The stromateiform fish *Parapropercarina multispinata* gen. et sp. nov. from the Eocene Fur Formation of Denmark

ANE ELISE SCHRØDER, TOMÁŠ PŘIKRYL & GIORGIO CARNEVALE

Schrøder, A.E., Přikryl, T. & Carnevale, G. 2025. The stromateiform fish *Parapropercarina multispinata* gen. et sp. nov. from the Eocene Fur Formation of Denmark. Bulletin of the Geological Society of Denmark, Vol. 74, pp. 251–266. ISSN 2245-7070. https://doi.org/10.37570/bgsd-2025-74-14

A new stromateiform fish from the earliest Eocene Fur Formation, northwestern Denmark, is described as *Parapropercarina multispinata* gen. et sp. nov. by using non-destructive μXRF-element mapping and standard comparative osteology. The new genus and species is diagnosed by a distinctive combination of characters: a moderately elongate, laterally compressed body; six branchiostegal rays, a single deeply notched dorsal fin with 15 spines and 18 rays; three supraneurals; anal fin with two or three spines and 24 soft rays; pectoral fin with 18 rays extending posteriorly approximately at the level of the 10th abdominal vertebra; pelvic fin containing one spine and five rays; 36 (15+21) vertebrae; well-developed parapophyses on posterior abdominal vertebrae; caudal skeleton comprising fused hypurals 1+2, partially fused hypurals 3+4, autogenous hypural 5, autogenous parhypural lacking parhypurapophysis, two uroneurals, and three epurals; oral jaw dentition uniserially arranged; body densely covered with thin, cycloid scales. *Parapropercarina multispinata* gen. et sp. nov. thus shows a mosaic of features, that clearly aligns it within the Stromateiformes (Stromateoidei). This new fossil extends the occurrence of a body plan similar to that of propercarinids back to the early Eocene of the eastern North Sea Basin.

Keywords: Stromateiformes, Stromateoidei, Propercarinidae, Nomeidae, North Sea realm.

Ane Elise Schrøder [aes@ign.ku.dk], Department of Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10, 1350 Copenhagen K, Denmark; also Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy [aneelise.schroder@unito.it]. https://orcid.org/0000-0001-9371-400X. Tomáš Přikryl [prikryl@gli.cas.cz], Department of Paleobiology and Paleoecology, Institute of Geology of the Czech Academy of Sciences, Rozvojová 269, 165 00 Praha 6 - Lysolaje, Czech Republic. https://orcid.org/0000-0002-7939-3622. Giorgio Carnevale [giorgio.carnevale@unito.it], Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy http://orcid.org/0000-0002-3433-4127.

Geological Society of Denmark
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Received 27 September 2025
Accepted in revised form 20 October 2025
Published online 06 November 2025

https://zoobank.org/urn:lsid:zoobank.org:pub:A96AD4C0-A884-4537-836E-4E5C44655AC7

The Fur Formation of Denmark is an early Eocene (Ypresian) offshore marine deposit within the eastern North Sea Basin. It is a world-famous Konservat-Lagerstätte renowned for the exceptional preservation of delicate organic remains, comprising both terrestrial and marine organisms, such as birds, insects, reptiles, plants, bony fishes, sharks, crustaceans, echinoderms, molluscs, and diatoms (for comprehensive overviews, see Larsson 1975; Homann 1991; Willumsen 2004; Schultz *et al*. 2011; Kristensen *et al*. 2012; Karl & Madsen 2012; Pedersen *et al*. 2012; Bourdon *et al*. 2016; Schrøder *et al*. 2023a). The diatom-rich sediments and intercalated volcanic ash layers characteristic of the formation have long been recognised as conducive to rapid burial and low-oxygen conditions, which allowed the preservation of remarkable details of both hard and soft tissues and the frequent occurrences of articulated skeletons (e.g. Gren *et al*. 2017; Lindgren *et al*. 2017; Schrøder *et al*. 2023b).

The ichthyofauna is notably diverse and in-

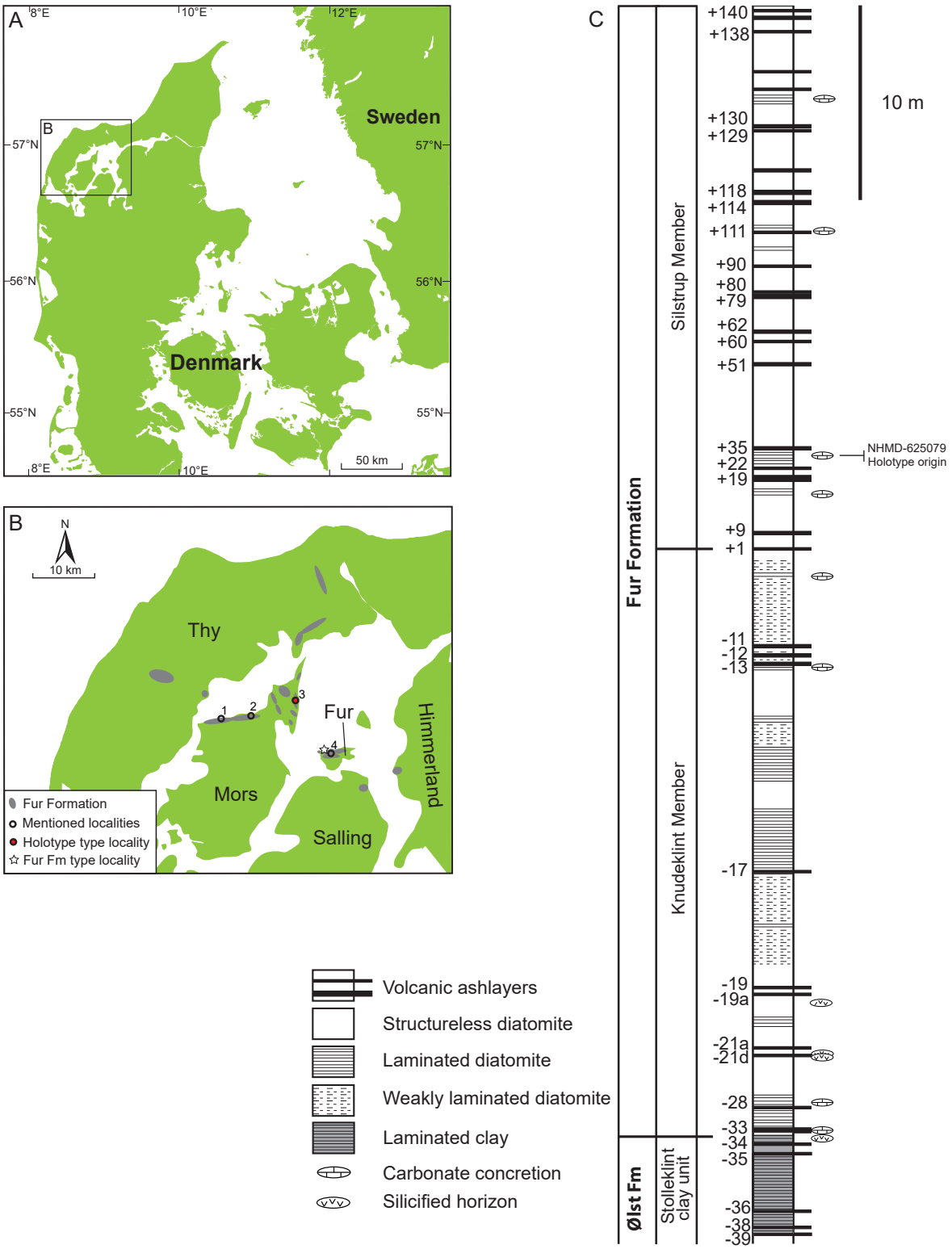

Fig. 1. A: Map of Denmark. The western Limfjord area where the Fur Formation is present. **B**: Outcrop localities and near-surface occurrences of the Fur Formation marked in grey. The localities from where the studied specimens originate are marked by circles designated with numbers: 1 = Klitgård Klint (NHMD-1351141); 2 = Bjørneborg (MM-9628); 3 = Ejerslev moclay pit, which is also the type locality of the holotype (NHMD-625079, FUM-N-10535); 4 = Graven at Stendal Høje. 'Graven' refers to the centrally located moclay pit at the locality. The white star indicates the type locality of the Fur Formation. **C**: Sedimentological log comprising the lowermost negative series of the Stolleklint clay unit, and the negative and positive ash series throughout the Fur Formation in northwestern Denmark. The stratigraphic position of the holotype is indicated. Modified from Schrøder and Carnevale (2023).

