



General Paleontology, Systematics and Evolution (Vertebrate Palaeontology)

A morid cod (Gadiformes, Moridae) from the early Oligocene deposits of the Czech Republic



Un moridé (Gadiformes, Moridae) en provenance de dépôts de l'Oligocène inférieur de la République tchèque

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ABSTRACT

An articulated skeleton of a morid cod (Gadiformes, Moridae) is described from the Oligocene Menilitic Formation, exposed in the Kelč-Strážné locality (Moravia; Subsilesian Unit; Western Carpathians). The fossil, preserved in dorsal view, is only partially complete, and lacking most of the postcranial part of the body. It shows a suite of features that clearly separate it from other gadiform taxa frequently found in the Oligocene-Miocene deposits of the region, and suggest its attribution to the family Moridae (mainly due to the general architecture of the skull). Due to the incompleteness of the fossil, it is not possible to define precisely its taxonomic status. However, the possession of two pterotic processes suggests that the fossil documented herein represents a member of the “Pseudophycis Group” (according to Paulin, 1989), related to the genus *Lotella* Kaup, 1858.

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R É S U M É

Un squelette de moridé (Gadiformes, Moridae) en connexion anatomique est décrit dans la formation ménilitique oligocène, affleurant dans la localité de Kelč-Strážné (Moravie, Unité sous-silésienne, Carpates occidentales). Le fossile, conservé en vue dorsale, n'est que partiellement complet, et la majeure partie postcrânienne du corps manque. Il montre un ensemble de caractères qui le différencie clairement des autres gadiformes fréquemment trouvés dans les dépôts oligo-miocènes de la région, et suggère son attribution à la famille des Moridae (principalement en raison de l'architecture générale du crâne). Du fait qu'il est incomplet, le statut taxonomique précis de ce fossile n'est pas définissable. Par ailleurs, la présence de deux processus ptérotiques suggèrent que le fossile présenté ici représente un membre du « groupe Pseudophycis » (selon Paulin, 1989), lié au genre *Lotella* Kaup, 1858.

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1. Introduction

Oligocene fish fossils of Moravia (Czech Republic; western Carpathians) have been described in numerous papers dealing with various groups of Elasmobranchii and Teleostei (e.g., Gregorová, 2011, 2013 and references therein), but only a few of these finds can be attributed to the order Gadiformes, and all of them belong to the single family Merlucciidae (namely, the genus *Palaeogadus* von Rath, 1859; Gregorová, 2013; Gregorová and Požár, 2003), although otoliths, as usual, suggest a much higher diversity of this order during the Oligocene within this region (for example, otoliths from the early Oligocene Pouzdřany Unit indicate the presence of Bregmacerotidae, Macrouridae, Melanonidae, Gadidae, Merlucciidae, Phycidae, and Lotidae; see Brzobohatý and Krhovský, 1998). Also, the coeval sediments from other parts of the Paratethys sedimentary basins preserved a wider diversity of gadiformes, including representatives of the family Moridae.

Moridae is a relatively small family with about 108 extant species, classified within 18 genera (Nelson et al., 2016). Přikryl (2015) briefly summarised the main skeletal fossil records of the family globally. Within the Paratethys, some of the taxa described earlier as Moridae (based mainly on results published by Daniltshenko, 1953, 1960) were later reconsidered and transferred to the Gadidae (for discussion, see Świdnicki et al., 1990), Bregmacerotidae or left *incertae sedis* (Přikryl et al., 2016, Prokofiev, 2005, respectively). Nevertheless, the Oligocene deposits of the Paratethys also preserve remains of true morids, today referred to *Eophycis* Jerzmańska, 1968. Up until now, three species of the genus have been described from various parts of the Paratethys (Jerzmańska, 1968; Pharisat, 1991; Rozenberg and Prokofiev, 2004). The definitive attribution of any fossil to this family is difficult because the significant characters are rarely preserved in fossil material (namely the contact of the anteriorly enlarged horns of the gas bladder and otic capsules, the horizontal septum of the gas bladder, the specific morphology of the otoliths, the unique architecture of the caudal skeleton, and, most likely, the possession of a parasphenoid with a transversely aligned ascending process, e.g., Fitch and Barker, 1972; Howes, 1991; Paulin, 1983, 1988, 1989; Svetovidov, 1967; however, *in situ* otoliths identified in *Eophycis* represent key arguments for the correct classification (Rozenberg and Prokofiev, 2004). Although the newly described fossil is only partially complete, it clearly differs from *Eophycis*. The main goal, therefore, is to describe and to document this new record of the family Moridae from the Rupelian deposits of Moravia (Czech Republic).

2. Material and methods

The material under consideration was discovered by Mr. Bronislav Novosad at the “Kelč-Strážné” locality in 2008. The fossil was partially prepared using small scalpels or needles. Examination was made of the fossil specimen, as well as plaster casts or latex peels (in some cases, coated with ammonium chloride for better visibility of features). Photographs were taken using a Canon EOS 1000D camera attached to a Leica MZ6 stereomicroscope. The drawings

were prepared using a camera lucida drawing tube and measurements of the specimens were based on the photos. The comparison with fossil and recent species of Moridae is based on the literature.

The fossil is housed in the collection of the National Museum in Prague (NMP).

Anatomical abbreviations: boc: basioccipital; br: brachioistegal rays; cl: cleithrum; co: circumorbitals; den: dentary; ect: ectopterygoid; end: endopterygoid; epio: epiotic; epn: epineural; exo: exoccipital; fr: frontal; hy: hyomandibula; le: lateral ethmoid; lpr: lower process of hyomandibula; mes: mesethmoid; mtp: metapterygoid; mx: maxilla; na: nasal; op: opercle; P: pectoral fin; pa: palatine; par: parietal; pcl: postcleithrum; pmx: premaxilla; pop: preopercle; prar: articular process of premaxilla; pras: ascending process of premaxilla; prop: opercular process of hyomanibula; prpm: postmaxillary process of premaxilla; pst: posttemporal; pter: pterotic; q: quadrate; r: ribs; rad: radials; scl: supracleithrum; soc: supraoccipital; sph: sphenotic; uh: urohyal; V: pelvic fin; vo: vomer; vert: vertebrae.

