

A reappraisal of the lampridiform *Palaeocentrotus boggildi* Kühne, 1941 from the Eocene Fur Formation, Denmark

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The systematic affinities of *Palaeocentrotus boggildi* within acanthomorph fishes have never been properly discussed. A comparative analysis of the skeletal anatomy of the genera *Cyttus* and *Zeus* was used by Kühne to support the placement of *Palaeocentrotus* within the zeiforms, despite certain features are completely different from those characteristic of zeiforms. Bonde (1966) was the first that recognised the lampridiform affinities of *Palaeocentrotus* and allocated the genus to its own family, Palaeocentrotidae. However, this hypothesis was not supported by a discussion of the relevant features to justify a possible relationship with the Lampridiformes. The anatomical survey of the known material of *Palaeocentrotus boggildi* presented here resulted in the identification of a suite of features that is regarded as diagnostic of the Lampridiformes, including: anterior palatine process absent, mesethmoid posterior to lateral ethmoids, elongate ascending premaxillary process longer than the alveolar process and inserting into the frontal vault, premaxilla and dentary edentulous, endopterygoid teeth absent, urohyal bearing a large ventral laminar expansion, second ural centrum free from fused first ural and preural centra and fused posteriorly to the upper hypural plate, presence of two supraneurals and of a single postcleithrum. The most striking feature of the Palaeocentrotidae, comprising only *Palaeocentrotus* and *Natgeosocus*, is the unique configuration of the dorsal fin wherein true spines occur exclusively in the central portion. This peculiar condition represents a further example of the remarkable plasticity of the acanthomorph median fins.

Keywords: Palaeocentrotidae, Paleogene, Ypresian, *Natgeosocus*, dorsal fin.

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The lampridiform *Palaeocentrotus boggildi* was the very first bony fish from the earliest Eocene Fur Formation to be described in detail (Kühne 1941). Fossils belonging to this taxon are rather rare in the Fur Formation. Between 1937 and the late 1960s, only two specimens including the holotype were known (Bonde 1966), while in the period from 1993 to 2018, six additional specimens have been recovered from two localities (the Ejerslev and Skarrethage mo clay pits) and deposited in officially recognised museums' collections. Two of these specimens have been collected by staff at the local Fossil- and Mo clay Museum on Mors. The other four specimens have been

recovered by private collectors, two of which have subsequently been acquired by local museums on the islands of Fur and Mors, and two have been declared Danekræ fossil trove, due to their exceptional scientific and exhibition value (Danekræ no. 79 and 1067). Danekræ are exceptional objects of fossil nature, meteorites or rare minerals found in Denmark, covered by national legislation and belong to the Danish state, and are entered into the Danekræ collection of the Natural History Museum Denmark (Christensen & Hald 1990; Bonde *et al.* 2008).

Lampridiforms constitute a well-defined clade within the acanthomorphs. However, as morpholog-

