic distribution inhabiting marine meso- and bathypelagic environment (Rass & Kashkina 1967; Borodulina 1968; Kobyliansky 1986; Nelson et al. 2016; Froese & Pauly 2021). The bathylagids are classified as a subfamily within Microstomatidae (Kobyliansky 1990; Johnson & Patterson 1996; Nazarkin 2018) or a separate family within Argentiniformes (Nelson et al. 2016; Betancur-R et al. 2017). Also larval characters suggest close relationships with argentinoids (see Ahlstrom et al. 1984).

The unambiguous fossil record of this group is rather poor and most of the earliest taxa should be carefully revised. The skeletal remains have been described from the Miocene deposits of California – *Bathylagus angelensis* (Jordan & Gilbert, 1919) and *Quaesitia quisquilia* Jordan & Gilbert, 1919 (David 1943; Fierstine et al. 2012); Japan – *Bathylagus sencta* Sato, 1962, *B. obesa* Sato, 1962, *B. toyohamaensis* Ohe, 1993, and *B.* sp. (Sato 1962; Ohe 1993; Yabumoto & Uyeno 1994); and Russia – *Leuroglossus kobylianskyi* Nazarkin, 2018 and several bathylagid taxa classified in open nomenclature (Nazarkin 2018; Voskoboinikova & Nazarkin 2018). As mentioned by Nazarkin (2018), the generic attribution of the fossil representatives from California and Japan should be

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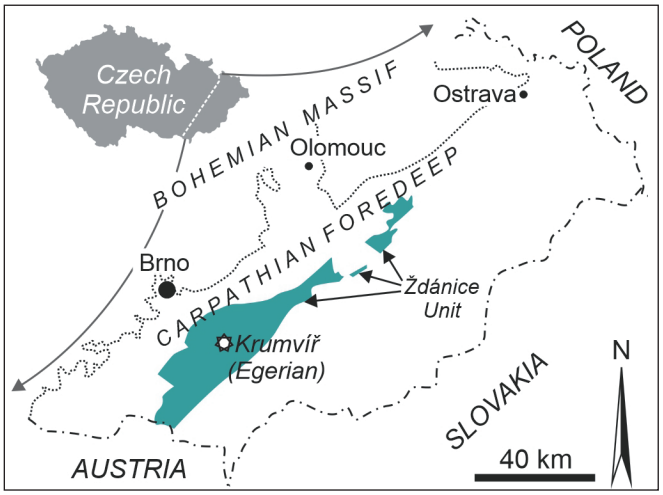

Fig. 1 - The geographic position of the Krumvíř locality within the Czech Republic. The distribution of the Žďánice Unit sediments follows Čtyřoký & Stráník (1995).

further examined. The otolith fossil record is surprisingly poor and only published records are represented by specimens from the Middle Pleistocene of Calabria (Italy; Girone 2003 and Nolf 2013) and Late Cretaceous of Bavaria (Germany; Schwarzhans 2010).

The deep-sea smelts are characterized by number of characters, but details in individual authors' attitudes may differ from one author to another. Herein combination of characters provided by Nazarkin (2018) is followed. Bathylagids are characterized by moderately elongated body with two or three branchiostegal rays, very large eyes and snout usually short, anal fin positioned in the posterior third of the body, pectoral fin at the ventral margin of the body, adipose fin usually present, swim bladder absent, lower jaw with continuous row of the identical densely spaced teeth, upper jaw teeth absent, and rod shaped premaxilla lacking processes (see Nazarkin 2018 for original source references).

The current publication presents description of the bathylagid remains recognized in the Egerian marlstones of the Krumvíř locality (Moravia, Czech Republic). The remains described herein (i) represent the oldest fossil skeletal record of this group, and (ii) document the distribution of the Bathylagidae within Paratethys during Oligo–Miocene.

Locality and associated fauna

The locality Krumvíř is located in the south eastern part of the Czech Republic, approximately 30 km SE from the center of the Brno (Figure 1) and preserves Egerian (Oligo-Miocene) deposits of the Ždánice-Hustopeče Formation of the Ždánice Unit (Čtyřoký & Stráník 1995; Gregorová 1997). The clayish marlstones preserved remains of cephalopds, insect, plants and mainly, fishes (Kalabis 1957; Knobloch 1969; Brzobohatý et al. 1975; Gregorová 2013; Přikryl & Carnevale 2018). The ichthyo-assemblage is represented by requiem sharks (Carcharhinidae: *Carcharhinus priscus*), herrings (Clupeidae: genus et species indetermined), lightfishes (Phosichthyidae: *Vinciguerria merklini*), lanternfish (Myctophidae: ?*Diaphus* sp.), true dories (Zeidae: ?*Zenopsis* sp.), hakes (Merlucciidae: *Merluccius* sp.), cusk eels (Bythitidae: *Kalabisia krumvirensis*; Ophidiiformes: genus et species indetermined), remoras (Echeneidae: genus et species indetermined), pipefish (Syngnathidae: *Syngnathus* sp.), snake mackerels (Gempylidae: *Hemithyrsites maicopicus*), cutlassfishes (Trichiuridae: *Anenchelum* sp.), unidentified perch-like fish (genus cf. *Oliganodon*), boarfishes (Caproidae: *Proantigonia radobojana*), and deep-sea smelts (Bathylagidae) described herein.