formative for early Eocene vertebrate evolution and diversification. The fish assemblage includes, among others, osteoglossiforms, argentiniforms, polymixiiforms, stromateiforms, zeiforms, lampridiforms, and syngnathiforms (e.g. Kuhne 1941; Tyler *et al*. 2000; Baciu *et al*. 2005; Bonde 2008; Schrøder *et al*. 2022, 2023a, 2025; Schrøder & Carnevale 2023, 2025a, 2025b), with bony fishes being the most abundant group of macrofossils. The fish assemblage exhibits a broad ecological spectrum, ranging from pelagic to demersal taxa, and provides a valuable high-latitude complement to the otherwise better-known, broadly coeval Tethyan faunas. In addition to their taxonomic breadth, the bony fishes of the Fur Formation preserve anatomical details that illuminate functional morphology, trophic strategies, and patterns of early Eocene teleost diversification.

Among the acanthomorph contingent, several stromateiforms have been recognised in Danish museums' collections by one of us (AES). The oldest known stromateiform fish, based on skeletal remains, was described by Schrøder *et al.* (2023a), and it is now accompanied by material reminiscent of the extinct stromateiform family Propercarinidae. The presence of a fish reminiscent of the propercarinids in the Fur Formation is significant because members of this stromateiform group are relatively rare in the fossil record, and their occurrences were previously restricted to the Oligocene deposits of the Paratethys. The material from Denmark thus provides an opportunity to reassess stromateiform diversity in the early Eocene.

The aim of the present paper is to 1) describe a new genus and species of stromateiform fish, *Parapropercarina multispinata* gen. et sp. nov., based on material housed in three natural history museums' collections in Denmark, and 2) discuss the potential systematic affinities of these propercarinid-like stromateiform remains from the earliest Eocene Fur Formation of Denmark.

Geological setting

The exposed formation localities and near surface occurrences of the earliest Eocene Fur Formation cover the region from the western part of Himmerland to the northern part of Salling, the islands of Fur and Mors, to the area of Thy (Fig. 1A). The Fur Formation is particularly exposed on Fur and Mors, and the sites include coastal cliff exposures and old digging pits around the two islands (Fig. 1B). It comprises a 60 m thick fossil-rich, marine diatomite, interbedded with ca. 180 and up to 200 ash layers (Bøggild 1918; Pedersen & Surlyk 1983) originating from the volcanic activity triggered by the opening of the Northeast Atlantic (e.g. Storey *et al.* 2007). The ash layer sequences were separated into a numbered negative and a numbered positive series by Bøggild (1918). The Knudeklint Member encompasses the negative sequence, and the Silstrup Member reflect the positive sequence. Later officially recognised ash layers have been assigned letters together with the original ash layer number (Fig. 1C, see also Pedersen & Surlyk 1983; Larsen *et al*. 2003). Calcareous carbonate concretions are present in certain horizons of the formation (Fig. 1C). They formed immediately below the sea-floor surface by precipitation of calcite before compaction of the surrounding sediment, commonly forming and growing around remains of dead organisms.

The Fur Formation largely replaces the Ølst Formation in this area of Denmark. Just the lowermost part of the Haslund Member, the Stolleklint clay unit, is exposed in the area. The section comprising ash layers around -39 to -34 belongs to this unit (Heilmann-Clausen *et al.* 1985; Heilmann-Clausen 1995). Radiometric dating of ash layers −17 and +19 of the Fur Formation, yielded $^{39}Ar/^{40}Ar$ age determinations of ~55.6 Ma and ~54.4 Ma, respectively (Westerhold *et al.* 2009). The Paleogene–Eocene boundary (P/E) is furthermore evident in the Stolleklint clay unit, based on the onset of the CIE (e.g. Heilmann-Clausen & Schmitz 2000; Schmitz *et al*. 2004; Stokke *et al*. 2020, 2021).

Material and methods

This study is based on material collected from the Ypresian, earliest Eocene, Fur Formation in northwestern Denmark. The fossil specimens have been collected at outcrop localities exposed on the islands of Mors and Fur in the western Limfjord area. The fossils are reposited in three Danish museums, namely the collections of Fur Museum and Museum Mors in northern Denmark, and in the Vertebrate palaeontology and Danekræ collections, respectively, of the Natural History Museum of Denmark. The holotype, NHMD-625079 (designated herein), was declared Danekræ fossil trove in 2008 (fossil trove no. DK-540) and thus kept in the Danekræ collection.

For an overview of the unique Danekræ fossil trove legislation pertaining to Denmark, see Schrøder *et al*. (2022) and Consolidated Act on Museums (2006).

All specimens were subjected to non-destructive μXRF-element mapping following the procedures of Schrøder and Carnevale (2023), applying a Bruker M4 Tornado Plus Amics at the Department of Geosciences and Natural Resource Management, Copenhagen University. The benchtop device was set to a maximum acceleration of 50 kV and an anode current of either 250 or 600 μA. The specimens were furthermore studied by conventional methods, using a Leica M80 equipped with a camera lucida drawing arm and by a Leica MZ75. Measurements were obtained on high-resolution specimen photos, applying ImageJ (Rasband 2018). Mapping of strontium and phosphorous reveals anatomical details of the body morphology not accessible by conventional methods; the strontium map exposes the intricate details of the body skeleton counting minute bone structures and skeletal parts hidden by scales on the fossils, whereas phosphorous commonly exposes and greatly enhances less strongly ossified or soft tissue elements, including soft rays and scales – even scales that may not be visible on the physical fossils (see also Schrøder *et al*. 2023b). The strontium maps were also directly applied for the interpretative reconstruction drawings along with the fossils.

Institutional abbreviations: FUM-N, Fur Museum, a division of Museum Salling; MM, Fossil and Moclay Museum, Museum Mors; NHMD, Natural History Museum of Denmark; DK, specimens declared Danekræ fossil trove, and kept in the Danekræ collection of the Natural History Museum of Denmark, University of Copenhagen.

Anatomical abbreviations: aa = anguloarticular; br = branchiostegal rays; cc = compound centrum; cl = cleithrum; co = coracoid; dn = dentary; ect = ectopterygoid; endt = endopterygoid; ep = epural; ffn = foramen of the facialis nerve; fr = frontal; hspu = haemal spine of preural; hyo = hyomandibula; hyp = hypural; le = lateral ethmoid; mtp = metapterygoid; mx = maxilla; ns = neural spine; op = opercle; pal = palatine; par = parietal; pas = parasphenoid; per = pectoral-fin radials; pcl = postcleithrum; phy = parhypural; pmx = premaxilla; pop = preopercle; ptm = posttemporal; pu = preural vertebra; qu = quadrate; ra = retroarticular; sc = scapula; scl = supracleithrum; scos = sclerotic ossicle; smx = supramaxilla; sn = supraneural; sph = sphenotic; soc = supraoccipital; sop = subopercle; sym = symplectic; uh = urohyal; un = uroneural

Morphometric abbreviations: AFB = anal-fin base; CPD = caudal peduncle depth; CPL = caudal peduncle length; DFB = dorsal-fin base; HD = head depth; HL = head length; MBD = maximum body depth; OD = orbit diameter (measured horizontally); PAD = preanal distance; PDD = predorsal distance; POD = preorbital distance; SL = standard length.

Systematic palaeontology

Division Percomorphacea *sensu* Wiley & Johnson, 2010

Order Stromateiformes *sensu* Pastana, Johnson & Datovo, 2022

Suborder Stromateoidei *sensu* Pastana, Johnson & Datovo, 2022

Genus *Parapropercarina* gen. nov.

Type species. *Parapropercarina multispinata* gen. et sp. nov. NHMD-625079A+B

Etymology. The name is derived from the prefix 'para' (from Greek 'ἀνά') meaning 'beside', 'at', 'together', 'alongside', 'against' or 'through', and the generic name '*Propercarina*', due to the numerous characteristics shared between the two genera.