3. Geological note

The Kelč locality (Moravia, Western Carpathians; Sub-silesian Unit) is historically well known for providing a rich fossil record (e.g., Kalabis, 1975; Knobloch, 1969; Prokop et al., 2007). Fossils were originally collected at “Kelč-Zámek” (Kalabis, 1975), but this area is now built up and as such is no longer accessible. All recently collected materials referred to the Kelč locality originate from the “Kelč-Strážné” area, situated about 1.5 km northwest of the city centre. Fragments of Dynów marlstones (one of the litho-stratigraphic members of the Menilitic Formation; for details regarding stratigraphy, see Bubík et al., 2016) are found in ploughed fields or meadows, and although no larger slabs of the sediments are available, the locality has provided relatively plentiful material (ongoing research).

4. Systematic section

Subdivision Teleostei Müller, 1845 *sensu* Arratia, 1999

Order Gadiformes Goodrich, 1909 *sensu* Endo, 2002

Family Moridae Goode and Bean, 1896

Genus et species unidentified

(Figs. 1–4a)

Referred specimens: NMP Pv 10054a and 10054b (part and counterpart).

Description: The fossil preserves the anterior part of the body and the dorso-ventrally flattened skull of a small fish. The length of the preserved portion is approximately 38 mm (measured on specimen NMP Pv 10054a), with an estimated standard length of not more than 80 mm.

The neurocranium is preserved in dorsal view. The frontal is narrow in the interorbital area, slightly wider in the ethmoid region and considerably wider in the postorbital region, making the lateral margins of the frontal broadly concave. Some parts of the supraorbital margin have a lobular, segmented appearance. The anterior-most tips of the frontal extend antero-laterally. The skull roof bears an X-shaped skull ridge (Figs. 3A, 4A). In the midline, anterior to the frontals, the remains of the mesethmoid are

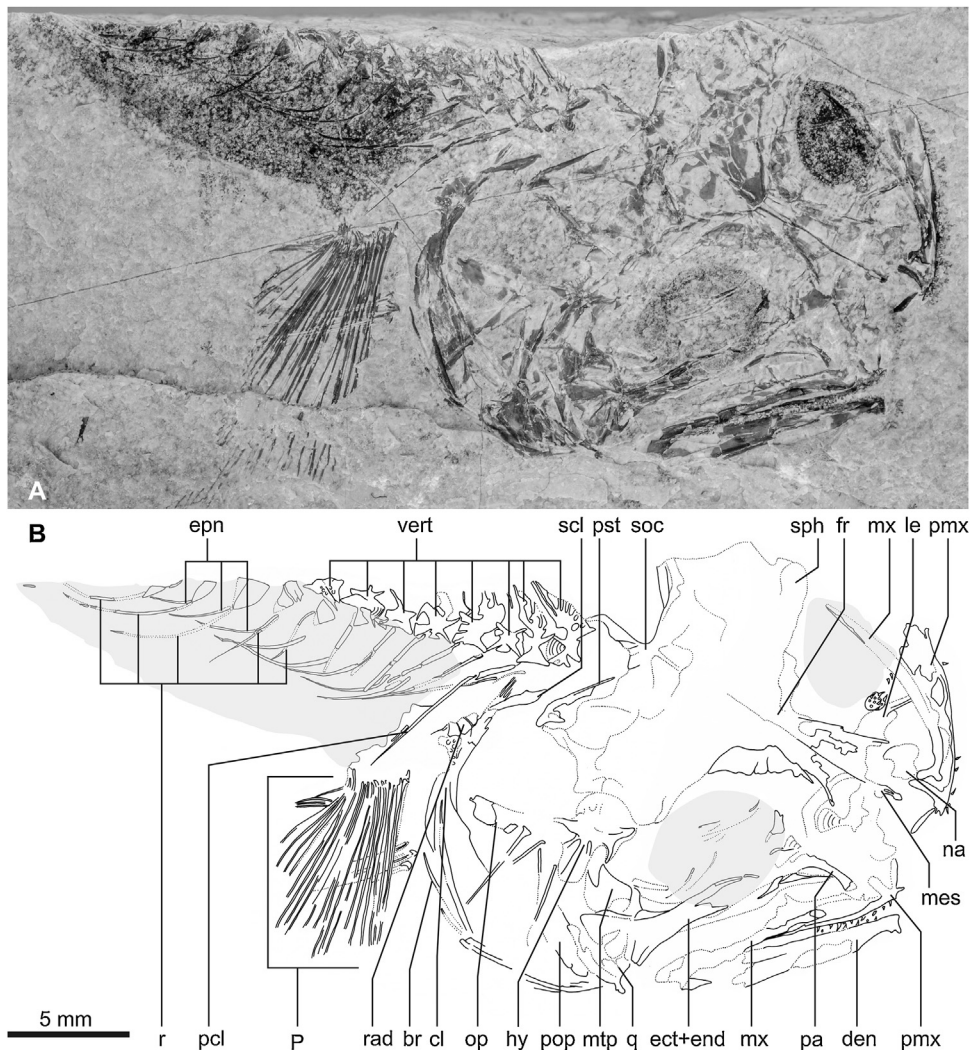


Fig. 1. Moridae, *gen. et sp. indet.*, specimen NMP Pv 10054a. A. Photo; B. Interpretative drawing. For abbreviations, see [Material and methods section](#).