The assemblage thus documents meso- to bathypelagic environment (supported also by the specimens under consideration), with relatively strong neritic influence – see Gregorová (1997, 2013).

Material and Method

The material is housed in the paleontological collection of the Department of Geological Sciences, Faculty of Sciences, Masaryk University in Brno (abbreviated by acronym MU and prefix PAL elsewhere). The list of material is included in the systematic section.

The fossils were prepared using small scalpels or needles before study. The photos were taken using a Canon EOS 1000D camera attached to a Leica MZ6 stereomicroscope. The drawings were prepared using a camera lucida drawing tube; the measurements of the specimens were based on the photos.

Systematic paleontology

Infraclass **TELEOSTEI** Müller, 1845, *sensu* Arratia, 1999

Superorder **Protacanthopterygii** Greenwood, Rosen, Weitzman & Myers, 1966

Order **Argentiniformes** Johnson & Patterson, 1996

Family Bathylagidae Gill, 1884

Genus *Krumvirichthys* gen. nov.

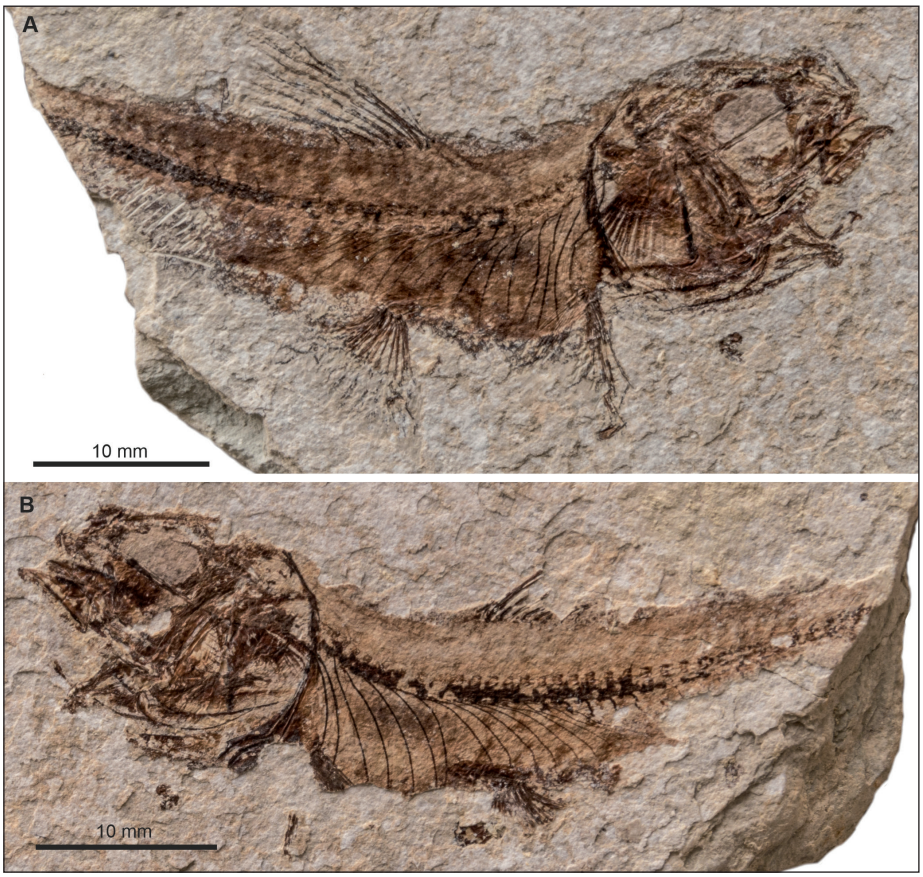

Fig. 2 - *Krumvirichthys brzobohatyi* gen. et sp. nov. Krumvíř, holotype. A) specimen MU PAL00353. B) counterpart specimen MU PAL00354.

Type species: *Krumvirichthys brzobohatyi* sp. nov.

Etymology: The generic name is composition of two words referring to "Krumvíř" (village name of the locality) and "ichthys" ("fish" in Greek, as a usual root for fish names).

Diagnosis: Bathylagid fish characterized by following unique combination of the characters: semicircular orbitosphenoid at the dorsal section of the orbit, basisphenoid developed, opercle bearing posterodorsally developed large process, opercle and subopercle posteroventrally finely radially grooved, preopercle with triangle-shaped process at the posteroventral margin of the bone, cleithrum with enlarged triangle-shaped posterior lamina, no postcleithra, pectoral fin with eight or nine rays reaching the level of the insertion of the dorsal fin, pelvic fin with nine rays inserted just below the middle of the dorsal fin base, dorsal fin with ten or eleven rays, up to eight supraneurals presented anteriorly to dorsal fin, vertebral column consist of at least 23 + 21 vertebrae, intermuscular bones presented, body covered by thin and large cycloid scales, and lateral line scales reinforced around tubular part.