Table 1. Type series, referred material and relevant collection data

Catalogue number	Type status	Formation	Member	Lithology	Ash-series	Locality
FUM-N-16161A+B	Paratype, p+cp	Fur Fm	Knudeklint?	Soft diatomite, laminated	N/A	Graven at Stendal Høje, Fur
FUM-N-10535	Paratype	Fur Fm	N/A	Carbonate concretion	N/A	Ejerslev moclay pit, Mors
FUM-N-17356	Paratype	Fur Fm	N/A	Carbonate concretion	N/A	Fur, no specific locality
NHMD-625079A+B (DK-540)	Holotype, p+cp	Fur Fm	Silstrup	Carbonate concretion	+26 or +27	Ejerslev moclay pit, Mors
NHMD-1351141	Referred specimen p+cp	Fur Fm	N/A	Carbonate concretion	N/A	Klitgård Klint, Mors
MM-9628	Referred specimen	Fur Fm	Silstrup	Carbonate concretion	+25 to +30	Bjørneborg, Mors

p = part, cp = counterpart

Stratigraphic and geographic range. Ypresian (earliest Eocene), Fur Formation, northwestern Denmark (Fig. 1).

Diagnosis. Stromateoid genus unique in having the following combination of characters: body moderately elongate; jaws with strong conical, uniserially arranged teeth; six branchiostegal rays; sclerotic ossicles present; ventral limb of preopercle with small, short spines; a single dorsal fin with a deep notch, long-based (~42% of SL) with 15 spines and 18 soft rays; three supraneurals, predorsal formula 0/0+0/2/1; anal fin with two or three spines and 24 rays; caudal fin forked with 17 (I,8+7,I) principal rays; procurrent spur absent; pectoral fin with 18 relatively long rays, reaching approximately the 10th abdominal vertebra; pelvic fin with a single spine and five rays; 36 vertebrae (15+21); posterior abdominal vertebrae bearing well-developed parapophyses; caudal-fin skeleton with fused hypurals 1 and 2, and partially fused hypurals 3 and 4, autogenous hypural 5, autogenous parhypural, parhypurapophysis absent, two uroneurals, and three epurals; cycloid scales thin, covering nearly the entire body.

***Parapropercarina multispinata* sp. nov.**
Figs 2, 3, 4, 5, 6, 7, 8, 9, Tables 1–2

2011 Fish of unknown affinity, Schultz *et al*., p. 75, fig. 15A

Holotype. NHMD-625079. Well-preserved and nearly complete articulated skeleton preserved in a carbonate concretion, in part (A) and counterpart (B), 70.1 mm SL. (Fig. 2). The specimen has not been prepared with or coated by protective chemical substances.

Etymology. The name is derived from the Latin words 'multi' meaning many and 'spina' meaning spine, due to the notable high number of spines in the dorsal fin.

Type locality of holotype. Fur Formation, lowermost Eocene. Collected from the Ejerslev moclay pit locality, northern part of the island of Mors, northwestern Limfjord area, Denmark (Fig. 1A–B). The stratigraphic level is around ash layer +26 or +27 (Fig. 1C).

Paratypes. FUM-N-16161A+B, well-preserved superficial three-dimensional impression in soft diatomite, in part and counterpart, 49.7 mm SL. The impression of the part (FUM-N-16161A) is nearly complete, whereas the area of the head anterior and ventral to the orbit is missing in the counterpart (FUM-N-16161B). The anal fin is also missing; FUM-N-10535, preserved in a single slab of carbonate concretion. Nearly the entire head is missing, but other characters, particularly those related to the squamation pattern, including the intricate organisation of different scale types, are preserved. The lateral-line scales are also evident in this specimen; FUM-17356, well-preserved nearly complete articulated skeleton in a single slab of carbonate concretion, 60.5 mm SL. The Sr-map of this specimen suggests it has undergone some kind of chemical preparation – however, the specimen is an old find and data to conclusively confirm this is not available (Fig. 3).

Referred material. NHMD-1351141, incompletely preserved specimen, in part and counterpart; MM-9628, moderately preserved specimen, missing major parts of the median fins, scales and the epaxial part of the caudal-fin skeleton (Fig. 4).

Table 2. Synopses of morphometric values of *Parapropercarina multispinata* gen. et sp. nov.

	Holotype NHMD-625079			Paratype FUM-N-16161			Paratype FUM-N-17536		
Morphometric characters	Measurements (mm)	% of SL	% of HL	Measurements (mm)	% of SL	% of HL	Measurements (mm)	% of SL	% of HL
SL	70.1	–	–	49.7	–	–	60.5	–	–
HL	22.0	31.4	–	14.1	28.4	–	16.3	26.9	–
HD	18.1	25.8	82.3	11.9	23.9	84.4	14.3	23.6	87.7
POD	5.9	8.4	26.8	3.9	7.8	27.7	4.7	7.8	28.8
OD	4.9	7.0	22.3	3.6	7.2	25.5	4.3	7.1	26.4
MBD	19.6	28.0	–	11.2	22.5	–	15.1	25.0	–
DFB	28.9	41.2	–	20.7	41.6	–	23.3	38.5	–
AFB	16.1	23.0	–	12.2	24.5	–	13.8	22.8	–
CPL	11.6	16.5	–	7.5	15.1	–	10.2	16.9	–
CPD	6.3	9.0	–	3.9	7.8	–	5.6	9.3	–
PDD	26.8	38.2	–	17.4	35.0	–	23.5	38.8	–
PAD	44.3	63.2	–	30.7	61.8	–	36.7	60.7	–