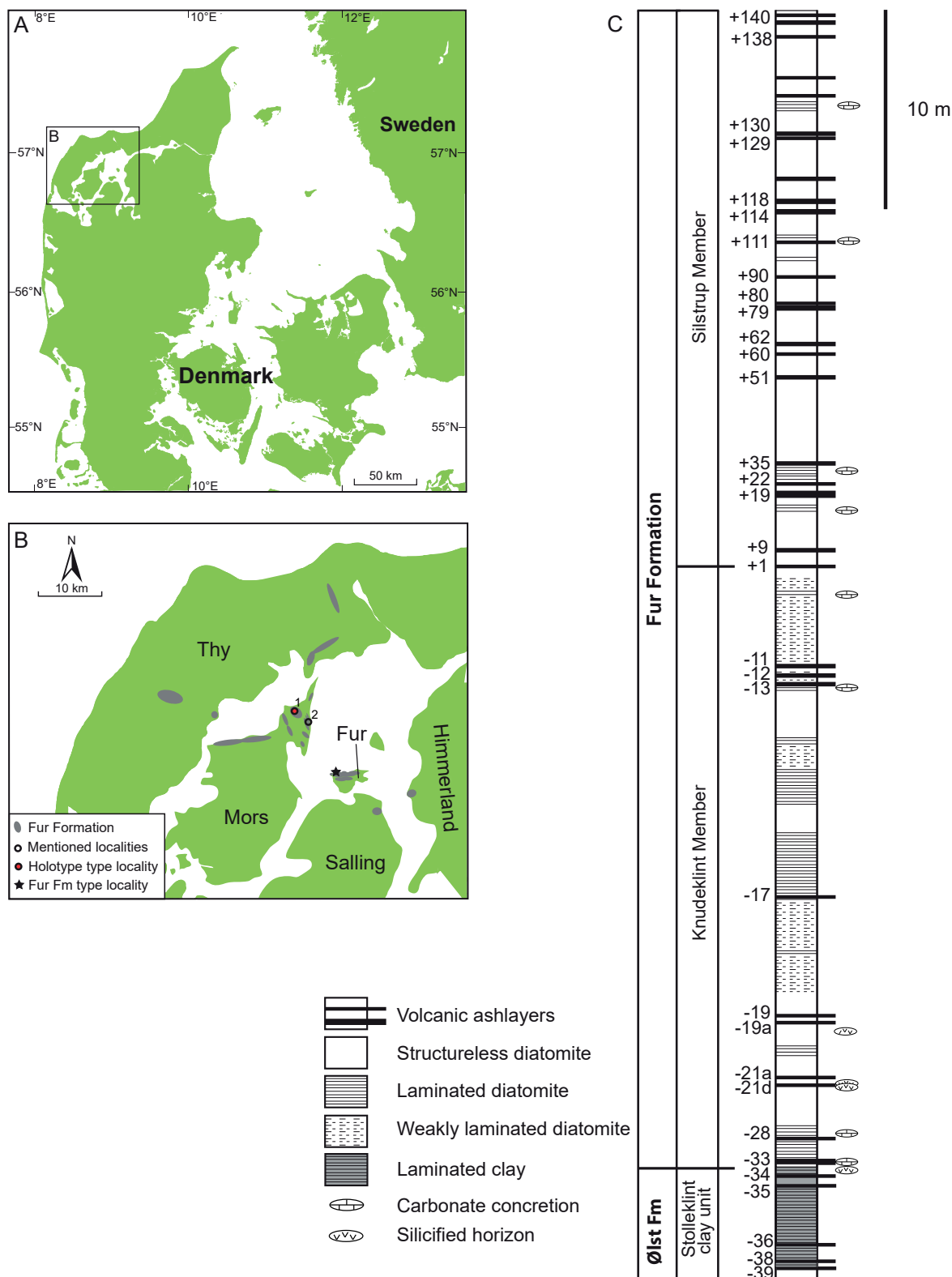


Fig. 1. A: Map of Denmark showing the area where the Fur Formation is present. **B:** Outcrop localities and near-surface occurrences of the Fur Formation. Circles mark the locations from where the examined specimens have been collected. 1 = Skarrebage moclay pit, which is also the type locality of the holotype; 2 = Ejerslev moclay pit. The star indicates the type locality of the Fur Formation. **C:** Sedimentological log comprising the positive and negative ash series throughout the Stolleklint clay unit of the Ølst Formation and the Fur Formation in northwestern Denmark. Modified from Schröder and Carnevale (2023).

ical and molecular evidence often provide contrasting results, the phylogenetic position of the order Lampridiformes is still debated. Most morphological studies concur to place Lampridiformes as sister to all the other acanthomorphs, i.e. Euacanthomorpha (e.g. Johnson and Patterson 1993; Olney *et al.* 1993; Wiley *et al.* 2000). Molecular studies have also placed Lampridiformes as sister group to Euacanthomorpha (e.g. Grande *et al.* 2013), as sister to the Acanthopterygii (e.g. Hughes *et al.* 2018), as sister to the Polymixiiformes (e.g. Li *et al.* 2009), as sister to the Paracanthopterygii (e.g. Betancur-R *et al.* 2013, 2017), as sister to the Polymixiiformes + Paracanthopterygii (Dettai & Lecointre 2005), and as sister to the Euacanthopterygii (Near *et al.* 2012). Molecular studies based on mitochondrial-DNA place Lampridiformes as sister to either Ateleopodiformes or Myctophiformes (see Miya *et al.* 2005, 2007; Poulsen *et al.* 2013).

Extant lampridiforms comprise strictly marine and pelagic taxa, exhibiting remarkable morphological diversity despite their comparatively limited species richness, currently comprising 26 species arranged in six families. These families are divided into the deep-bodied bathysomes (Veliferidae and Lamprididae) and the elongate-bodied taeniosomes (Lophotidae, Radiicephalidae, Regalecidae, Trachipteridae; Oelschläger 1983; Olney *et al.* 1993; Davesne *et al.* 2014, 2016; Brownstein & Near 2024). To date, not less than 15 fossil genera of Lampridiformes have been described (e.g. Sorbini & Sorbini 1999; Bannikov 1991, 1999, 2014; Carnevale 2004; Delbarre *et al.* 2016; Carnevale & Bannikov 2018; Micklich & Bannikov 2022; Davesne *et al.* 2023). Davesne *et al.* (2014) and Delbarre *et al.* (2016) found that Lampridiformes + *Pharmacichthys* Woodward, 1942 + *Aipichthyoidea* + *Pycnosteroidea* Woodward, 1942 form a clade, the Lampridomorpha, representing the sister group to the Euacanthomorpha, with the oldest representatives of Lampridomorpha dating back to the Cenomanian.