Krumvirichthys brzobohatyi sp. nov.

Figs. 2-8, Tab.1

Holotype: Specimen preserved as a part (MU PAL00353 – head pointed to right; Fig. 2A) and counterpart (MU PAL00354 – head pointed to left; Fig. 2B).

Type horizon and locality: Oligocene–early Miocene, Egerian, NN1 (Gregorová 1997); Krumvíř (Ždánice Unit).

Material: MU PAL00355 (paratype; isolated head in right lateral view; counterpart of the MU PAL00356, Fig. 3A1); MU PAL00356 (paratype; isolated head in left lateral view; counterpart of the MU PAL00355, Fig. 3A2); MU PAL00357 (paratype; anterior body fragment with the dorsal and pectoral fins as well as the posterior part of the head preserved in right lateral view, Fig. 3B); MU PAL00358 (paratype; anterior body fragment with the pectoral fin and the almost complete head in right lateral view, Fig. 3C) – all specimens from the type horizon and locality.

Etymology: In honor of Professor Rostislav Brzobohatý (Masaryk University in Brno), for his paleoichthyological studies in the Paleogene and Neogene of the Europe.

Diagnosis: As for the genus.

	measurement (in mm)
preserved length	ca 50
estimated length	ca 80
head length	16
head depth	13.3
orbit diameter	4.2
preorbital length	3.4
orbitosphenoid length	1.5
predorsal length	22.5
longest ray of D	12
length of D base	6.2
longest ray of P	9
longest ray of V	6.4

Tab. 1 - *Krumvirichthys brzobohatyi* gen. et sp. nov. Krumvíř. Measurements of the holotype MU PAL00353.

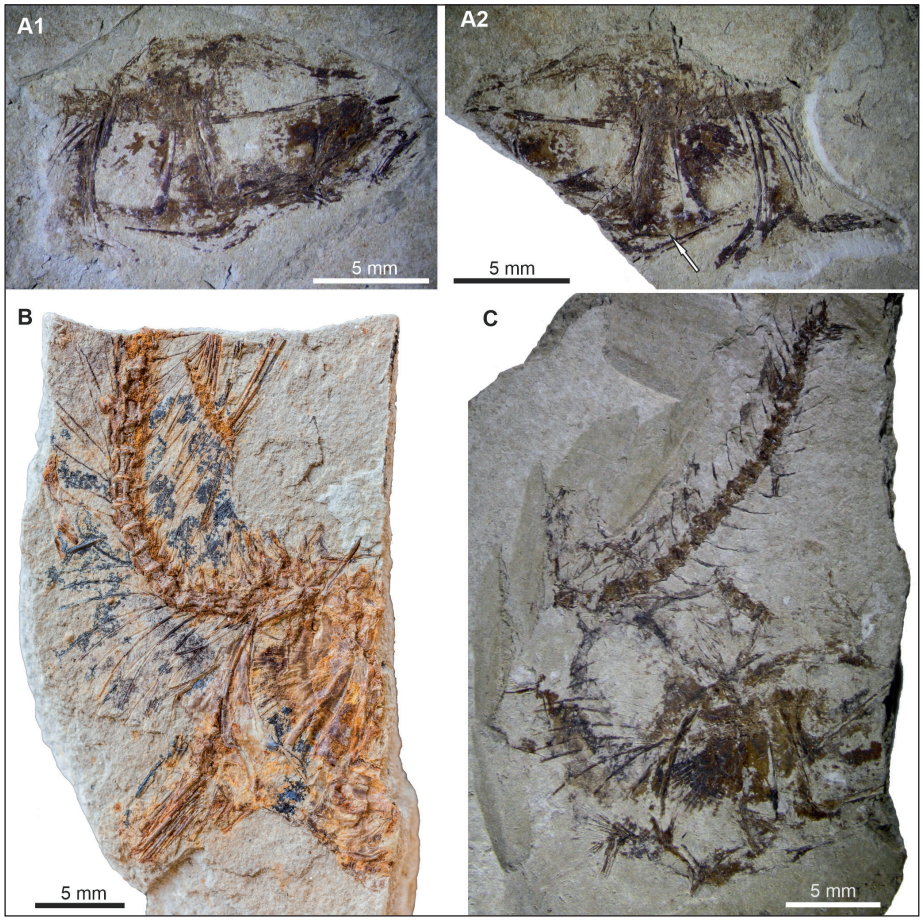

Fig. 3 - *Krumvirichthys brzobohatyi* gen. et sp. nov. Krumvíř. A) Specimen MU PAL00355. B) Counter-specimen MU PAL00356. C) Specimen MU PAL00357. D) Specimen MU PAL00358. The arrow shows the postero-ventral process of the preopercle.