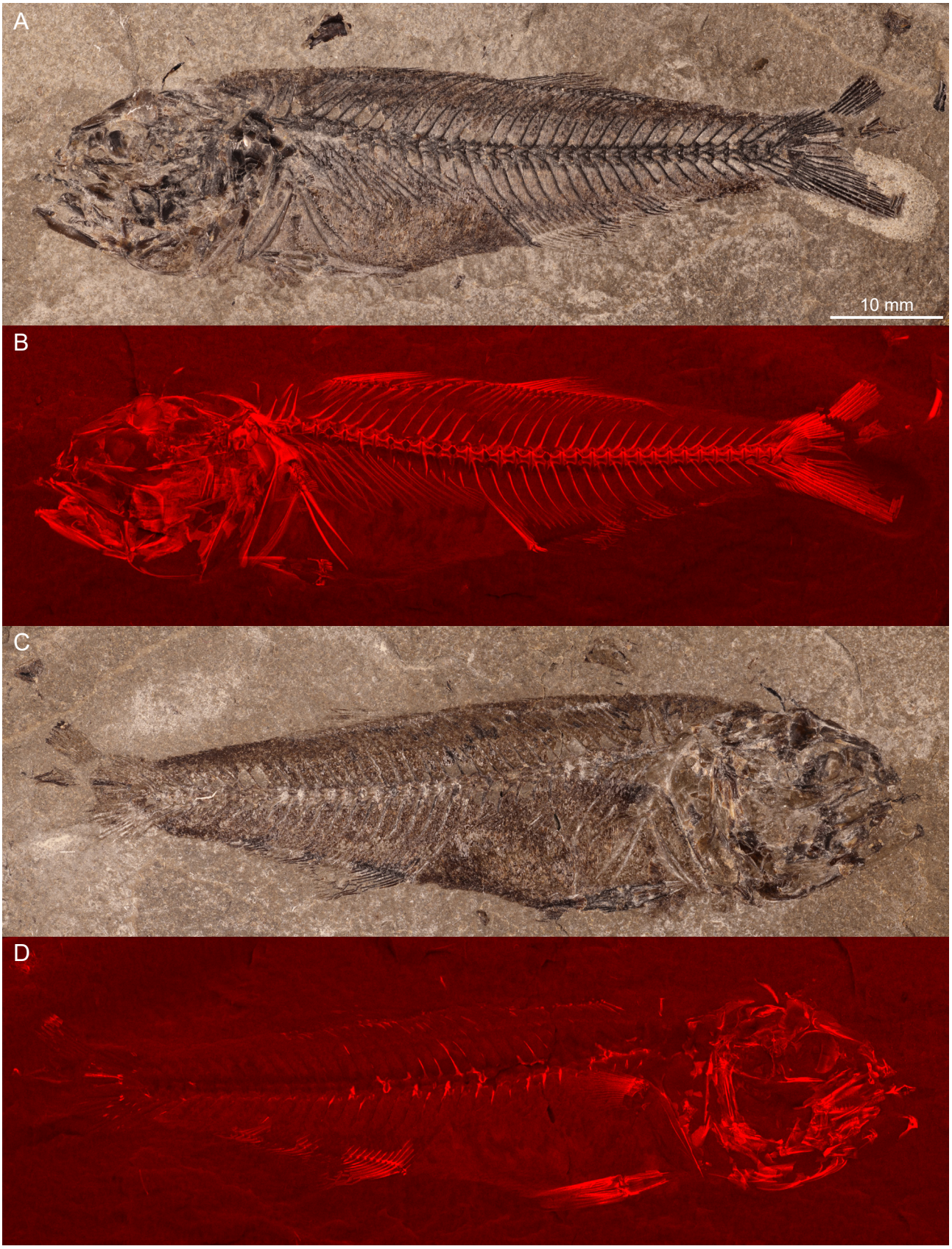

Fig. 2. *Parapropercarina multispinata* gen. et sp. nov., holotype NHMD-625079 (DK-540). **A–D**: High-resolution photo images and strontium element maps, respectively, of the holotypic part (A–B, NHMD-625079A) and counterpart (C–D, NHMD-625079B). Note particularly the rounded vertebral foramen, located slightly above each centrum (B).

Diagnosis. As for the genus.

Description. The body is elongate, relatively slender and laterally compressed, SL about 70 mm. The head is moderately large, representing nearly 29% of SL. The maximum body depth is contained about four times in SL, measured between the head and the first spines of the dorsal fin; the minimum depth is just in front of the caudal fin. The predorsal distance represents slightly less than 40% of SL. The preanal distance represents slightly more than 60% of SL. The head is nearly triangular in shape with the dorsal margin either straight or slightly convex, and the ventral margin convex. The mouth is terminal, slightly dorsally oriented. The orbit is large, representing about one-fourth of the head length, and is nearly the same size as the preorbital distance. The caudal peduncle is relatively short, representing slightly more than 15% of SL and caudal peduncle depth about 10% of SL (Table 2).

Neurocranium. The neurocranium is moderately deep. The ethmoid region in lateral view is rhomboid-shaped. What appears to be the vomer articulates with the ventral surface of the ethmoid region. The vomer bears several tiny teeth. The lateral ethmoid bears a clear concavity posterolaterally. The frontals are narrow in the anterior part, while about three times wid-

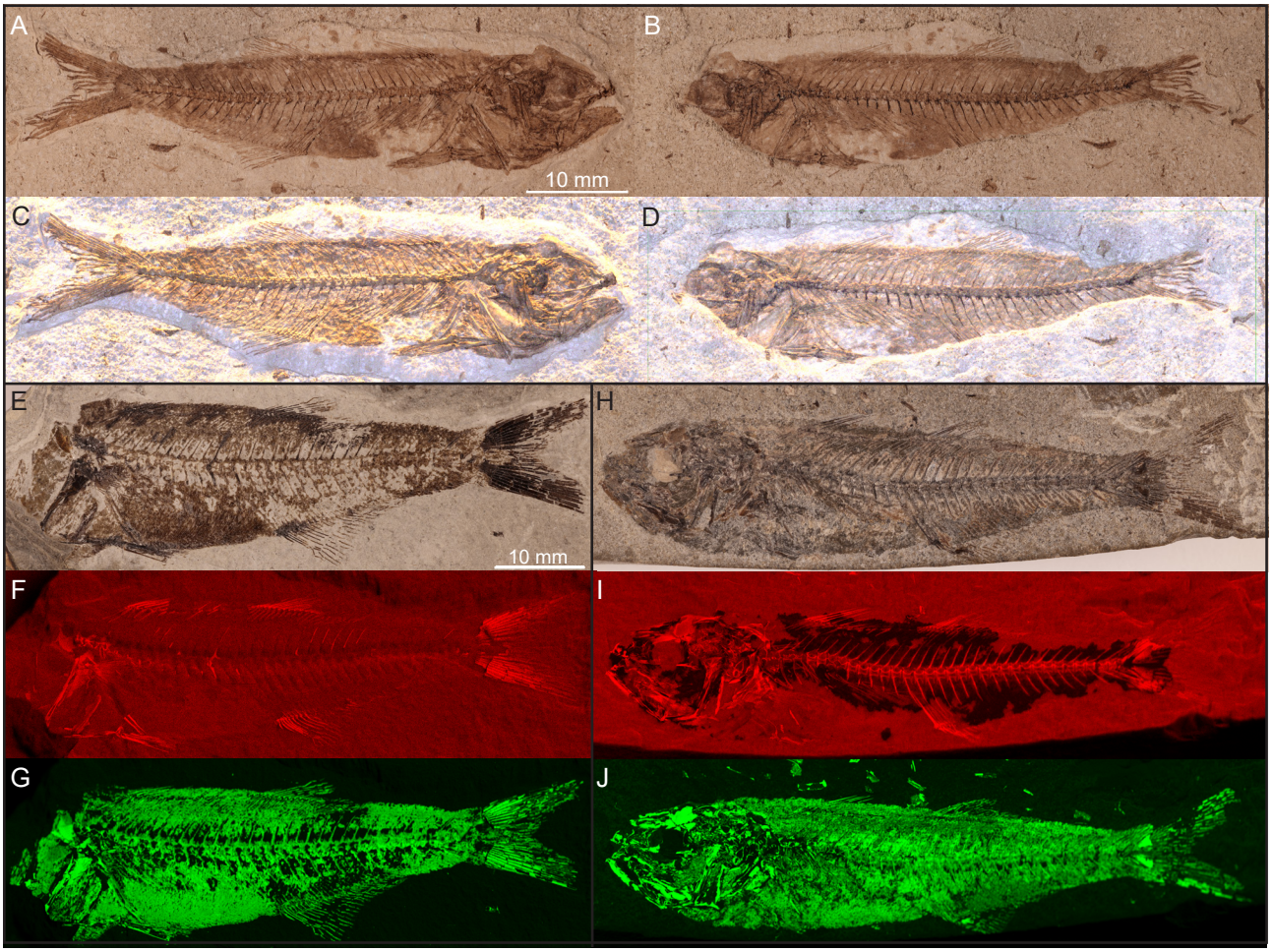

Fig. 3. *Parapropercarina multispinata* gen. et sp. nov. Paratypes. **A–D**: Paratype FUM-N-16161, the scale bar in A applies also to B, C and D. **A**: High-resolution photo image of the part FUM-N-16161A. **B**: High-resolution photo image of the counterpart FUM-N-16161B. **C–D**: Mosaic image of FUM-N-16161A (C) and FUM-N-16161B (D) in different illumination to make the bone imprints appear inverted, thereby enhancing the visibility of the individual bone element morphologies. **E–G**: Paratype FUM-N-10535, high-resolution image (E), strontium element map, note the lack of Sr-signals as the bones are mostly preserved as imprints with exception of the paired and median fins (F), whereas the scales are preserved and clearly visible in the phosphorous map (G). The scale bar in E applies also to F, G, H, I, J. **H–J**: Paratype FUM-N-17356, high-resolution photo image (H), strontium element map (I), note the taphonomic modification of the postcranial portion of the body, including the supraneurals where only two of the three are visible, and the dislocated anteriormost vertebrae, where several are now visible in anterior view.

er in the postorbital region. The posterodorsal corner of the orbit is delimited by the sphenotic; it articulates with the posterolateral margin of the frontal. The frontals articulate with the parietals posteriorly. The supraoccipital crest is short and low. The otic part of the neurocranium is about twice as deep as the ethmoid part. The ventral margin of the neurocranium is occupied by the parasphenoid, which is ventrally curved in the central part; there are well recognisable lateral processes at the postorbital section of the bone (e.g. FUM-N-17356, NHMD-1351141, Figs 2–3). Other parts of the neurocranium are not recognisable.