The earliest known lampridiform (Campanian), *Nardovelifer altipinnis* Sorbini & Sorbini, 1999, was resolved as a stem-lampridiform based on the presence of a suite of plesiomorphic characters absent from the crown-group (Davesne *et al.* 2014; Delbarre *et al.* 2016). Morphologically, this taxon represents the most derived Cretaceous lampridomorph taxon, exhibiting the closest affinity to extant veliferids (Sorbini & Sorbini 1999). Another putative stem-lampridiform (earliest Eocene) was recently described from the Fur Formation by Schröder and Carnevale (2025a), with several characters overlapping with *Nardovelifer altipinnis*. *Bathysoma lutkeni* Davis, 1890, from the Paleocene strata of Denmark and Sweden, is presently regarded the oldest Cenozoic lampridiform (Patterson 1964, 1968; Davesne *et al.* 2014). The most recent integrative morphological and molecu-

lar phylogenetic studies support the hypothesis that the diversification of extant lampridiform morphotypes occurred approximately ten million years after the Cretaceous-Paleogene mass extinction event (Brownstein & Near 2024), roughly corresponding to the earliest Eocene Fur Formation of Denmark (Storey *et al.* 2007; Westerhold *et al.* 2009; Stokke *et al.* 2020), in the immediate aftermath of the Paleocene-Eocene Thermal Maximum (Stokke *et al.* 2021).

The aim of the present study is therefore to provide a descriptive analysis of the morphology of *Palaeocentrotus boggildi* and discuss its affinities within the Lampridiformes.

Geological setting

The earliest Eocene Fur Formation is exposed at several places in the western Limfjord area of northern Denmark (Fig. 1A). The bulk of localities are exposed on the islands of Mors and Fur, represented by old and active digging pits and costal cliff exposures. Other notable exposures are present in the western part of Himmerland, the northern part of Salling, and in Thy (Fig. 1B). The Fur Fm comprises a fossil-rich, marine argillaceous diatomite, approximately 60 m in thickness, interbedded with possibly up to 200 ash layers, originating from the volcanic activity related to the opening of the Northeast Atlantic (e.g. Bøggild 1918; Pedersen & Surlyk 1983; Storey *et al.* 2007; Baumann 2024). Bøggild (1918) assigned the layers individual numbers and subdivided them into a negative and a positive series from -39 to +140. The series from -39 to just below -33 is now considered part of the lowermost section of the Haslund Member, Ølst Formation. This section of silicified hardened clay is commonly referred as the 'Stolleklint clay unit' (Heilmann-Clausen *et al.* 1985; Heilmann-Clausen 1995), which also comprises the Paleocene-Eocene boundary, based on the onset of the CIE (Schmitz *et al.* 2004; Stokke *et al.* 2020, 2021). The section from -33 to just below +1 reflects the lower Knudeklint Member of the Fur Fm, whereas the section from +1 to +140 reflects the upper Silstrup Member of the Fur Fm. The lower Knudeklint Mb is mainly laminated with relatively few ash layers, and the upper Silstrup Mb predominantly consists of structureless beds with numerous ash layers (Fig. 1C). Later recognised ash layers, not included in the series of Bøggild, have been assigned letters together with the number of the closest original ash layer (Fig. 1C; e.g. Gry 1940; Larsen *et al.* 2003; Pedersen *et al.* 2004). The Fur Formation was ostensibly deposited in a local nutrient-rich upwelling area, causing intermittently massive diatom blooms. The lamination of beds, general scarcity of benthic fauna together with other indicators, such as jaw tetany and other types

of muscle contractions, evident from the fossil bony fishes, suggests a fluctuating oxygen level, varying from anoxic to slight dysoxic conditions throughout the sequences (Pedersen 1981; Pedersen and Surlyk 1983; Heilmann-Clausen *et al.* 1985; Schröder *et al.* 2022; Schröder and Carnevale 2023).

With a few and rare exceptions (e.g. Schröder *et al.* 2023b, fig. 9G–J; Schröder and Carnevale 2025b, fig. 2), fossils from the soft diatomite are commonly preserved as flattened or shallow carbonaceous 3D impressions, where the original elements of the fossils have been entirely dispersed to the enclosing diatomite matrix – even if bone fragments are still present (Schröder *et al.* 2023b, figure 9A–E).

Carbonate concretions are present in certain stratigraphical horizons throughout the formation (Fig. 1C). These were formed just below sea-floor level by precipitation of calcite before compaction of the surrounding sediment. The concretions occasionally formed and grew around dead organisms, leaving the fossils within preserved predominantly as calcium phosphate or calcite (Pedersen and Buchart 1996; Pedersen *et al.* 2004). Later examinations have further shown that other original elements are preserved within the carbonate concreted fossils as well, relating to the body anatomy of the organisms (Schröder *et al.* 2023b). The fossils preserved in carbonate concretions, particularly the fishes, are usually exquisitely preserved, commonly retaining at least part of their original three-dimensional morphology (Schröder *et al.* 2022, 2023a, 2023b; Schröder and Carnevale 2023, Schröder and Carnevale 2025b). Only a single specimen, MM-108, described in this paper, is preserved in a carbonate concretion.

Material and methods

This study is based on museum collection material from the Eocene Fur Formation of northwestern Denmark. A total number of eight specimens have been examined. (Table 1). The material is deposited in four public recognised institutions, including the

collections of the Fur Museum and Museum Mors in northern Denmark, the Natural History Museum Denmark, and the Natural History Museum, London (United Kingdom). All material originates from the Ypresian Fur Formation in Denmark.