Description. Small fish (preserved length is about 50 mm; estimated standard length is about 80 mm), moderately elongated and slightly laterally compressed. The head is rounded (head length to head depth ratio is 1.2), and the mouth terminal. The lower jaw joint is located at the level of the anterior margin of the orbit. The orbit is large (orbit diameter represents ca 26% of the head length), located relatively anteriorly (preorbital length represents slightly more than 20% of the head length). Measurable dimensions are summarized in the Table 1.

The neurocranium is fragmentarily preserved and only few individual bones are identifiable. The lateral ethmoid is well recognizable ossification just in front of the orbit, with rounded lateral extensions and convex dorsal margin. The orbitosphenoid is a semicircular ossification in the dorsal part of the orbit (its antero-posterior length represents ca 35% of the orbit diameter). The remains of basisphenoid are recognizable, but its actual shape is unclear (due to its partial covering by other skeletal elements). The parasphenoid is straight and running through the middle of the orbit (Fig. 4A).

The preopercle is L-shaped with the vertical limb about twice longer than the horizontal one. The postero-ventral margin of the bone bears recognizable triangle-shaped posterior process (well discernable at the specimen MU PAL00356; Fig. 5A). The opercle articulate with the hyomandibula in the antero-dorsal part of the bone. The postero-dorsal edge bears large process that dorsally delimits deep notch at the posterior margin of the bone. The postero-ventral corner of this bone bears the shallow radial grooves which border better-ossified "rays" between them. The antero-dorsal margin of the opercle is wave shaped, with distinctive concavity in the postero-dorsal margin of the bone. The subopercle is sickle-shaped and its postero-ventral margin is finely radially grooved (see Fig. 4A).

The entopterygoid is large, more or less rounded, making main element forming the roof of the mouth cavity and anteroventrally articulated with ectopterygoid. The ectopterygoid has shape of strongly elongated thin triangle (both its limbs are almost same long and meeting under the angle of the 70 degrees) that is well recognizable at the specimen MU PAL00355. The metapterygoid is missing.