Fig. 1. Moridae, *gen. et sp. indet.*, spécimen NMP Pv 10054a. A. Photo. B. Dessin interprétatif. Pour les abréviations, se référer à la section [Matériel et méthodes](#).

recognisable; no traces of the vomer are identifiable. The lateral ethmoids are well developed, expanded laterally and have concave anterior margins (the lateral extremities reach half of the orbit diameter). The small, oval sphenotic is identifiable in the antero-lateral portion of the postorbital region. The supraoccipital with a well-developed crest is identifiable. The supraoccipital separates the left and right parietals and the posteriorly located epiotics, while the parietals and the epiotics are in contact with each other. No remains of the exoccipitals, nor a basioccipital, are recognizable. The pterotic is large (medially it contacts the epiotic, parietal and frontal, and anteriorly it contacts the sphenotic), bearing two horn-like processes (the ventrolateral and posterior; white and black arrows respectively in [Fig. 3A, B](#)). The remains of the oval-shaped nasals are recognisable between the mesethmoid and the lateral ethmoids. Specimen NMP Pv 10054b shows well-preserved remains of four small ossifications in the orbital region, ten-

tatively interpreted as circumorbitals. The hyomandibula has a single articulation with the neurocranium (the articular facet of the neurocranium is located just anterior to the ventro-lateral process of the pterotic). The hyomandibula bears well-developed opercular and (possibly also) anterior processes ([Fig. 3C](#)). The metapterygoid bears two dorsally oriented processes, the posterior one probably serving for articulation with the main hyomandibular body, while the anterior process serves for articulation with the presumed lower process of the hyomandibula. The details of the quadrato-ptyergo-palatal complex are not clear, but it seems to be relatively strongly built and generally in the shape of an elongated, posteriorly expanded strap. The palatine seems to be well developed, with a long, antero-laterally oriented articular process. The lower jaw joint is located at the level of the posterior margin of the orbit. The lower jaw is insufficiently preserved, but seems to be relatively straight. The premaxilla is slightly bent, with

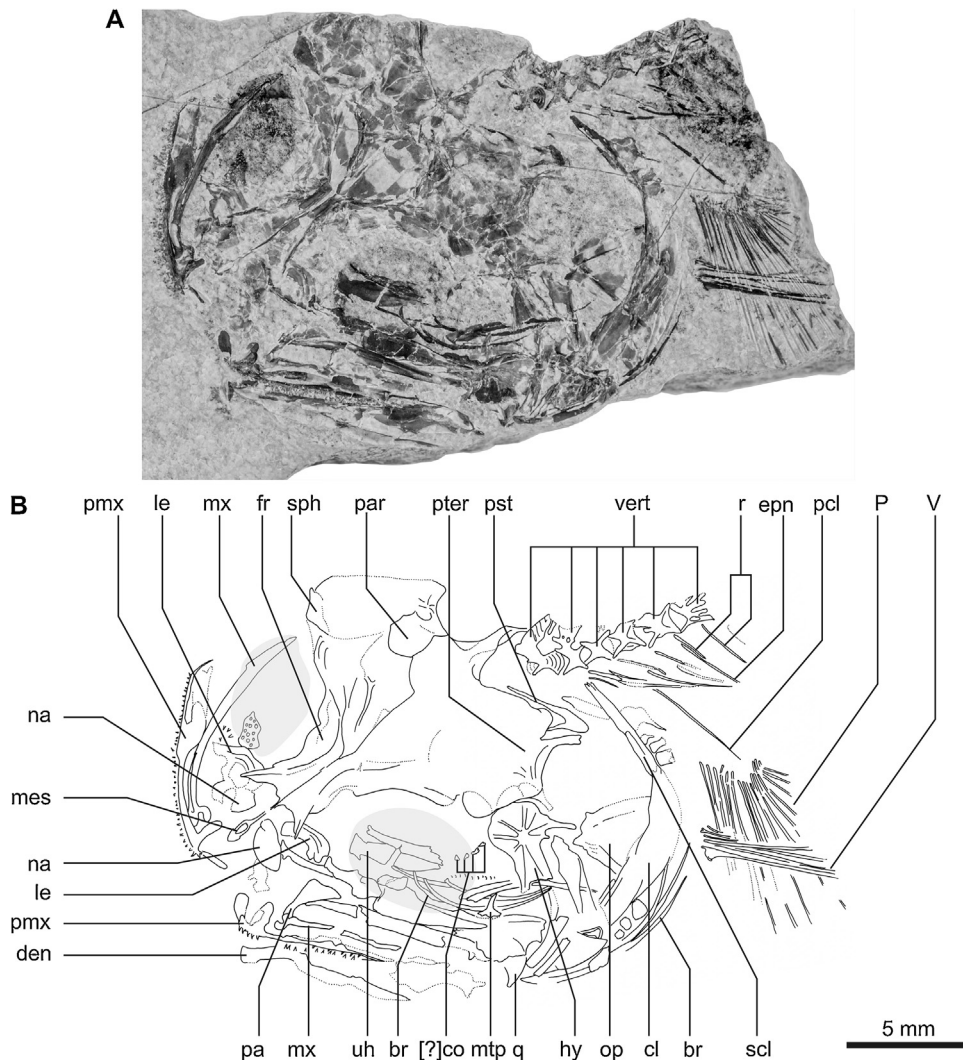


Fig. 2. Moridae, *gen. et sp. indet.*, specimen NMP Pv 10054b. A. Photo; B. Interpretative drawing. For abbreviations, see [Material and methods section](#).
Fig. 2. Moridae, *gen. et sp. indet.*, spécimen NMP Pv 10054b. A. Photo ; B. Dessin interprétatif. Pour les abréviations, se référer à la section [Matériel et méthodes](#).

broadly separated and well-developed articular, ascending and postmaxillary processes, and a postmaxillary notch (Fig. 3E). The dentary and premaxillae bear numerous small teeth (the latter all along the ventro-lateral margins; the distribution of the teeth on the dentary is not clear); some of the teeth seem to be somewhat larger than others, but these are randomly placed. The maxillae (Fig. 3E) show a well-developed articular groove within the articular head; the posterior part of the maxilla is spear-shaped. The precise shape of the preopercle is not clearly recognisable, but preserved fragments suggest it was a broad sickle-shaped bone. The opercle is more or less triangular, with a concave postero-ventral margin. The urohyal shows a typical gadooid shape (Fig. 3D). Fragments of branchiostegal rays and remains of the branchial arches (and associated toothed patches) are recognisable, but their detailed morphology and numbers are not clear.