The holotype NHMUK PV P 22956 + PV P 22957 is kept at the Natural History Museum, London, and is part of the Walter Kühne collection. The holotype was collected by Charlotte Petsche in 1937 from the Skarrethage moclay pit on the island of Mors (Figs 1B, 2). The collection of Kühne, including this holotype, was purchased by the British Museum (=Natural History Museum, London) in October 1937. A second specimen, NHMD-2002586, from the Fur Formation (locality unknown) was collected by seminary teacher Frits Hastrup in 1942 and entered the collections of the Mineralogical Museum, University of Copenhagen (merged into NHMD in 2004) as an exchange possibly for another fossil in the 1960s. No further specimens referred to *Palaeocentrotus* were recorded for almost 50 years until two other specimens were recovered by private collectors from the Skarrethage moclay pit in 1993, NHMD-624663, and the Ejerslev moclay pit in 2016, NHMD-625274; these were subsequently declared Danekræ fossil trope (DK-79 and DK-1067, respectively). Local museums have acquired two further specimens from private collectors, one in 2001 from the Skarrethage moclay pit, now kept in the Fossil- and Moclay Museum (MM-94), and one in 2008 from the Ejerslev moclay pit, now kept in the collections of Fur Museum (FUM-N-16193a+b). Moreover, the staff at the Fossil- and Moclay Museum recovered two specimens in 2007 and 2018, MM-108 and MM-11959, respectively, both from the Ejerslev moclay pit.

The material was examined with a Leica M80 stereomicroscope equipped with a camera lucida drawing arm, a Nikon SMZ1000 stereomicroscope, a Wild Heerbrugg M7A equipped with a camera lucida drawing arm, and a Leica MZ75.

Photos of NHMUK PV P-specimens were taken with a Canon EOS 600D, while a Canon EOS R5 was applied for all remaining specimens.

Table 1. *Palaeocentrotus boggildi* Kühne, 1941. Studied material comprising the holotype, referred material and relevant specimen collection data

Catalogue number	Type status	Formation	Member	Lithology	Ash-series	Locality
NHMUK PV P 22956	Holotype (part)	Fur Fm	Knudeklint	Soft diatomite	2 m below -18a	Skarrethage moclay pit, Mors
NHMUK PV P 22957	Holotype (counterpart)	Fur Fm	Knudeklint	Soft diatomite	2 m below -18a	Skarrethage moclay pit, Mors
FUM-N-16193a	Referred material	Fur Fm	N/A	Soft diatomite	N/A	Ejerslev moclay pit, Mors
FUM-N-16193b (cp to 16193a)	Referred material	Fur Fm	N/A	Soft diatomite	N/A	Ejerslev moclay pit, Mors
MM-94	Referred material	Fur Fm	N/A	Soft diatomite	N/A	Skarrethage moclay pit, Mors
MM-108	Referred material	Fur Fm	Silstrup	Carbonate concretion	+25	Ejerslev moclay pit, Mors
MM-11959 (p & cp)	Referred material	Fur Fm	Silstrup	Soft diatomite	+25	Ejerslev moclay pit, Mors
NHMD-624663 (DK-79) (p & cp)	Referred material	Fur Fm	N/A	Soft diatomite	N/A	Skarrethage moclay pit, Mors
NHMD-625274 (DK-1067) (p & cp)	Referred material	Fur Fm	N/A	Soft diatomite	N/A	Ejerslev moclay pit, Mors
NHMD-2002586	Referred material	Fur Fm	N/A	Soft diatomite	N/A	Unknown

cp = counterpart, p = part.

Selected specimens, MM-108 and MM-11959 (only the counterpart) were subjected to μ XRF-element mapping. We followed the procedures, settings and machinery outlined in Schröder *et al.* (2023b) and Schröder and Carnevale (2023), i.e. applying a Bruker M4 Tornado Plus Amics at the Department of Geosciences and Natural Resource Management, University of Copenhagen, with a maximum acceleration of 50 kV and an anode current of either 250 or 600 μ A. With a few and rare exceptions fossils from the soft diatomite are commonly preserved as flattened or shallow carbonaceous 3D impressions, where the original elements of the fossils have been entirely dispersed to the enclosing diatomite matrix (e.g. Schröder *et al.* 2023b, fig. 9G–J; Schröder and Carnevale 2025b, fig. 2). Considering these results, we sent loan applications to the NHMUK, concerning the holotype specimen kept in London, for it to undergo non-destructive μ XRF in Denmark. However, for several reasons it was not possible to get it to Denmark.

Measurements were obtained either directly on the specimens with a digital calliper or with ImageJ due to the fragility of the specimens. Standard length (SL) is used throughout.

Institutional abbreviations: DK, Danekræ fossil trove collection, Natural History Museum Denmark (University of Copenhagen); FUM-N, Fur Museum, a division of Museum Salling (Denmark); MM, Fossil- and Moclay Museum, a division of Museum Mors (Denmark); NHMD, Natural History Museum Denmark, University of Copenhagen; NHMUK PV P, Fossil Fish Collection (=PV P, Palaeontology Ver-

tebrates, Pisces), Natural History Museum, London, United Kingdom.