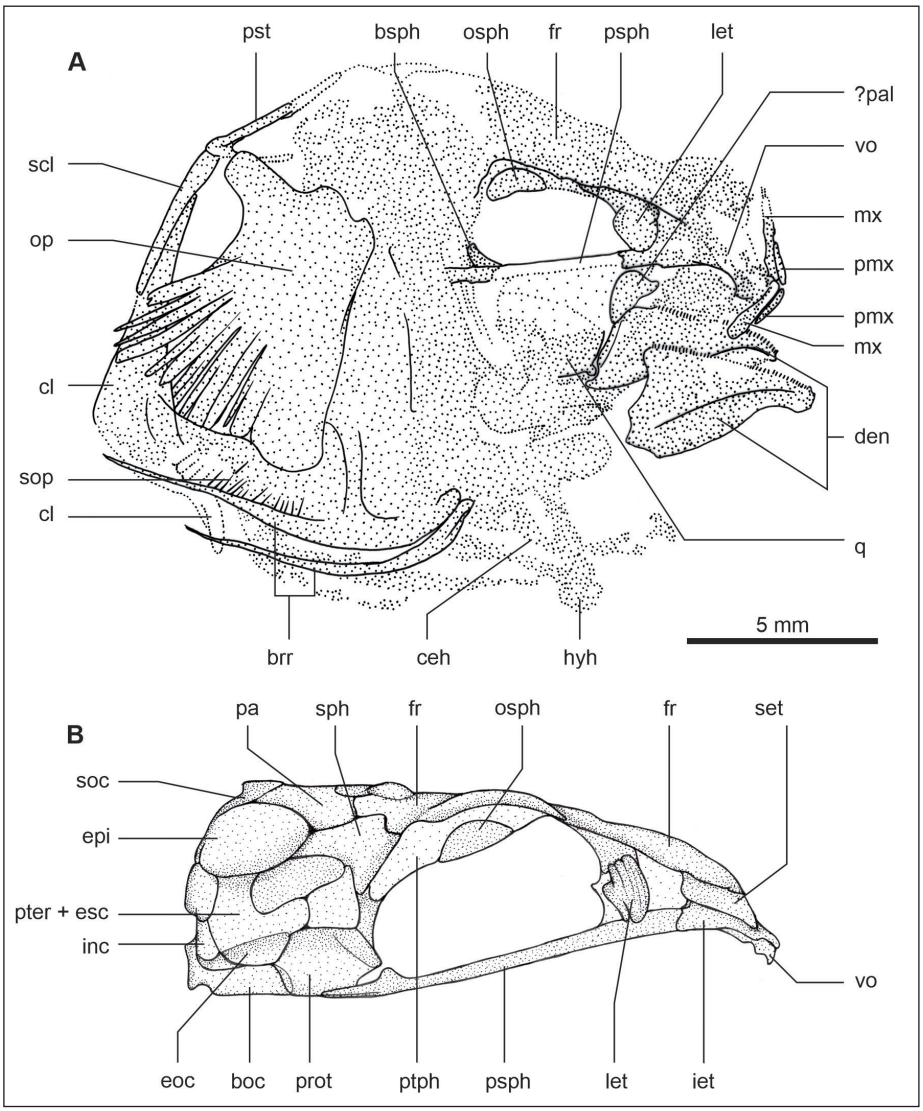

Fig. 4 - A) *Krumvirichthys brzobohatyi* gen. et sp. nov. Krumvíř. Holotype specimen MU PAL00353. B) *Dolicholagus longirostris* (Maul, 1948) – adopted and modified from Kobyliansky (1986). Anatomical abbreviations: boc – basioccipital; brr – branchiostegal rays; bsph – basisphenoid; ceh – anterior ceratohyal; cl – cleithrum; den – dentary; eoc – exocipital; epi – epiotic; esc – extrascapular; fr – frontal; hyh – hypohyal; iet – infraethmoid; inc – intercalar; let – lateral ethmoid; mx – maxilla; op – opercle; osph – orbitosphenoid; pa – parietal; pal – palatine; pmx – premaxilla; prot – prootic; psph – parasphenoid; pst – posttemporal; pter – pterotic; ptph – pterosphenoid; q – quadrate; scl – supracleithrum; set – supraethmoid; soc – supraoccipital; sop – subopercle; sph – sphenotic; vo – vomer; ? – uncertain element. Anterior to right.

A sickle shaped skeletal element in the anterior part of the mouth roof (preserved at the holotype specimen MU PAL00353) is tentatively interpreted to be toothless palatine.

The oral jaws are only partially preserved. The premaxillae (same as the maxillae) are preserved from both side of the head and suggesting simple, stick-like morphology. The maxilla is more robust than premaxilla, about one third to one half longer and with no recognizable details. None of the upper jaw bones bears teeth. The lower jaw is relatively short, triangular, with concave ventral and convex dorsal margins. In the lower third of the dentary, parallel to the ventral margin, is recognizable mandibular sensory canal. The anterior third of the dorsal margin of the dentary bears teeth, arranged in single row. The teeth are simple, cone-like with simple and sharp tips.

The hyoid bar is fragmentarily preserved, with few recognizable details (such as general shape of anterior ceratohyal and rounded hypohyals). There are clearly recognizable two sabre like branchiostegal rays (Fig. 4A) and urohyal with shape of antero-posteriorly elongated drop (Fig. 5B). The specimen MU PAL00354 preserves imprint of the first (?) branchial arch with associated gill rakers (Fig. 5C) – there are six or seven and approximately nine in dorsal and ventral parts of the branchial arch respectively.

The vertebral column is incomplete in all of the available specimens, but fragments in various specimens suggest at least 23 abdominal vertebrae (holotype specimen MU PAL00353) and 21 caudal vertebrae (MU PAL00358). However, these numbers probably represent the minimum value for these meristic data. The specimen MU PAL00358 preserves remains of fragmentarily preserved caudal skeleton, but without any discernable details.