The pectoral girdle is represented by remains of a relatively robust crescent-shaped cleithrum, articulating dorsally with the stick-like supracleithrum. The whole pectoral girdle articulates with the neurocranium via the V-shaped posttemporal. The postcleithrum is straight, needle-shaped, with a slightly enlarged proximal part. Remains of the scapula and coracoid are not recognisable. There are recognisable fragments of three proximal radials, but this area of the fossil is partly covered with sediment and their actual number may thus be higher. The pectoral fin has a more or less rounded margin and is composed of about 15 rays. The pelvic girdle is not preserved, but the preserved remains of the pelvic fin rays suggest the fins were relatively short, and composed of about five rays each.

The axial skeleton is far from complete and preserves only the remains of eight vertebral centra, followed by remains of four parapophyses (the parapophyses are

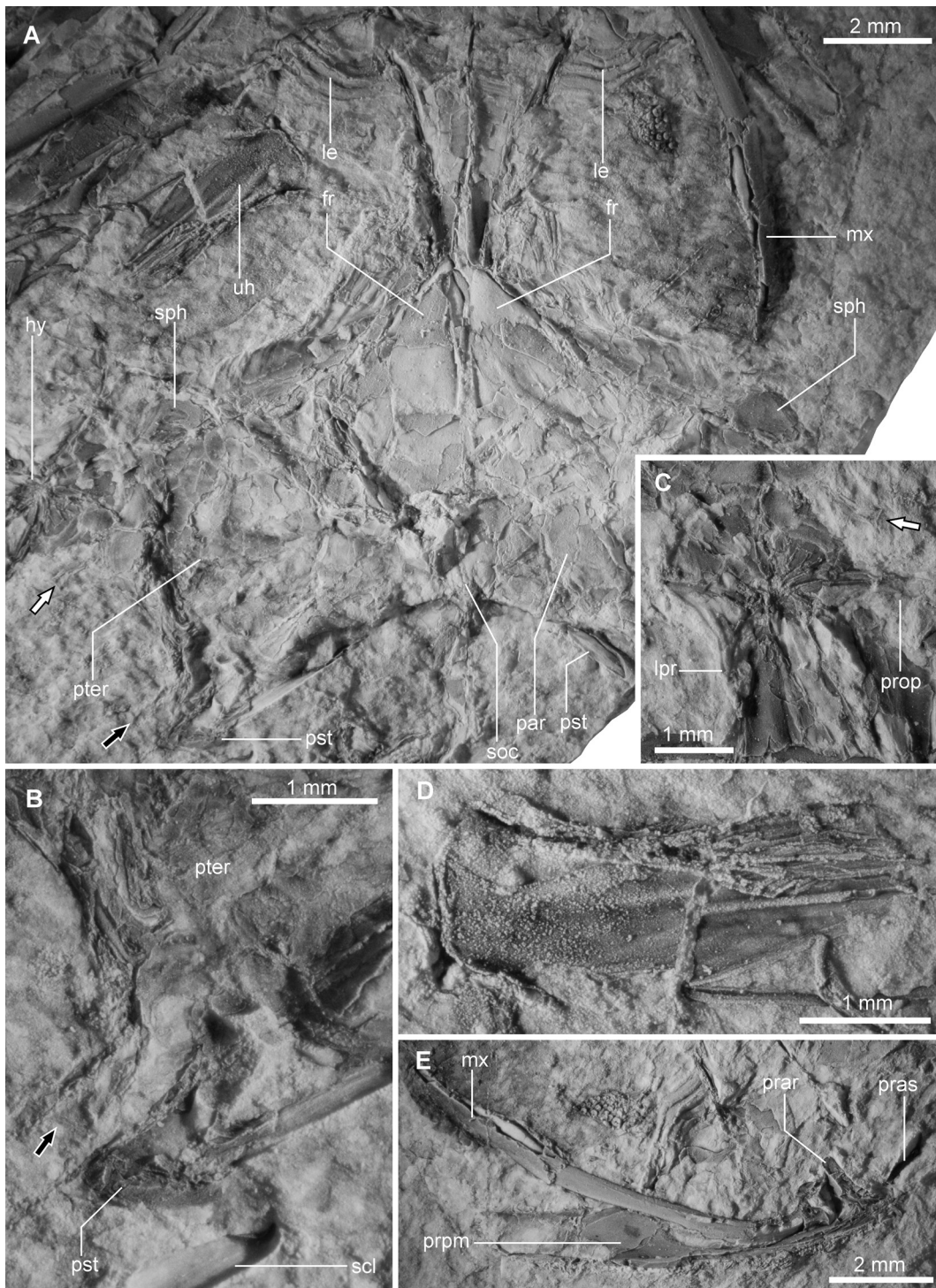


Fig. 3. Moridae, *gen. et sp. indet.*, specimen NMP Pv 10054b. A. Dorsicranium; B. Posterior part of the pterotic and posttemporal; C. Hyomandibula; D. Urohyal; E. Maxilla and premaxilla. The ventro-lateral and posterior processes of the pterotic are marked by white and black arrows, respectively. For abbreviations, see [Material and methods section](#).

Fig. 3. Moridae, *gen. et sp. indet.*, spécimen NMP Pv 10054b. A. Dorsicranium ; B. Partie postérieure du ptérotique et post-temporale ; C. Hyomandibulaire ; D. Urohyal ; E. Maxillaire et prémaxillaire. Les processus ventro-latéraux et postérieurs du ptérotique sont indiqués par des flèches blanches et noires, respectivement. Pour les abréviations, se référer à la section [Matériel et méthodes](#).