Anatomical abbreviations: aa, anguloarticular; ab, accessory bone; ach, anterior ceratohyal; ba, basipterygium; br, branchiostegal rays; clt, cleithrum; co, coracoid; dhh, dorsal hypohyal; dfs, dorsal-fin spine; dn, dentary; ect, ectopterygoid; enpt, endopterygoid; ep, epural; fr, frontal; hh, hypohyals; hspu, haemal spine of preural vertebra; hyo, hyomandibula; hyp, hypural; ob, orbitosphenoid; iop, interopercle; le, lateral ethmoid; me, mesethmoid; mtp, metapterygoid; mx, maxilla; na, nasal; op, opercle; pa, palatine; pas, parasphenoid; pch, posterior ceratohyal; pcl, postcleithrum; pfr, pectoral-fin radials; phy, parhypural; pmx, premaxilla; pop, preopercle; ptm, posttemporal; pu, preural centrum; qu, quadrate; sc, scapula; scl, supracleithrum; sop, subopercle; soc, supraoccipital; sym, symplectic; u, ural centrum; un, uroneural; uh, urohyal; vhh, ventral hypohyal.

Systematic palaeontology

Order Lampridiformes Goodrich, 1909

Family Palaeocentrotidae Bonde, 1966

Emended diagnosis. A lampridiform family unique and derived in having spines only in the middle of the dorsal fin, and first dorsal-fin pterygiophore in the first interneural space. The family is further distinguished from all other lampridiform families in having the following combination of features: body

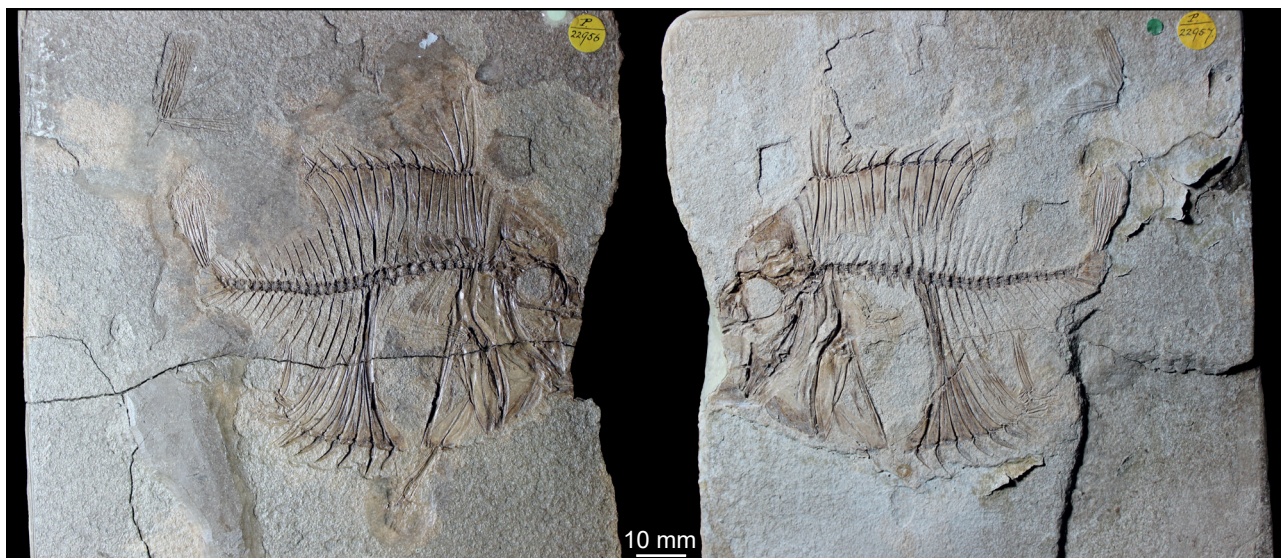
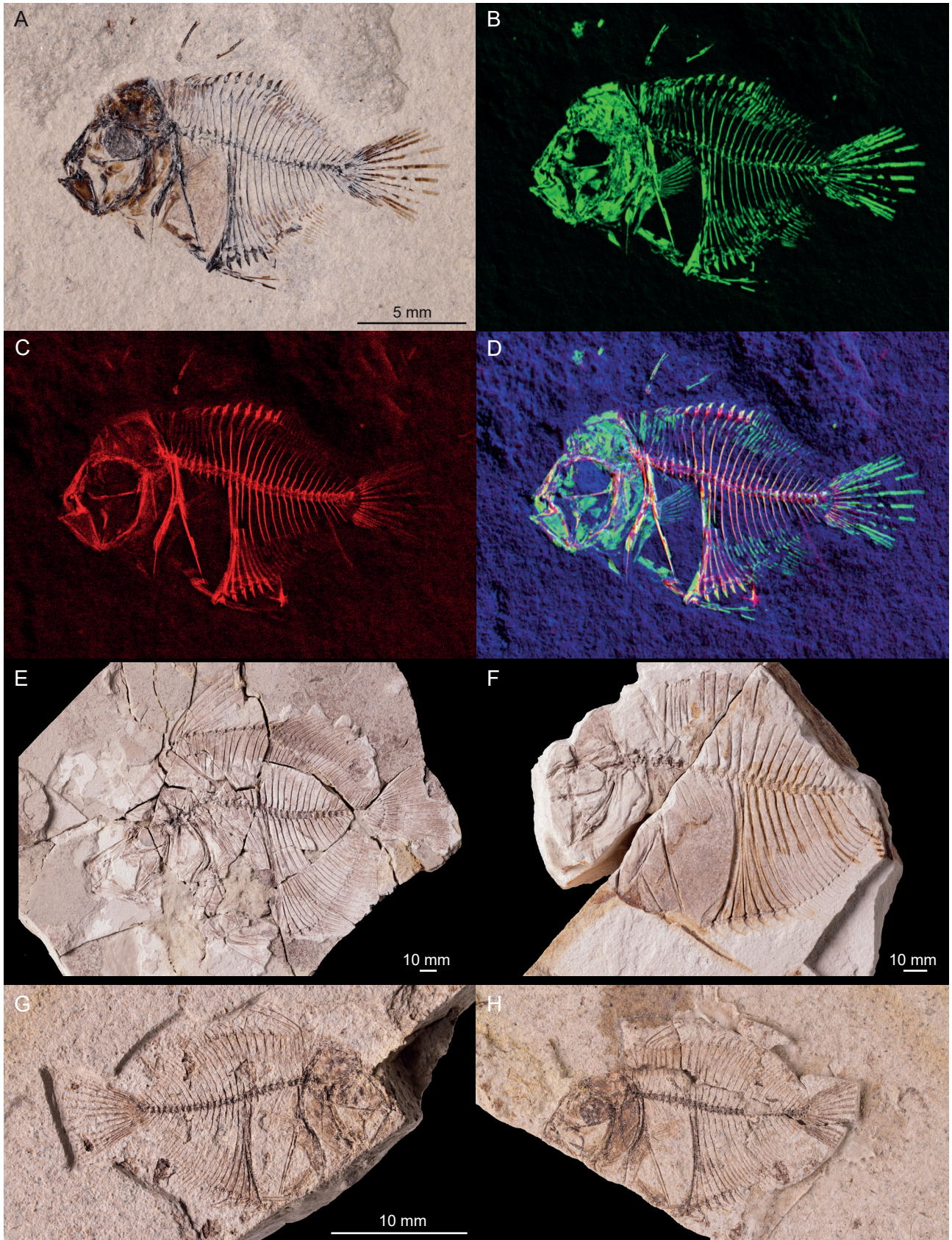