Infraorbital series and sclerotic bones. None of the circumorbital bones is recognisable. The sclerotic ossicles are large, bowl-shaped and located in the anterior and posterior parts of the orbit. The anterior sclerotic ossicle seems to be slightly larger than the posterior one (compare NHMD-625079 and NHMD-1351141, Figs 2, 4, 5, 6).

Jaws. The oral jaws are strong and massive. The alveolar process of the premaxilla is relatively straight, bearing a single row of small conical teeth. It is not possible to determine the precise number of teeth in any of the examined specimens. Both the ascending and articular processes are short and blunt (NHMD-625079, Fig. 2). Posteriorly, the premaxilla seems to be in close connection with the posterior section of the maxilla. Anterodorsally, the maxilla exhibits a slight curvature and has well-developed ethmoid and premaxillary processes; just above the posterior margin of the maxilla, there are feebly ossified skeletal remains that are tentatively interpreted herein as a partially preserved supramaxilla (NHMD-625079, MM-9628, Figs 2, 4, 6). The lower jaw articulation is located at the level of the posterior half of the orbit. The dentary is relatively deep, V-shaped and with a straight alveolar margin and a single row of relatively large and spaced conical teeth; at least 12 teeth can be recognised in the paratype FUM-N-16161 (Fig. 3A–D). The anterodorsal corner of the symphysis is slightly curved ventrally, whereas the ventral margin is somewhat convex; its posterior margin reaches the level of the central part of the orbit. There is a large foramen at midheight of the symphysis, probably for the facialis nerve (Fig. 6). The anguloarticular is rhomboid in shape, anteriorly articulating with the dentary and posterodorsally with the quadrate. There seems to be a small retroarticular in the posteroventral corner of the anguloarticular.

Suspensorium. The hyomandibula is elongated with a straight shaft exhibiting an anteriorly developed lamina that is in contact with the metapterygoid. The articular head is massive with a rounded margin and appears to be inclined slightly forward (FUM-N-17536, Fig. 3H–J) bearing a relatively short opercular process. The maximum width of the artic-

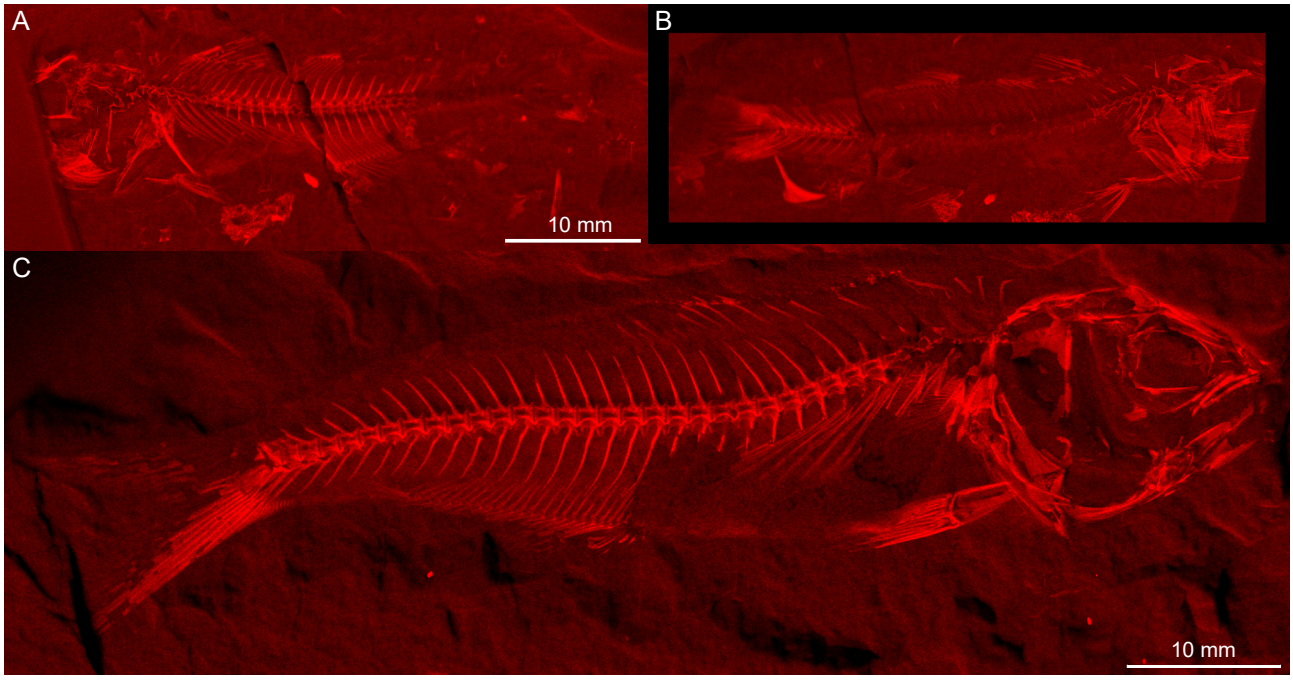

Fig. 4. *Parapropercarina multispinata* gen. et sp. nov. Referred material shown in their strontium element maps. **A–B**: NHMD-1351141, part (A) and counterpart (B). **C**: MM-9628.

ular head is contained about 3.5 times in the shaft of the bone. The palatine articulates dorsally with what appears to be the lateral ethmoid and posteroventrally with the ectopterygoid. Several tiny teeth are recognisable along the medial surface of the palatine in the holotype (Fig. 2). The ectopterygoid is L-shaped, with the horizontal limb being slightly longer than the vertical one; posteriorly, it contacts the anterior margins of the quadrate and the metapterygoid. The endopterygoid articulates with the dorsal margin