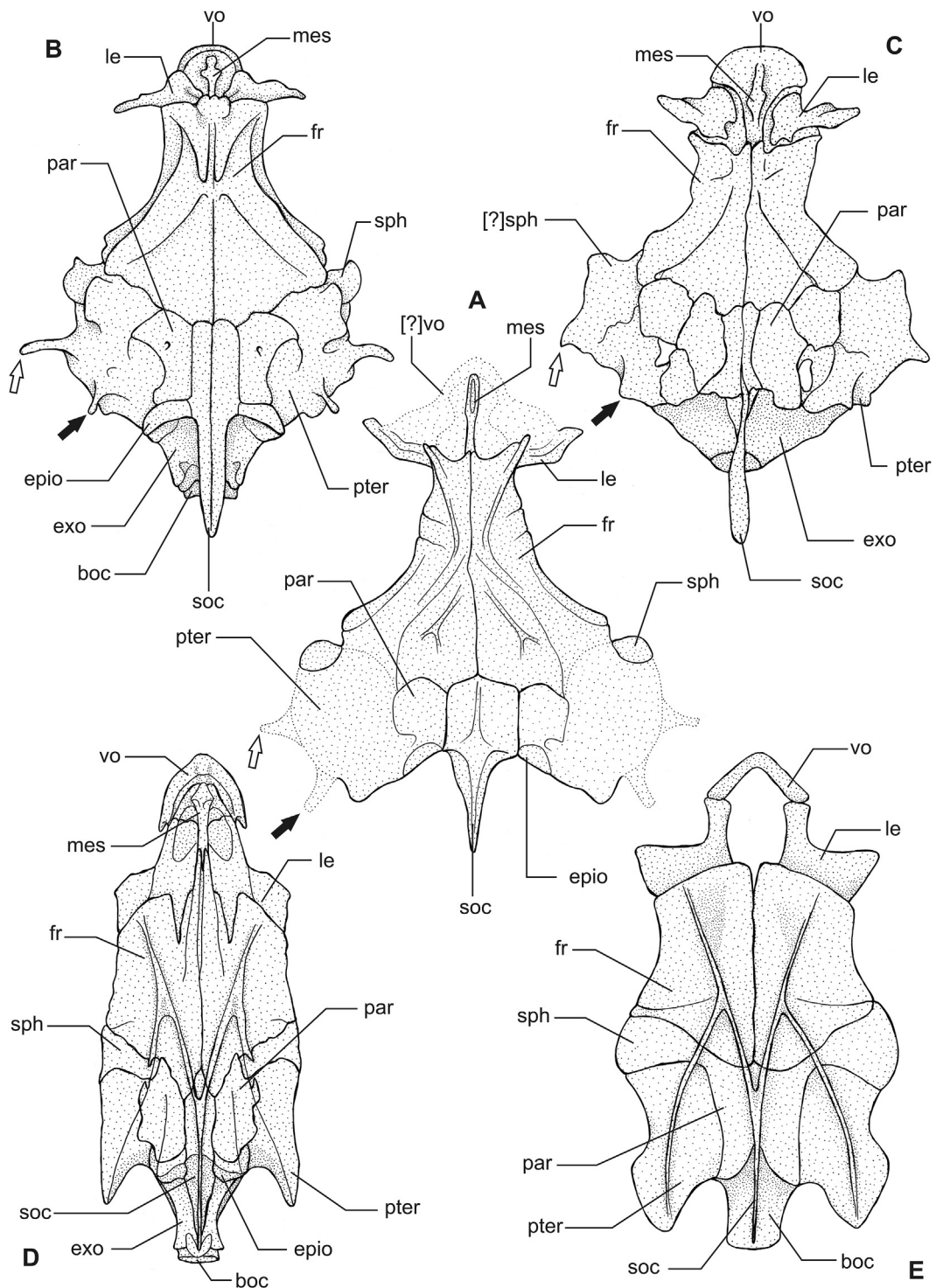


Fig. 4. Dorsicrania of selected Gadiformes; Moridae (of the “Pseudophycis group”; A–C) and Merlucciidae (D–E; *Merluccius* and *Palaeogadus* as common genera of the Oligocene–Miocene of the region). A. Moridae, *gen et sp. indet.*, restoration based on specimens NMP Pv 10054a and b (nasal, exoccipital and basioccipital are omitted); B. *Lotella phycis* (Temminck and Schlegel, 1846) according to Svetovidov (1948: 251); C. *Eeyorius hutchinsi* Paulin, 1986 according to Paulin (1986: 205); D. *Merluccius merluccius* Linnaeus, 1758 according to Inada (1981: fig. 28); E. *Palaeogadus intergerinus* Daniltshenko, 1947 according to Fedotov (1976: 61). The ventro-lateral and posterior processes of the pterotic are marked by white and black arrows, respectively. For abbreviations, see *Material and methods section*.

easily recognisable from the seventh preserved vertebra). The first preserved vertebra is expected to be in fact the second one of the column, while the first vertebra is coalesced with the occipital part of the skull (as described in morids, e.g., in *Lotella cf. tosaensis* by Prokofiev, 2008 or in *Eophycis jammensis* by Přikryl, 2015). The neural arches of the anteriorly preserved vertebrae are well developed, broad, and relatively robust. From the second preserved vertebra, the epipleural bones are attached to the ventro-lateral margins of the centra (and more posteriorly on the parapophyses). The first six epipleurals are straight, while those more posteriorly located are slightly bent. Ribs are clearly recognisable, attaching to the epipleurals or (in two penultimate cases) the parapophyses. The last preserved parapophysis bears an epipleural, but no rib. Neither scales nor otoliths are recognisable. Soft-tissue remains are partly preserved as a dark film in the eye and abdominal areas.