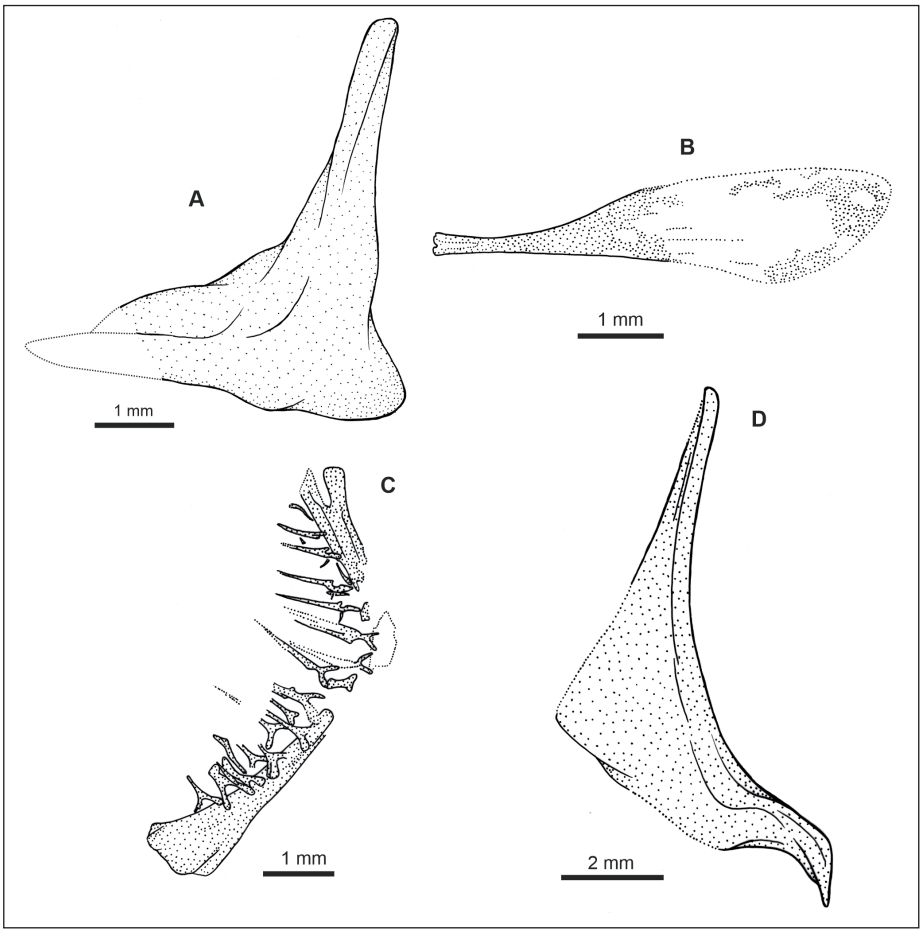

Fig. 5 - *Krumvirichthys brzobohatyi* gen. et sp. nov. Krumvíř. A) Specimen MU PAL00356. Interpretative drawing of the preopercle. Anterior to left. B) Specimen MU PAL00358. Interpretative drawing of the urohyal. Anterior to left. C) Holotype specimen MU PAL00354. Interpretative drawing of the first (?) branchial arch associated with gill rakers. Anterior to left. D)Specimen MU PAL00357. Interpretative drawing of the cleithrum. Anterior to right.

There are preserved approximately eleven pairs (or slightly more as suggest MU PAL00357) of ribs. Remains of the intermuscular bones (tentatively interpreted to be epineurals and epipleurals) are recognizable in the holotype specimen, but preservation is too fragmentary to be more accurate.

Although none of the specimen is complete, it is possible to say that the dorsal fin inserts in the anterior half of the body (predorsal length of the holotype MU PAL00353 is 22.5 mm). The base of the dorsal fin represents more than 25% of the predorsal length. The fin is composed by ten or eleven rays, with first two rays significantly shorter than the posterior ones. The length of the longest ray represents slightly more than 50% of the predorsal length (and 75% of the head length). The dorsal fin in MU PAL00357 is supported by ca 13 posteriorly shortening pterygiophores (the first one is the shortest, but incomplete preservation does not allow to confirm its original state). Anteriorly to dorsal fin remains of several supraneurals (up to eight?) are recognizable. The individual supraneuralia are stick-like and inserted in the interneural spaces (but exact numbers and distribution is not clear). The anal fin is almost unrecognizable due to preservation, but its origin is obviously posteriorly to the dorsal fin.

The pectoral girdle is well preserved in almost all specimens. The posttemporal is well developed, with dorsal ramus about twice longer and more robust than the ventral one. The posttemporal is posteroventrally articulated with stick-like straight supracleithrum that articulates ventrally with cleithrum. No remains of sensory canal associated with supracleithrum are recognizable. The cleithrum is sigmoidally shaped, with enlarged triangle-shaped posterior lamina (Fig. 5D). The remains of the scapula and coracoid mark triangle-like darker spot postero-ventrally to cleithrum with no recognizable details. There are no postcleithra. The pectoral fin is composed by eight or nine rays articulated with pectoral girdle closely to the ventral profile of the body. The pectoral fin is relatively long, with the posterior-most tip reaching the level of the insertion of the dorsal fin (the longest pectoral ray represents more than 56% of head length).

The preserved remains of the basipterygia seem to be relatively simple, posteriorly widened plates, unfused in midline. The pelvic fin is formed

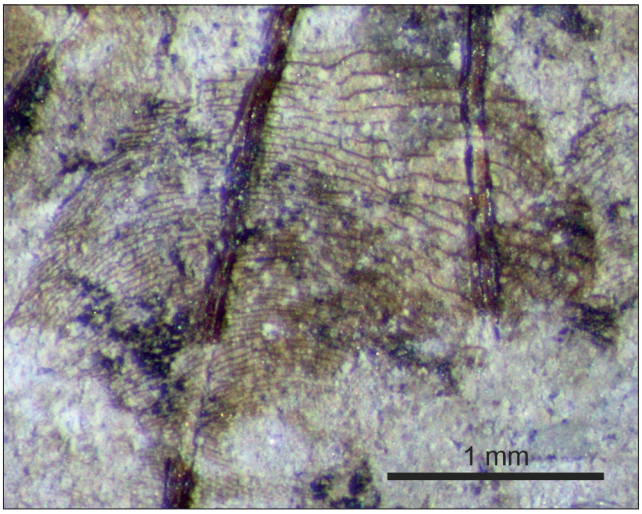

Fig. 6 - *Krumvirichthys brzobohatyi* gen. et sp. nov. Krumvíř. Specimen MU PAL00358. Abdominal scale on the ventral portion of the body (at the level between second and third ribs). Anterior to right.