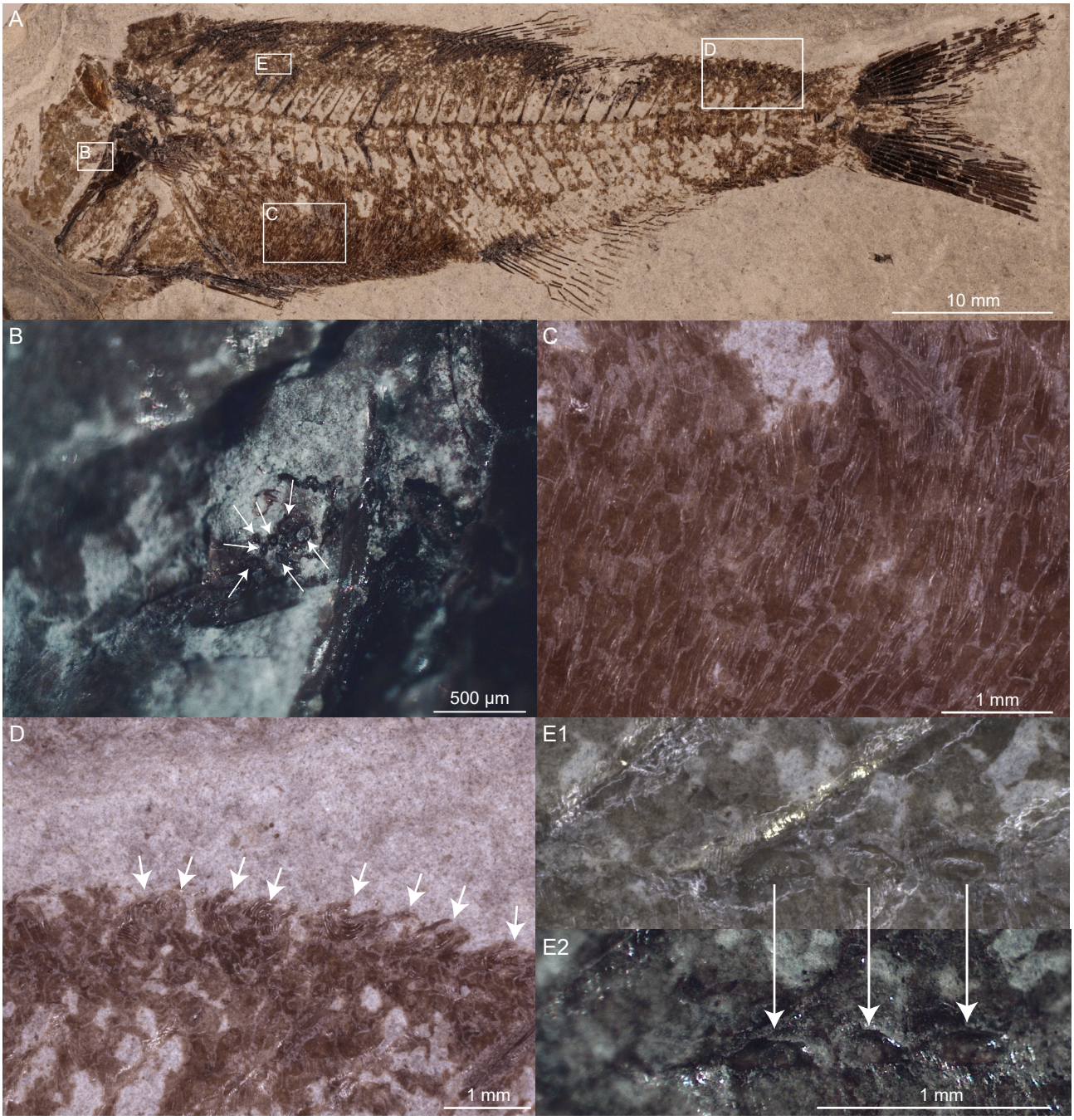

Fig. 5. *Parapropercarina multispinata* gen. et sp. nov. Micrographs of the branchial tooth plate and different scale types, paratype FUM-N-10535. **A**: High-resolution photo image showing the entire paratype, with each frame indicating the magnified sections in this figure. **B**: A partly preserved branchial tooth plate in transverse section. Arrows indicate the most noticeable teeth. **C**: The overlapping scales covering most of the body, of which only the posterior portion is exposed showing the longitudinally oriented circuli. **D**: Ovoid cycloid scales by the posterodorsal body margin are indicated with arrows. **E**: Three elliptic lateral-line scales. The upper (E1) and lower (E2) micrographs were taken of the exact same portion, but on two different micro-setups, highlighting the glasslike appearance of these scales.

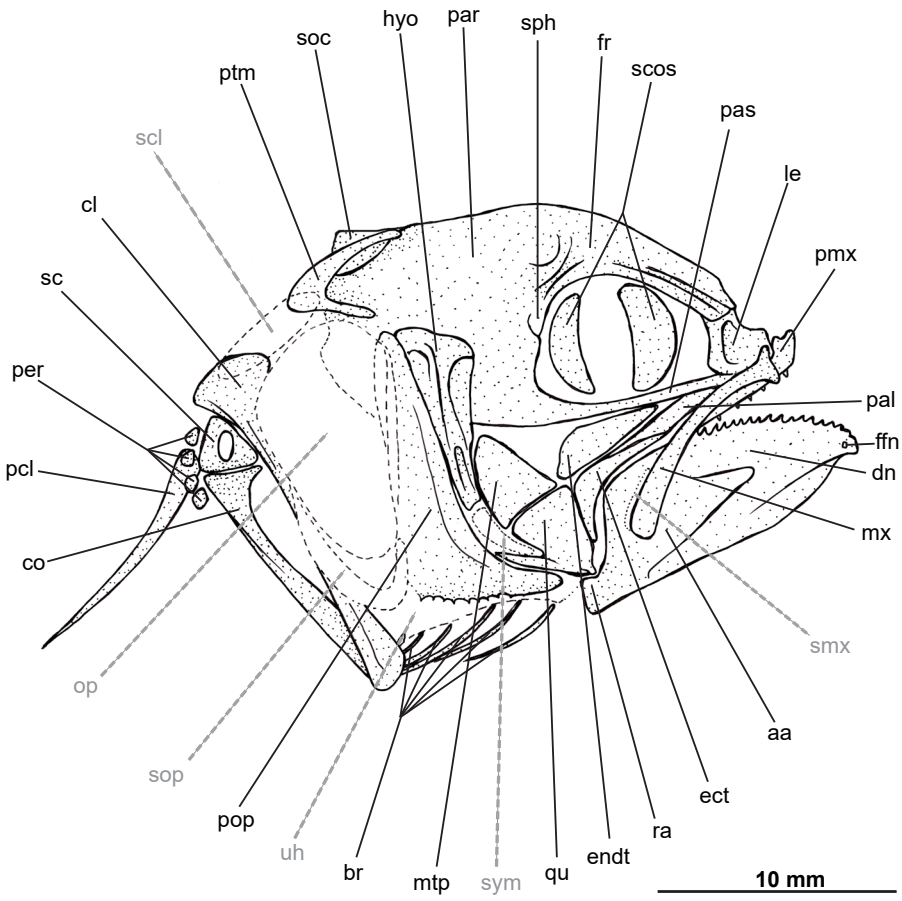

Fig. 6. *Parapropercarina multispinata* gen. et sp. nov. Interpretative reconstruction of the head, based on the holotype NHMD-625079.

of the ectopterygoid (NHMD-625079). There is no evidence of pterygoid teeth. The quadrate is shaped as an isosceles triangle and has a well-developed, rounded articular head for the lower jaw.

Opercular series. The bones of the opercular series are generally poorly preserved in the available material. The preopercle is L-shaped; the vertical limb appears to be more than twice as long as the horizontal one. The ventral margin and posteroventral corner of the bone bear several small, short spines (NHMD-625079, NHMD-1351141). The morphology of the posterior margin is not clearly recognisable. The opercle is very thin and appears to be rhomboid-shaped, and deeper than wide; no ornamentations or spines can be recognised along its posterior border. The dorsal margin of the subopercle has a deeply notched shape, but no other details of the subopercle and of the interopercle are recognisable.

Hyoid apparatus and branchial skeleton. The hyoid bar has a straight dorsal and a slightly concave ventral margin (NHMD-625079, FUM-N-17356, partially visible also in NHMD-1351141). The hypohyals and the articulation between the anterior and posterior ceratohyals cannot be recognised. Six branchiostegal rays appear to be present. Although some branchial remains are faintly recognisable in NHMD-1351141, including several well-developed gill rakers, the morphology of the branchial arches is not clear. In the paratype FUM-N-10535 (Figs 3E, 5), a small fragment of bone with evident presence of tiny teeth is preserved in the region between the posterior opercular margin and the anterior margin of the cleithrum; these are mostly preserved in transversal section and it is reasonable to assume that this tooth bearing structure represents a partly preserved branchial tooth plate (Fig. 5A–B). None of the available material shows any evidence of the pharyngeal sacs or individual pharyngeal sac rakers (Fig. 6).

Vertebral column and intermuscular bones. The vertebral column comprises 36 vertebrae, including the compound centrum (15 abdominal and 21 caudal). The morphology of the first and second vertebrae is not entirely clear. The dorsal prezygapophyses of the vertebrae from the 3rd through the 33rd exhibit an anterior articular surface for the respective dorsal postzygapophyses of the preceding neural arch. On the lateral side of the neural arches, including those of the second preural vertebra, slightly above the

vertebral centrum, there is a rounded foramen. There are ventral parapophyses developed from the eighth up to fifteen abdominal vertebrae, which gradually increase in size posteriorly. The haemal spines of the caudal vertebrae are slightly longer and more curved backwards than the opposite neural spines, which are shortened posteriorly in the series.

Twelve pairs of ribs occur from the fourth to the fifteen abdominal vertebrae, being strongly developed and posteriorly inclined. From the fourth to the seventh vertebrae, the ribs articulate with the ventral margin of the centra, moving subsequently to the posteroventral surface of the parapophyses. Anteriorly, the ribs are generally more massive and elongate reaching one third of the body depth, while they are thinner and shorter posteriorly. Remains of at least three pairs of epineurals, associated with the dorsal portions of the anterior ribs, are visible in the holotype (Fig. 2).

Caudal skeleton and fin. The caudal skeleton consists of a compound centrum, fused hypurals 1 and 2, partially fused hypurals 3 and 4, autogenous hypural 5, autogenous parhypural (without parhypurapophysis), two uroneurals, and three epurals. The parhypural has a massive proximal portion. The haemal spines of PU2 and PU3 are autogenous. The neural spine of PU3 is fully developed. The neural spine of PU2 is strongly reduced to a low, blade-like crest. The caudal fin is deeply forked. There are 17 (1,8 + 7,1) and eight or nine upper and nine to ten lower procurrent rays. There is no evidence of a procurrent spur (Figs 2, 7).