5. Discussion and conclusion

The preservation of the specimen in dorsal view and its incomplete condition impedes adequate interpretation and comparisons. Nevertheless, the fossil under consideration shows one feature considered to be diagnostic for the Paracanthopterygii and Anacanthini, namely the absence of the parapophyses on the anteriorly located centra (Patterson and Rosen, 1989). The inclusion of the fossil in the Gadiformes is supported by its overall appearance, the presence of a single articulation between the hyomandibula and neurocranium (Wiley and Johnson, 2010), and by the absence of the epipleural bones on the first and second centra (Ford, 1937; Murray and Wilson, 1999; Patterson and Rosen, 1989).

The familial status of the specimen differs from that of any other gadiform described earlier from the region (family Merlucciidae with the genera *Palaeogadus* from the Oligocene and *Merluccius* from the early Miocene; Gregorová, 2013; Jaroš, 1937; Gregorová and Požár, 2003), mainly due to the generally different architecture of the skull (compare Fig. 4A, D and E): while the merlucciids are characterised (among others) by a V-shaped neurocranial crest opening anteriorly (Cohen, 1984; Inada, 1981; Lloris et al., 2005), the fossil studied here clearly shows an X-shaped neurocranial crest (Fig. 4A). Although the inclusion of the specimen in the family Moridae is not corroborated directly by any of the diagnostic characters mentioned above, such a classification is supported by the proportions of the skull, with the orbito-rostral portion being larger than or of a similar size to the postorbital portion (Daniltschenko, 1960) and a generally similar morphology of the dorsicranium. Unfortunately, no detailed comparative osteology of the family Moridae has been published yet, but some of the morid crania figured by

Table 1

Comparison of fin ray numbers of the paired fins in the “*Pseudophycis* group” (according to Paulin, 1989).

Tableau 1

Comparaison du nombre de rayons des nageoires paires chez le « groupe *Pseudophycis* » (d’après Paulin, 1989).

	P	V
Specimens NMP Pv 10054a, b	ca 15	ca 5
<i>Pseudophycis</i>	19–27	5–6
<i>Lotella</i>	19–26	7–9
<i>Eeyorius</i>	24–25	6

Svetovidov (1948; namely *Uraleptus* Costa, 1846 (= *Gadella* Lowe, 1843), *Lotella* Kaup, 1858, and *Physiculus* Kaup, 1858) share several important characters with this fossil, namely: the lateral ethmoids expanding laterally at the level of half the height of the orbit; the sphenotics being located more laterally than the lateral-most margins of the lateral ethmoids; the sphenotics being significantly smaller than the pterotics; the pterotics being expanded anteriorly; and an X-shaped neurocranial crest present.

The pterotic of the genus *Lotella* in dorsal view (as figured by Svetovidov, 1948) bears two processes, one ventro-lateral and one posterior, similar to the fossil under consideration (white and black arrows, respectively, in Figs. 3 and 4). A somewhat similar condition was figured also for the genus *Eeyorius*, where both processes have the form of slight ridges (see Paulin, 1986; Fig. 4B).

The fossil is therefore most probably a member of the “*Pseudophycis* group” (including the genera *Pseudophycis* Günther, 1862, *Lotella* Kaup, 1858 and *Eeyorius* Paulin, 1986), which is characterised by “otoliths, with the ostium approximately equal to the cauda and a crista superior more than three-fourths as long as the crista inferior” (Paulin, 1989). Unfortunately, otoliths are not preserved, and such definitive confirmation of this conclusion is not possible.

The fossil is reminiscent of the genus *Lotella*, based on the features mentioned above and the shape of the postcleithrum, which is simple and straight (see Endo, 2002: fig. 38). The genus *Lotella* consists of four valid extant species (Cohen et al., 1990), two questionable fossil species based on articulated skeletons (Daniltschenko, 1953, 1960, but see also revision by Świdnicki et al., 1990) and relatively few otolith-based occurrences (e.g., Schwarzzhans et al., 2012, 2017), but a closer comparison with any of these taxa is not possible due to the preservation of the fossil.

The number of fin rays in the paired fins of the fossil, compared with data published for the “*Pseudophycis* group”, suggests a strong similarity with the genus *Pseudophycis* (see Table 1).

The fossil studied here cannot be included in the genus *Eophycis*, mainly due to the different morphology of the

Fig. 4. continued.

Dorsicrania des Gadiformes sélectionnés ; Moridae (du « groupe *Pseudophycis* » ; A–C) et Merlucciidae (D–E ; *Merluccius* et *Palaeogadus* en tant que genres communs de l’Oligocène–Miocène de la région). A. Moridae, *gen et sp. indet.*, reconstruction basée sur les spécimens NMP Pv 10054a et b (nasal, exoccipital et basioccipital ont été omis) ; B. *Lotella phycis* (Temminck et Schlegel, 1846) d’après Svetovidov (194 : 251) ; C. *Eeyorius hutchinsi* Paulin, 1986 d’après Paulin (1986: 205) ; D. *Merluccius merluccius* Linnaeus, 1758 d’après Inada (1981 : fig. 28) ; E. *Palaeogadus intergerinus* Daniltschenko, 1947 d’après Fedotov (1976: 61). Les processus ventro-latéraux et postérieurs du ptérotique sont indiqués par des flèches blanches et noires, respectivement. Pour les abréviations, se référer à la section *Matériel et méthodes*.

hyomandibula, the shape of the lower jaw and the pterotic, and the number of fin rays in the paired fins (Přikryl, 2015).