Fig. 2. *Palaeocentrotus boggildi*, holotype NHMUK PV P 22956 + NHMUK PV P 22957. Moderately preserved, incomplete part and counterpart in soft diatomite, collected from the Skarrehage moclay pit (locality 1 in Fig. 1B). High-resolution photo images of the holotype, NHMUK PV P 22956, part (left), and counterpart NHMUK PV P 22957 (right).



deep and laterally compressed; vertebrae 29–32 (including second ural centrum); second preural vertebra with fully developed neural spine; caudal fin rounded, containing 10–13 principal rays; dorsal fin long-based, with an anterior crescent lobe; coracoid not expanded ventrally.

Genus *Palaeocentrotus* Kühne, 1941

Type species. *Palaeocentrotus boggildi*, from the Skarrehage molay pit, Island of Mors, Northern Denmark.

Stratigraphic and geographic range. Ypresian (earliest Eocene), Fur Formation, northwestern Denmark (Fig. 1). Holotype NHMUK PV P 22956–22957 was recovered approximately 2 metres below volcanic ash layer -18a, which corresponds to the lower part of the Knudeklint Mb.

Emended diagnosis. A palaeocentrotid genus unique in having the following combination of characters: body depth about half of SL; head length exceeds 65% of SL; ventral keel of orbitosphenoid absent; basisphenoid absent; beryciform foramen absent; 29 (10+19) vertebrae; parapophyses on posterior four abdominal vertebrae; two supraneurals, both inserting in the preneural space; predorsal formula 0+0/2/1+1/1/; dorsal-fin with six elongate rays followed by eight or nine spines and 21–24 rays; anal fin with six or seven spines and 21–22 rays; three epurals; accessory autogenous bone between haemal spines of the second and third preural vertebrae; caudal fin with 13 principal rays plus two to four dorsal and two or three ventral procurent rays; distal end of the postcleithrum very close to the anterior margin of the first anal-fin pterygiophore; pelvic fin containing up to nine rays, of which the outer two or three are thicker and notably elongate.