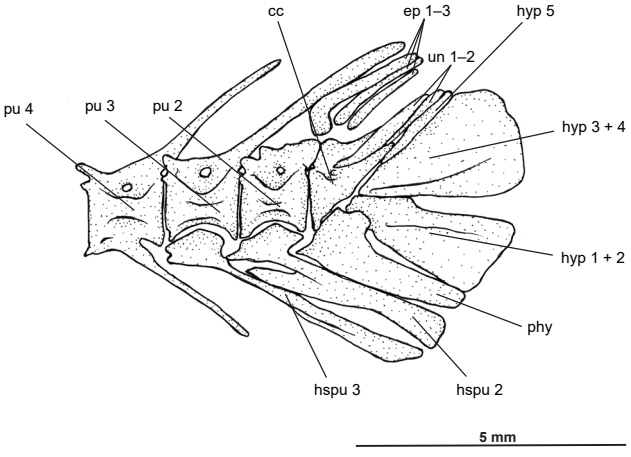

Fig. 7. *Parapropercarina multispinata* gen. et sp. nov. Interpretative reconstruction of the caudal-fin skeleton, based on the holotypic part NHMD-625079A.

Median fins and supports. There are three tiny supraneurals, about one mm in length each (FUM-N-16161 and MM-9628, Figs 3–4, 8); in some specimens, including the holotype NHMD-625079 and paratype FUM-N-17536, only two supraneurals can be recognised, most likely the missing one being hidden under other skeletal elements or not preserved at all (note this region in particular in FUM-N-17536). The first supraneural is nearly T-shaped, with a larger anteriorly projecting process. The second supraneural is faintly enlarged anteriorly, and the third supraneural is rod-like. The predorsal formula is 0/0+0/2/1. The dorsal fin is continuous and contains 15 spines plus 18 rays supported by 33 pterygiophores (Fig. 9). The first spine is in supernumerary association on the first dorsal-fin pterygiophore. The second to fifth dorsal-fin spines are much longer than the others. The 9th to 13th spines are nearly equal in length, much shorter than the preceding ones. This condition is also supported by the preserved impression of this part of the dorsal fin in the paratype FUM-N-10535 in which an indented outer profile of the dorsal fin is recognisable. The 14th spine is very short, and the 15th is significantly longer and thinner. The rest of the dorsal fin comprises 18 distally branched and segmented rays, the longest being the 16th and the following ones decrease in length posteriorly. The dorsal-fin formula cannot be determined in the holotype, due to taphonomic modification of the anterior postcranial portion of the body.

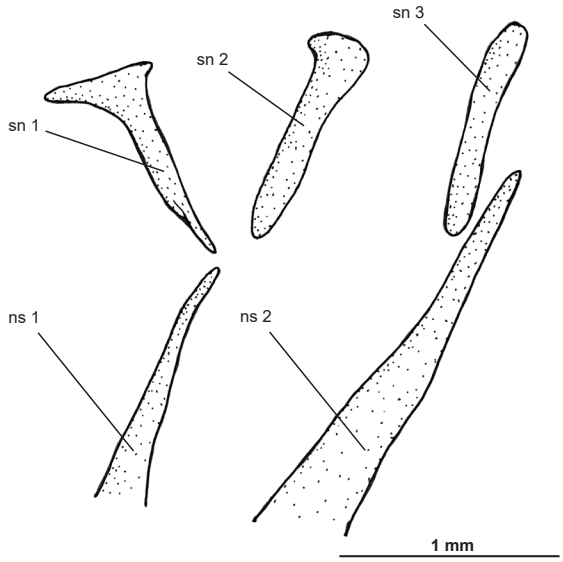

Fig. 8. *Parapropercarina multispinata* gen. et sp. nov. Interpretative reconstruction of the three supraneurals with the first being nearly T-shaped and the two following rod-like. Based on the paratypic counterpart FUM-N-16161B.

The anal fin consists of two (FUM-N-17536, NHMD-1351141, Figs 3–4) or three (holotype NHMD-625079, FUM-N-10535, FUM-N16161, Figs 2–3) spines plus 24 rays that decrease in length posteriorly. The posterior anal-fin spine is considerably longer than the preceding ones.

Paired fins and girdles. The posttemporal has two limbs, the dorsal one being massive, slightly arched and more than twice as long as the ventral limb. The limbs form an angle of about 50°. The supracleithrum articulates with the dorsal extremity of the cleithrum and the posteroventral margin of the posttemporal. The cleithrum is crescent-shaped and bears an expanded bony lamina along its posterodorsal margin. The scapula is rounded and centrally pierced by the scapular foramen. The ventral margin of the scapula and surface of the cleithrum just below it articulate with the coracoid, which has an expanded and curved ventral limb. The postcleithrum is rod-like and reaches almost the ventral margin of the body. The pectoral fin inserts at midheight of the body and contains about 18 rays supported by four radials, two of which articulate with the scapula and two with the coracoid. The distal portions of the pectoral-fin rays reach the level of the 10th abdominal vertebra (see MM-9628).

The basipterygium is elongate and triangular, with a well-developed postpelvic process. The pelvic fin comprises a single spine plus five rays, extending back up to the 10th or 11th vertebra.

Squamation. The body, including the proximal portion of the median fins, is densely covered by overlapped scales, of which only the posterior field is exposed showing longitudinally oriented circuli (Fig. 5C). Along the dorsal and ventral margins of the body, three or four rows of small ovoid cycloid scales form a very dense sheath (Fig. 5D). The same type of scales is also recognisable in the proximal part of the caudal fin, extending to the level of first bifurcation of the caudal-fin rays, as well as along the basal portion of the dorsal and anal fins. Cycloid scales of larger size cover most of the head, including the cheek, opercular series, and nape, being absent on the frontals, orbital area and the snout. Furthermore, the lateral-line series can be recognised in the paratype FUM-N-10535 between the dorsal body profile and the vertebral column. The lateral-line scales are recognisable based on the impression on their internal canal; there are approximately three lateral-line scales per interneural space (Fig. 5E), at least in the anterior half of the body.

The nomenclatural acts of this paper are registered on ZooBank. LSID of the new genus *Parapropercarina*: https://zoobank.org/urn:lsid:zoobank.org:act:85FF6F95-495B-460D-95C0-7494083DEDAA
and the LSID of the new species *Parapropercarina multispinata*:
https://zoobank.org/urn:lsid:zoobank.org:act:440E329F-9BF2-4303-AE61-1027AFFD0A02

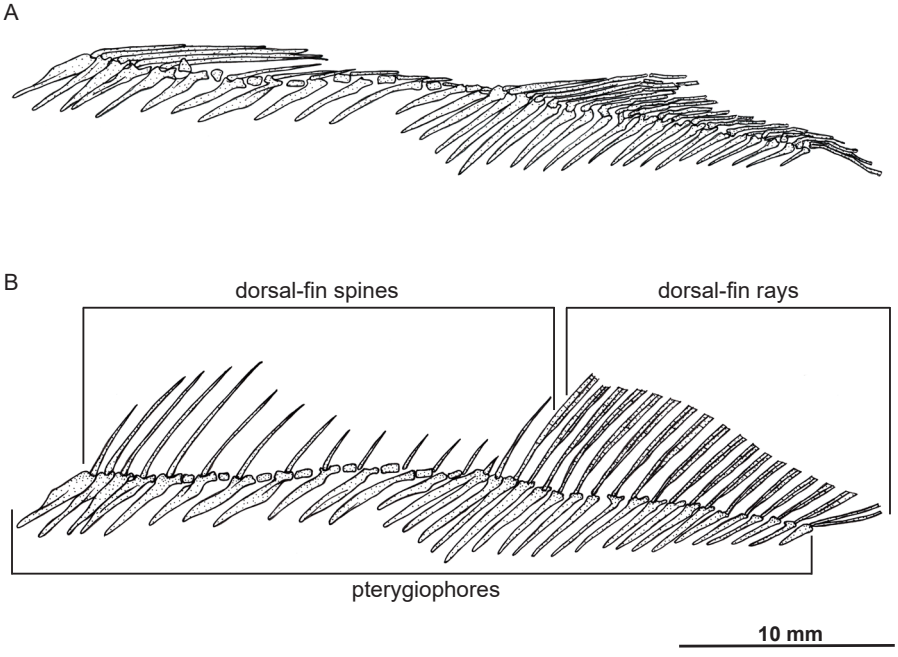

Fig. 9. *Parapropercarina multispinata* gen. et sp. nov. **A**: Interpretative drawing of the dorsal fin, based on the holoptypic part, NHMD-625079A. **B**: Reconstruction of the dorsal fin, with dorsal-fin spine section, dorsal-fin rays and pterygiophores indicated.