Some characters of the fossil are unknown (such as the total number of vertebrae, number of rays in the unpaired fins and morphology of their skeletal supports, otoliths, and soft tissue features) or are difficult to interpret correctly (such as the presumed circumorbitals, which seem to be relatively unusual; compare Fig. 2 and e.g., Endo, 2002: fig. 29). Nevertheless, these problems are related to the fragmentary state of the specimen and poor preservation, as well as to our limited understanding of the osteology of extant morid species. The preservation of the fossil does not allow a full comparison and proper description of a new taxon; such a description must wait until new, better preserved specimens become available. However, it is possible to conclude that the Central Paratethys was inhabited by a morid fish morphologically closely related to *Lotella* during the Rupelian.

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References

- Arratia, G., 1999. The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements. In: Arratia, G., Schultze, H.-P. (Eds.), *Mesozoic Fishes 2—Systematics and Fossil Record*. Verlag Dr. Friedrich Pfeil, München, pp. 265–334.
- Brzobohatý, R., Krhovský, J., 1998. A synopsis of the Teleost taxa (otoliths) from the Pouzdřany Formation (West Carpathians, Pouzdřany Unit, Early Oligocene). *Zemní plyn a nafta* 43, 279–289.
- Bubík, M., Franců, J., Gilliková, H., Otava, J., Švábenická, L., 2016. Upper Cretaceous to lower Miocene of the Subsilesian Unit (Western Carpathians, Czech Republic): stratotypes of formations revised. *Geol. Carpath* 67, 239–256.
- Cohen, D.M., 1984. Gadiformes: Overview. In: Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall, A.W., Richardson, S.L. (Eds.), *Ontogeny and systematics of fishes*, Am. Soc. Ichthyol. Herpetol. Gainesville, pp. 259–265.
- Cohen, D.M., Inada, T., Iwamoto, T., Scialabba, N., 1990. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. FAO, Rome.
- Costa, O.G., 1829–1853. *Fauna del regno di Napoli*. Napoli.
- Daniiltschenko, P.G., 1947. O filogenetičeskoj svyazi mezdu rodami *Palaegadus* i *Merluccius*. *Dokl. Akad. Nauk SSSR* LVIII, 659–662 [In Russian].
- Daniiltschenko, P.G., 1953. *Iskopaemie predki sovremennykh Moridae*. *Vop. Ikhtiol.* 1, 117–127 [In Russian].
- Daniiltschenko, P.G., 1960. Bony fishes from Maikop deposits of the Caucasus. *Trudy paleontologičeskogo instituta* 78, 1–208 [In Russian].
- Endo, H., 2002. Phylogeny of the order Gadiformes (Teleostei, Paracanthopterygii). *Mem. Grad. School Fish. Sci. Hokkaido Univ.* 49, 75–149.
- Fedotov, V.F., 1976. *Treskovye paleogen-neogenovych otloženij SSSR*. *Trudy paleontologičeskogo instituta* 157, 1–83 [In Russian].
- Fitch, J.E., Barker, L.W., 1972. The fish family Moridae in the eastern north Pacific with notes on morid otoliths, caudal skeletons, and the fossil record. *Fish. Bull.* 70, 565–584.
- Ford, E., 1937. Vertebral variation in teleostean fishes. *J. Mar. Biol. Assoc. UK* 22, 1–60.
- Goode, G.B., Bean, T.H., 1896. *Oceanic ichthyology, a treatise on the deep-sea and pelagic fishes of the world, based chiefly upon the collections made by the steamers Blake, Albatross, and Fish Hawk in the northwestern Atlantic*. Smithsonian Institution United States National Museum, Washington.
- Goodrich, E.S., 1909. *Vertebrata craniata. Fascicule I. Cyclostome and fishes*. In: Lankaster, E.R. (Ed.), *A Treatise on Zoology. Part 9*. Adam & Charles Black, London, pp. 1–518.
- Gregorová, R., 2011. Fossil fish fauna (Teleostei, Selachii) from the Dynów marlstone (Rupelian, NP 23) of the Menilitic Formation at the locality of Litěnice (Czech Republic). *Acta Mus. Moraviae. Sci. Geol.* 96, 3–33.
- Gregorová, R., 2013. *Tajemné moře v Karpatech*. Moravské zemské museum, Brno [In Czech].
- Gregorová, R., Požár, M., 2003. Rybí fauna Menilitového souvrství (střední oligocén) na nové lokalitě Rysova Hora (Rožnov pod Radhoštěm). *Acta Mus. Moraviae. Sci. Geol.* 88, 191–206 [In Czech].
- Günther, A., 1862. *Catalogue of the fishes in the British Museum, Vol. IV*. Trustees of British Museum, London.
- Howes, G.J., 1991. Anatomy, phylogeny and taxonomy of the gadoid fish genus *Macruronus* Günther, 1873, with a revised hypothesis of gadoid phylogeny. *Bull. Br. Mus. Nat. Hist. Zool.* 57, 77–110.
- Inada, T., 1981. Studies on the merlucciid fishes. *Bull. Nat. Res. Inst. Far Seas Fisher.* 18, 1–172.
- Jaroš, Z., 1937. Paleogenní rybí fauna z Linhartských Vážan od Slavkova u Brna. *Čas. Vlast. Spol. Mus. v Olomouci* 49, 99–106 [In Czech].
- Jerzmańska, A., 1968. Ichtyofaune des couches à Ménilité (Fylsch des Karpathes). *Acta Palaeontol. Pol.* 13, 379–489.
- Kalabis, V., 1975. Makropaleontologické zhodnocení menilitových vrstev se zvláštním zřetelem k ichtyofauně lokalit Špiček u Hranic na Moravě a Kelče. Část druhá: Kelč. *Zpr. Vlastivěd. Úst. v Olomouci* 175, 1–9 [In Czech].
- Kaup, J.J., 1858. *Uebersicht der Familie Gadidae*. *Arch. Naturgesch.* 24, 85–93.
- Knobloch, E., 1969. *Tertiäre Floren von Mähren*. *Musejní spolek Brno, Brno*.
- Linnaeus, C., 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, 10th ed. Holmiae, Stockholm.
- Lloris, D., Matallanas, J., Oliver, P., 2005. *Hakes of the World (Family Merlucciidae)*. An annotated and illustrated catalogue of hake species known to date. FAO, Rome.
- Lowe, R.T., 1843. Notices of fishes newly observed or discovered in Madeira during the years 1840, 1841, and 1842. *Proc. Zool. Soc. Lond.* 1843, 81–95.
- Müller, J., 1845. Über den Bau und die Grenzen der Ganoiden, und über das natürliche System der Fische. *Abh. Königl. Akad. Wissensch. Berlin* 1845 (for 1844), pp. 117–216.
- Murray, A.M., Wilson, M.V.H., 1999. Contributions of fossils to the phylogenetic relationships of the percopsiform fishes, (Teleostei: Paracanthopterygii): order restored. In: Arratia, G., Schultze, H.P. (Eds.), *Mesozoic Fishes 2 – Systematics and Fossil Record*. Verlag, Dr. Friedrich Pfeil, München, Germany, pp. 397–411.
- Nelson, J.S., Grande, T.C., Wilson, M.V.H., 2016. *Fishes of the World*. Fifth Edition. John Wiley & Sons, Inc, Hoboken.
- Patterson, C., Rosen, D.E., 1989. The Paracanthopterygii Revisited: Order and Disorder. In: Cohen, D.M. (Ed.), *Papers on the systematics of gadiform fishes*. *Nat. Hist. Mus. of Los Angeles County, Sci. Ser.*, 32, pp. 5–36.
- Paulin, C.D., 1983. A revision of the family Moridae (Pisces: Anacanthini) within the New Zealand region. *Rec. Nat. Mus. New Zealand* 2, 81–126.
- Paulin, C.D., 1986. A new genus and species of morid fish from shallow coastal waters of southern Australia. *Mem. Mus. Victoria* 47, 201–206.
- Paulin, C.D., 1988. Swimbladder structure in morid cods (Pisces: Gadiformes). *Copeia* 1988, 450–454.
- Paulin, C.D., 1989. Moridae: overview. In: Cohen, D.M. (Ed.), *Papers on the systematics of gadiform fishes*. *Nat. Hist. Mus. of Los Angeles County, Sci. Ser.*, 32, pp. 243–250.
- Pharisat, A., 1991. La paleoichthyofaune du Rupelian marin de Froidefontaine. *Ann. Soc. Univ. Franche-Comté Besançon Géol.* 4, 13–97.
- Prokofiev, A.M., 2005. O sredneocenovom vozraste dvuch vidov kostistych ryb (Teleostei), oschibocna ukazanyh dlja nižnego oligocena. *Integr. Sci. J.* 7, 61–62 [In Russian].
- Prokofiev, A.M., 2008. Moridae, Neobythitidae, and Bythitidae (Gadiformes: Moridae, Ophidiiformes) of Nha Trang Bay, South China Sea, central Vietnam. *J. Ichthyol.* 48, 860–875.
- Prokop, J., Přikryl, T., Dostál, O., Nel, A., 2007. *Oligaeschna kvaceki* sp. nov., a new fossil dragonfly (Odonata: Aeshnidae) from the middle Oligocene