Remarks. The family Palaeocentrotidae comprises two taxa, the Eocene *Palaeocentrotus boggildi* from Denmark examined herein, and the Oligocene *Natgeosocus sorini* from the Pshekha Horizon of northern Caucasus, Russia (Bannikov 2014). These two taxa are unique within the lampridiforms and share a unique configuration of the dorsal fin with spines restricted to its middle portion, and the first dorsal-fin pterygiophore that inserts in the first interneural space. However, they can be easily separated from

each other based on a series of morphological and meristic features. *Palaeocentrotus* differs from *Natgeosocus* in having body depth comprised between 60 and 72% SL (vs. not less than 80% SL), 29 (vs. 32) vertebrae, three (vs. two) epurals, accessory autogenous bone lying between the haemal spines of the second and third preural vertebrae (not present in *Natgeosocus*), 13 (vs. 10) principal caudal-fin rays, two (vs. none) supraneurals, predorsal formula 0+0/2/1+1/1/ (vs. /1/1/1+1/), dorsal-fin with six elongate rays followed by eight or nine spines and 21–24 rays (vs. six rays followed by eight spines and 20 rays), anal fin with six or seven spines and 21–22 rays (vs. 5 spines and 22 rays), distal end of the postcleithrum close to the anterior margin of the first anal-fin pterygiophore (vs. well separated).

Palaeocentrotus boggildi, Kühne, 1941

(Figs 2, 3, 4, 5, 6, 7, 8, Table 1, Table 2)

- 1941 *Palaeocentrotus böggildi*: Kühne, p. 374–386, text-figs 1–3.
- 1964 *Palaeocentrotus* Kühne: Rosen, p. 251.
- 1966 *Palaeocentrotus boeggildi* Kühne: Bonde, p. 200
- 1968 *Palaeocentrotus* Kühne: Patterson, p. 97
- 1969 *Palaeocentrotus* Kühne: Rosen & Patterson, p. 367, 418
- 1983 *Palaeocentrotus böggildi* Kühne: Oelschläger, p. 31, 89, 99, 106, 109, text-fig. 80
- 1992 *Palaeocentrotus boeggildi* Kühne: Bonde, p. 36–37, text-fig. 2
- 1995 *Palaeocentrotus boeggildi* Kühne: Bonde, p. 1–2, frontpage + figure text
- 1997 *Palaeocentrotus* Kühne: Bonde p. 39 & text-table p. 48
- 1999 *Palaeocentrotus boeggildi* Kühne: Bannikov, p. 68–69, text-fig. 1a
- 2008 *Palaeocentrotus boeggildi* Kühne: Bonde *et al.*, p. 97, text-fig.
- 2010 *Palaeocentrotus* Kühne: Bonde *et al.*, p. 31, text-figs 21–22
- 2012 *Palaeocentrotus boeggildi* Kühne: Pedersen *et al.*, p. 91, text-fig. 44G
- 2014 *Palaeocentrotus boeggildi* Kühne: Bannikov p. 625–627, text-fig. 1
- 2021 *Palaeocentrotus boeggildi* Kühne: Madsen & Rasmussen, p. 49, text-fig.
- 2023 *Palaeocentrotus boeggildi* Kühne: Schröder, p. 252, text-fig.
- 2025a *Palaeocentrotus böggildi* Kühne: Schröder & Carnevale, p. 33, 35, 42–43

Fig. 3. *Palaeocentrotus boggildi* Kühne, 1941, referred specimens. High-resolution photo images and μ XRF-element maps. **A–D:** MM-108, the smallest specimen available and preserved in a slab of carbonate concretion. **A:** High-resolution photo image. **B:** Phosphorous element map (green). **C:** Strontium element map (red). **D:** Combined strontium, phosphorous, and calcium maps; note the visuals of the dorsal- and anal-fin spines (yellowish) versus the soft, segmented rays (green). The scale bar in A also applies to B–D. **E:** NHMD-625274 (DK-1016) the largest specimen known from the soft diatomite. **F:** MM-94, incomplete specimen, soft diatomite. **G–H:** FUM-N-16193a+b in part and counterpart, soft diatomite. Scale bar in G also applies to H.

Etymological note. Kühne (1941) originally named the taxon *Palæocentrotus böggildi*. However, according to ICZN nomenclature code Article 27, the correct genus name should be *Palaeocentrotus*, as the ligature ‘æ’ of the letters a and e is forbidden (ICZN 1999). Kühne (1941) named the species *böggildi* in honour of the Danish professor Ove Balthasar Bøggild (1872–1956) and used the German letter ‘ö’ (o with an umlaut) for the linguistically same Danish letter ‘ø’. However, since the origin being the Danish ‘ø’, and not the German ö, the correct spelling of the specific name is therefore *boggildi* and not ‘*boeggildi*’ as reported by several authors since the publication of Bonde (1966; pers. comm. Thomas Pape, president of the International Commission on Zoological Nomenclature, July 2025; see also the ICZN nomenclatural code Article 32.5.2.1).

Holotype. NHMUK PV P 22956 + NHMUK PV P 22957, a moderately well-preserved incomplete articulated skeleton, in part and counterpart, estimated SL of 84.6 mm. This specimen is preserved in soft diatomite as a superficial 3D impression, comprising

also minute skeletal fragments. The part, PV P 22956, was treated with a form of stabilising varnish, resulting in a dark-coloured, shiny surface. Similarly, the counterpart, PV P 22957, was treated with a non-colouring/non-staining consolidant allowing a latex cast to be made (Fig. 2, Table 1).