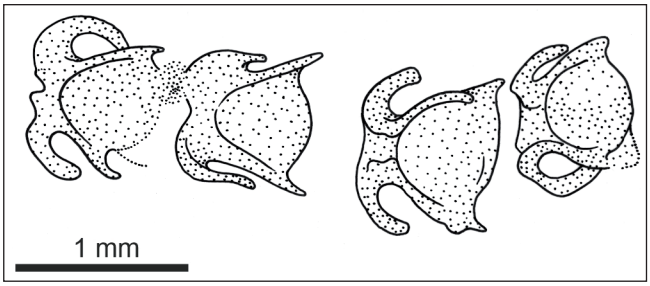

Fig. 7 - *Krumvirichthys brzobohatyi* gen. et sp. nov. Krumvíř. Holotype specimen MU PAL00353. Interpretative drawing of the lateral line scales. Anterior to right.

by nine rays and inserts just below the middle of the dorsal fin base. The length of the longest pelvic rays represents more than 70% of the longest pectoral rays.

The body is covered by thin and large cycloid scales, preserving numerous circuli (Fig. 6). The scales are fully comparable with those of bathylagid fishes figured by Nazarkin (2018: fig. 5). The lateral line seems to be located just above the level of vertebral column – the preserved structures allow to recognize the morphology of reinforced tissue around individual tubular part (Fig. 7) and it seems that the lateral line scales are reduced to these "simple" structures.

The holotype specimen MU PAL00353 preserves remains of the dark pigmentation (Figs. 2A and 8). There are several roughly vertically oriented stripes and spots in the dorsal part of the body. Moreover, there are several larger pigmentation spots preserved at the body flanks, approximately below the lateral line level.

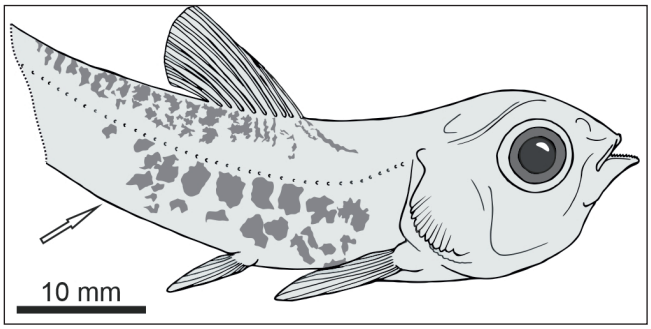

Fig. 8 - *Krumvirichthys brzobohatyi* gen. et sp. nov. Krumvíř. Interpretative drawing of preserved dark pigmentation based on the holotype specimen MU PAL00353. Arrow marks position of the anal fin (omitted).

Discussion and conclusion

Taxonomic remarks and affinities. The attribution of the considered fossils to the family Bathylagidae is supported by the overall physiognomy of the body, short mouth gape, presence of two branchiostegal rays, toothless maxilla and premaxilla, uniformly toothed lower jaw, large orbit, short snout, and pectoral fin positioned closely to the ventral margin of the body − see list of the characters in Nazarkin (2018) and original references mentioned therein.

Although the fossil remains are incomplete and partly disarticulated, a number of characters support their affinity with contemporary bathylagids. Kobyliansky (1986) presented osteological framework for all bathylagid genera, including a number of details on skull and postcranial skeleton; the combination of morphological characters has been established to define individual genera and although not all of them have good potential for fossilization, combination of absence or presence of orbitosphenoid, basisphenoid, metapterygoid and postcleithra gave enough information to clearly separate individual genera each from other (Table 2).

The studied fossils show a combination of presence of orbitosphenoid and basisphenoid, but metapterygoid and postcleithra are obviously missing (see description above). The combined presence of the orbitosphenoid and basisphenoid observed in the *Krumvirichthys* gen. nov. is typical for Recent bathylagid genera *Lipolagus*, *Melanolagus*, and *Bathylagichthys*, but none of them may be associated with fossils under the consideration. The genera *Lipolagus* and *Melanolagus* are monospecific taxa (Froese

	Krumvirichthys gen. nov.	*Bathylagichthys* Kobyliansky, 1986	*Lipolagus* Kobyliansky, 1986	*Melanolagus* Kobyliansky, 1986	*Dolicholagus* Kobyliansky, 1986	*Bathylagus* Gunther, 1878	*Pseudobathylagus* Kobyliansky, 1986	*Leuroglossus* Gilbert, 1890	*Bathylagoides* Whitley, 1951
orbitosphenoid	developed	developed	developed	developed	developed	developed	none	reduced	none
basisphenoid	developed	developed	developed	developed	none	none	none	none	almost completely reduced
metapterygoid	none	developed	developed	none	none	none	none	none	developed
postcleithrum	none	three elements	two elements	two strongly reduced elements	none	one, highly reduced dorsal element	none	none	none

Tab. 2 - Comparison of the selected characters of the bathylagid genera. Based on Kobyliansky (1986) and personal observation.