- sediments of northern Moravia (Western Carpathians). *Geol. Carpat.* 58, 181–184.
- Pfikryl, T., 2015. Skeletal anatomy of the early morid fish *Eophycis* (Gadiformes, Moridae) from an Oligocene deposit in Poland. *C. R. Palevol* 14, 625–635.
- Pfikryl, T., Brzobohatý, R., Gregorová, R., 2016. Diversity and distribution of fossil codlets (Teleostei, Gadiformes, Bregmacerotidae): review and commentary. *Palaeobiodiv. Palaeoenviro.* 96, 13–39.
- von Rath, G., 1859. Beitrag zur Kenntniss der fossilen Fische des Plattenberges im Canton Glarus. *Zeitschr. Deutsch. Geol. Ges.* 11, 108–132.
- Rozenberg, A., Prokofiev, A.F., 2004. The first finding of fish of the family Moridae (Gadiformes) in the lower Oligocene of the Caucasus with otoliths in situ. *J. Ichthyol.* 44, 732–740.
- Schwarzahns, W., Scotfield, R.P., Tennyson, A.J.D., Worthy, J.P., Worthy, T.H., 2012. Fish remains, mostly otoliths, from the non-marine early Miocene of Otago, New Zealand. *Acta Palaeontol. Pol.* 57, 319–350.
- Schwarzahns, W., Lee, D.E., Gard, H.J.L., 2017. Otoliths reveal diverse fish communities in Late Oligocene estuarine to deep-water paleoenvironments in southern Zealandia, New Zealand. *J. Geol. Geophys.* 60, 433–464.
- Svetovidov, A.N., 1948. Treskoobraznye [Gadiformes]. *Fauna SSSR, Zool. Inst. Akad. Nauk SSSR* 34, Ryby [Fishes] 9, 1–222 [In Russian; English translation 1962: 304 pp. Israel Program for Scientific Translation, Jerusalem].
- Svetovidov, A.N., 1967. Contribution to the knowledge of Moridae (Pisces, Gadiformes). *Zool. Zh.* 46, 1684–1693 [In Russian].
- Świdnicki, J., Fedotov, V.F., Bannikov, A.F., 1990. Placement of Caucasus Miocene fishes—previously considered in the family Moridae—in Gadidae. *J. Ichthyol.* 30, 138–142.
- Temminck, C.J., Schlegel, H., 1846. Pisces. In: *Fauna Japonica*, Leiden, The Netherlands.
- Wiley, E.O., Johnson, G.D., 2010. A teleost classification based on monophyletic groups. In: Nelson, J.S., Schultze, H.-P., Wilson, M.V.H. (Eds.), *Origin and Phylogenetic Interrelationships of Teleosts*. Verlag Dr. F. Pfeil, Munich, Germany, pp. 123–182.