Comparative discussion

The new taxon described herein, *Parapropercarina multispinata* gen. et sp. nov., possesses a number of characters that unequivocally place it within the Percomorphacea, including the absence of a separate second ural centrum, presence of five hypurals, pelvic fins with less than six rays, and the caudal fin composed by 17 (I,8+7,I) principal rays (see Wiley & Johnson 2010).

The overall morphology of *Parapropercarina multispinata* gen. et sp. nov. is strongly reminiscent of that of stromateiform fishes. The monophyly of the order Stromateiformes is supported by eight synapomorphies (Pastana *et al*. 2022), including: 1) at least 24 distally branched anal-fin rays; 2) number of ventral procurrent caudal fin rays10–12; 3) premaxillary teeth uniserial; 4) palatine teeth absent; 5) medial bony suture between the dorsal and ventral hypohyals absent, 6) adductor mandibulae pars malaris subdivided into retromalaris and promalaris subsections, 7) anteroventral section of epaxialis present; and 8) interdermal canal plexus present, with the first three being clearly recognisable in the studied material of *Parapropercarina* gen. nov., thereby supporting its attribution to the Stromateiformes. The majority of the other features refer to soft structures that can be preserved in fossils only in exceptional cases. The order Stromateiformes comprises six extant families, the Amarsipidae, Ariommatidae, Centrolophidae, Tetragonuridae, Stromateidae, and Nomeidae (see Haedrich 1967, 1969; Pastana *et al*. 2022), one extinct family, the Propercarinidae (see Bannikov 1995, Přikryl *et al*. 2014, Micklich & Přikryl 2025), plus several fossil taxa of uncertain familial affinities [see Bannikov (2018) for review and critical comments]. The oldest skeletal record of this lineage is represented by *Butyrumichthys henricii* (see Schrøder *et al*. 2023a), which also originates from the Eocene deposits of the Fur Formation. The recognisable characters of *Parapropercarina* gen. nov. listed above, support its attribution within the suborder Stromateoidei (=non-Amarsipidae Stromateiformes *sensu* Pastana *et al*. 2022).

The attribution of *Parapropercarina* gen. nov. to Ariommatidae, Tetragonuridae, and Stromateidae can be ruled out based on the higher number of dorsal-fin spines (15 vs. 11), which Pastana *et al*. (2022) considered an unambiguous synapomorphy of these families. The Centrolophidae can be ruled out as well, including *Butyrumichthys*, based on the general morphological features, such as an elongated body (vs. deep), low supraoccipital crest (vs. high supraoccipital crest), a single dorsal fin exhibiting a deep notch, containing 15 spines and 18 rays (vs. notch absent and 3–7 spines plus 23–50 rays).

The overall morphology of *Parapropercarina* gen. nov. most closely resembles that of the Nomeidae and the extinct family Propercarinidae (Table 3).

The Nomeidae has traditionally been considered as a stromateoid group, characterised by two dorsal fins, teeth on the vomer and palatines, six branchiostegal rays, four hypurals and three epurals in the caudal-fin skeleton, and papillae in the pharyngeal sacs with stellate bases, arranged in about five broad longitudinal bands (Haedrich 1967; see also interpretative comments by Pastana *et al*. 2022: 947). The definition of this family based on unambiguous synapomorphies was detailed by Pastana *et al*. (2022) and includes the ventral limb of the coracoid being curved, dorsal surface of the head with scales, interradial membrane of the pectoral fin covered by scales, and modified pectoral girdle, which reflects the specialisation of the pectoral fin (Pastana *et al*. 2022). Conversely, six branchiostegal rays, palatine teeth, presence of some cycloid scales on the dorsal surface of the head, partial fusion of some of the hypurals, and a single dorsal fin with a deep notch, are present in both *Parapropercarina* gen. nov. and in nomeids. The other characters appear not to be present in the examined material of *Parapropercarina* gen. nov. However, it cannot be ruled out that some of

Table 3. Comparative overview of *Parapropercarina*, Propercarinidae and Nomeidae

Characters	*Parapropercarina*	Propercarinidae	Nomeidae
Elongated body	+	+	+/–
Low supraoccipital crest	+	+	–
Vomerine and palatine teeth	+	+	+
Single dorsal fin with deep notch	+	–	+/–
Rayless pterygiophores	–	+	?
Six branchiostegal rays	+	+	+
Vertebral column 35–37	+ (36)	+ (35≤37)	+ (30≤42)
Modified pectoral girdle	–	–	+
Slightly curved ventral limb of coracoid	+	+	+

these may have been present in origin and lost due to the fossilisation processes.

As mentioned above, *Parapropercarina* gen. et sp. nov. also exhibit considerable morphological similarities to the monotypic family Propercarinidae, which was recently emended by Micklich and Přikryl (2025) as a lineage of stromateoid fishes with elongated body, pelvic fin present in adults, number of anal fin-rays that exceeds the number of rays in the second dorsal fin, presence of about 36 vertebrae, posterior abdominal ones with well-developed parapophyses, caudal-fin skeleton non-oligomerized, teeth rather strong, scales thin, cycloid or ctenoid, and the lateral line high, running parallel to the dorsal margin of the body. The most striking differences between *Parapropercarina* gen. nov. and *Propercarina* are represented by the possession of a single vs. two deeply separated dorsal fins; no free rayless pterygiophores vs. five free rayless pterygiophores in between the first and second dorsal fins; and relatively long pectoral fins vs short.

Concluding remarks

Parapropercarina multispinata gen. et sp. nov. clearly exhibits morphological characters shared with representatives of both families, Propercarinidae and Nomeidae. This confirms the hypothesis by Micklich & Přikryl (2025) that the propercarinids are likely much closer to the nomeids, than to the amarsipids, as suggested earlier (compare Bannikov 1995 and Přikryl *et al*. 2014). Up to date propercarinid-like stromateiforms are known from Oligocene Paratethyan deposits (Bannikov 1995; Přikryl *et al*. 2014; Micklich & Přikryl 2025). The new taxon described herein suggests that a body plan similar to that of propercarinids was in existence at much higher northern latitudes in the immediate aftermath of the PETM, thereby expanding both the temporal and latitudinal distribution. Due to the preservation of all current available material kept in the museum collections in Denmark, it is not possible to conclusively resolve the attribution at the family level of *Parapropercarina multispinata* gen. et sp. nov.

Acknowledgements

René Lyng Sylvestersen and Bo Schultz (Fur Museum, Museum Salling) are warmly thanked for organising and authorising the loan of specimens FUM-N-16161A+B, FUM-10535 and FUM-N-17356. Bent Erik Kramer Lindow is cordially thanked for organising the loans of NHMD-625079A+B and NHMD-1351141, and authorising access to the photolab at the Zoological Museum in early 2024. Ida Bonnevier Wallstedt is thanked for providing specify data on the NHMD specimens. Thanks to Henrik Madsen for organising the loan of MM-9628, and many thanks to Kristoffer Szilas for access to the μXRF facilities and equipment at the Department of Geosciences and Natural Resource Management, University of Copenhagen. The research of AES was supported by the Carlsberg Foundation grant no. CF23-1059. The research of GC was supported by grants (ex-60% 2024) from the Università degli Studi di Torino. The research of Tomáš Přikryl was supported by the Institute of Geology of the Czech Academy of Sciences (RVO67985831). We greatly appreciate the comments and suggestions by journal reviewers, Ionuţ Grădianu and Giuseppe Marramà.

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