& Pauly 2021) and contrary to *Krumvirichthys* gen. nov., both of them show two postcleithra (strongly reduced in *Melanolagus*); furthermore the genus *Lipolagus* shows an ossified metapterygoid (Kobyliansky 1986). The genus *Bathylagichthys* consist of six species (Gon & Stewart 2014) and contrary to *Krumvirichthys* gen. nov., it is characterized by the presence of metapterygoid and three postcleithra (Kobyliansky 1986).

Krumvirichthys brzobohatyi gen. et sp. nov. is clearly different from all bathylagid genera known up to date. On the other hand, the considered fossils show certain level of similarity with *Dolicholagus longirostris* (Maul, 1948), mainly by (i) shape and position of the sickle shaped orbitosphenoid and (ii) general proportions of the neurocranium in lateral view (cf. Figs. 4A and B). The new bathylagid genus differs from *Dolicholagus longirostris* in presence of basisphenoid and rather untypical pigmentation at the body, together with relatively long pectoral fins (reaching the level of the dorsal fin origin contrary to short pectorals in *Dolicholagus*; Kobyliansky 1985). On the contrary, the long pectoral fins partly remind its morphology in *Bathylagichthys longipinnis* (Kobyliansky, 1985).

Nazarkin (2018) presented a hypothesis of the relationships of bathylagids based on a set of morphological characters and the phylogram (Nazarkin 2018: fig. 8; L=67; Ci=59; Ri=60) has been used with attempt to provisionally accommodate the phylogenetic position of the *Krumvirichthys* gen. nov., on the base of the preserved characters. The suggested position (Fig. 9) reflects absence of the postcleithra (character 35 of Nazarkin 2018) but obviously before loss of ossified basisphenoid (see Table 2). In such case, the presence of "almost completely reduced" basisphenoid (as described by Kobyliansky 1986) in *Bathylagoides* would be considered as "taxic atavism", same as in case of the single, highly reduced dorsal element of postcleithrum in the *Bathylagus* – see Stiassny (1992) for discussion of the phenomenon and references.

It would be also noted, that the new genus and species is clearly different from *Idrissia carpathica* Jerzmańska, 1960 from Oligocene deposits of Polish Carpathians, assumed to be Bathylagidae by Jerzmańska & Kotlarczyk (1981) and consequently by Kotlarczyk et al. (2006). Several characters mentioned in the original description of *Idrissia carpathica* is in direct contradiction with diagnostic characters of the bathylagids (such as teeth on upper jaw and relatively high number of branchiostegal rays visible in the interpretative drawings – see Jerzmańska 1960: 374, fig. 3) and such a classification is not supported by any argument. Therefore, until detailed morpho-anatomical revisions of the type material will be available, such an attribution cannot be seriously taken into account.

Based on the foregoing, the specimens from Krumvíř locality represent the oldest verifiable record of the bathylagid fishes and document the distribution of this group during Oligo–Miocene within Central Paratethys. The material is distinctively different from all other known fossil and Recent bathylagids, supporting its separated taxonomic status. Furthermore, the classification increased the diversity of the Bathylagidae to nine genera.

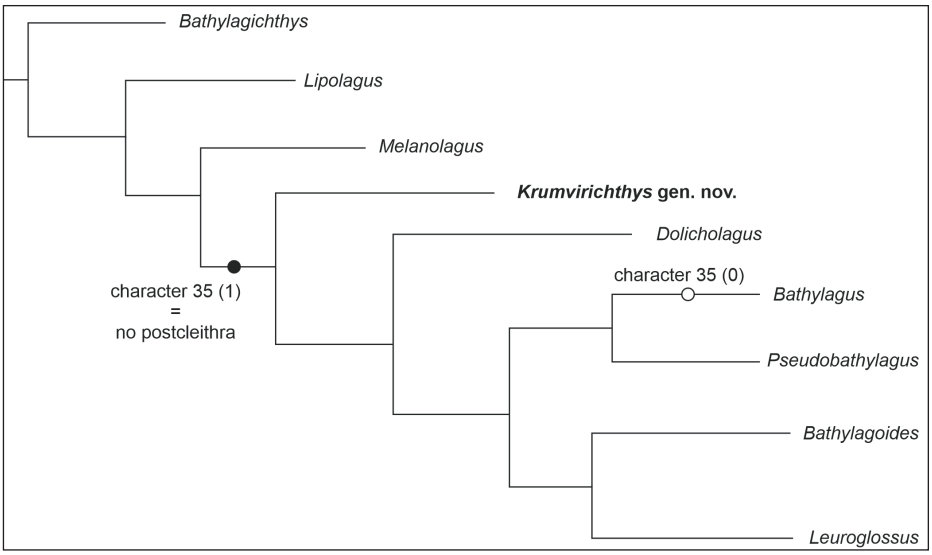

Fig. 9 - Expected phylogenetic position of the *Krumvirichthys* gen. nov. in the phylogram produced by Nazarkin (2018) – simplified and modified. Note atavistic nature of the character 35.

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