Diagnosis. As for the genus.

Type locality of holotype. Knudeklint Member of the Fur Formation, lowermost Eocene (Ypresian). Collected from the Skarrethage mo clay pit on the island of Mors, northwestern Limfjord area, Denmark (Fig. 1). Excavated about 2 m below volcanic ash layer -18a (Kühne 1941).

Referred material. FUM-N-16193a+b, nearly complete well-preserved articulated skeleton preserved as impression in soft diatomite, in part and counterpart, 20 mm SL; MM-94, incomplete, articulated skeleton showing part of the head and axial skeleton, preserved as impression in soft diatomite, with faint cycloid scale imprints exposed in the abdominal region;

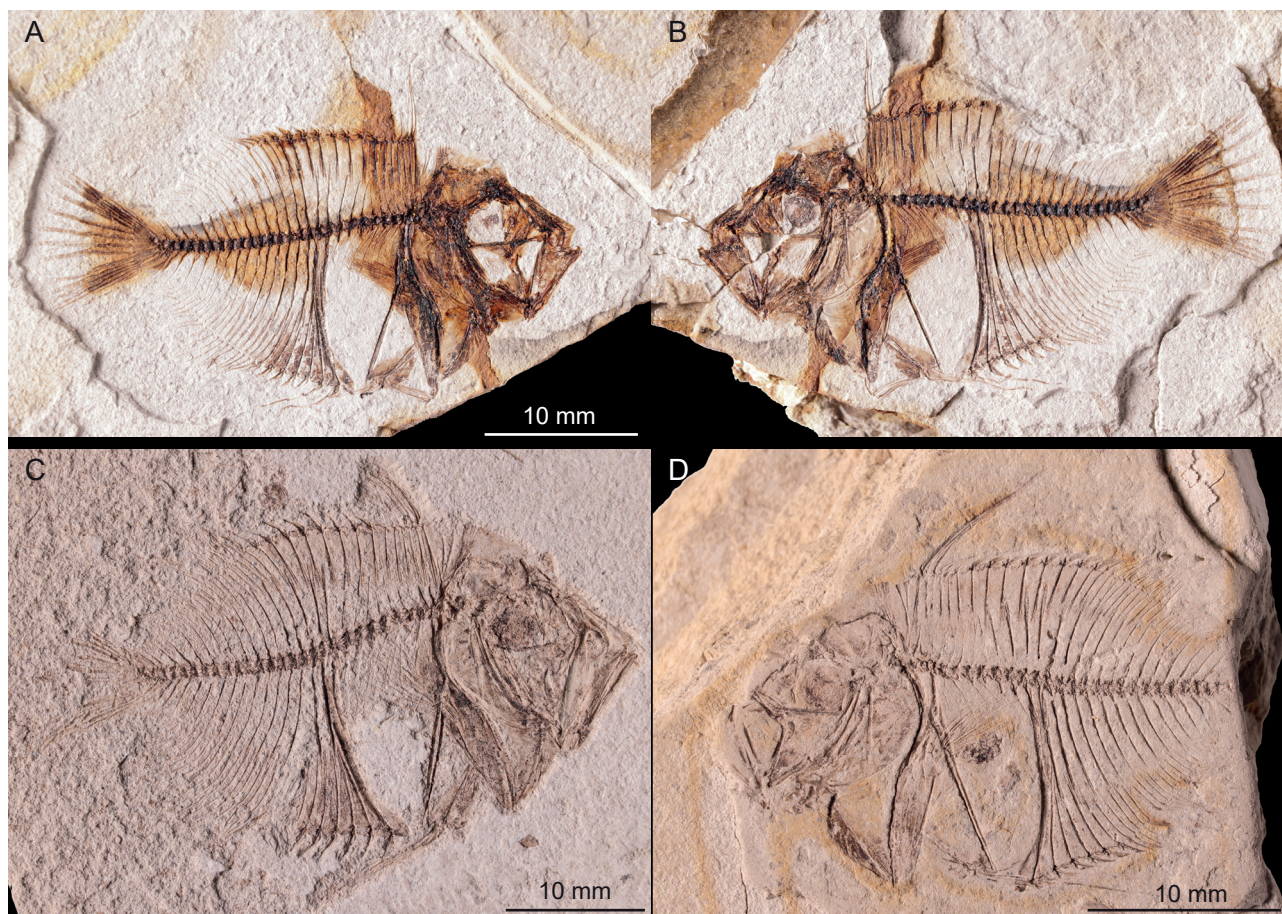


Fig. 4. *Palaeocentrotus boggildi* Kühne, 1941. High-resolution photo images of referred material, continued. **A–B:** MM-11959, part (A) and counterpart (B). **C:** NHMD-624663, the most well-preserved part of the superficial three-dimensional impression in soft diatomite. **D:** NHMD-2002586, incomplete, superficial three-dimensional impression, soft diatomite.

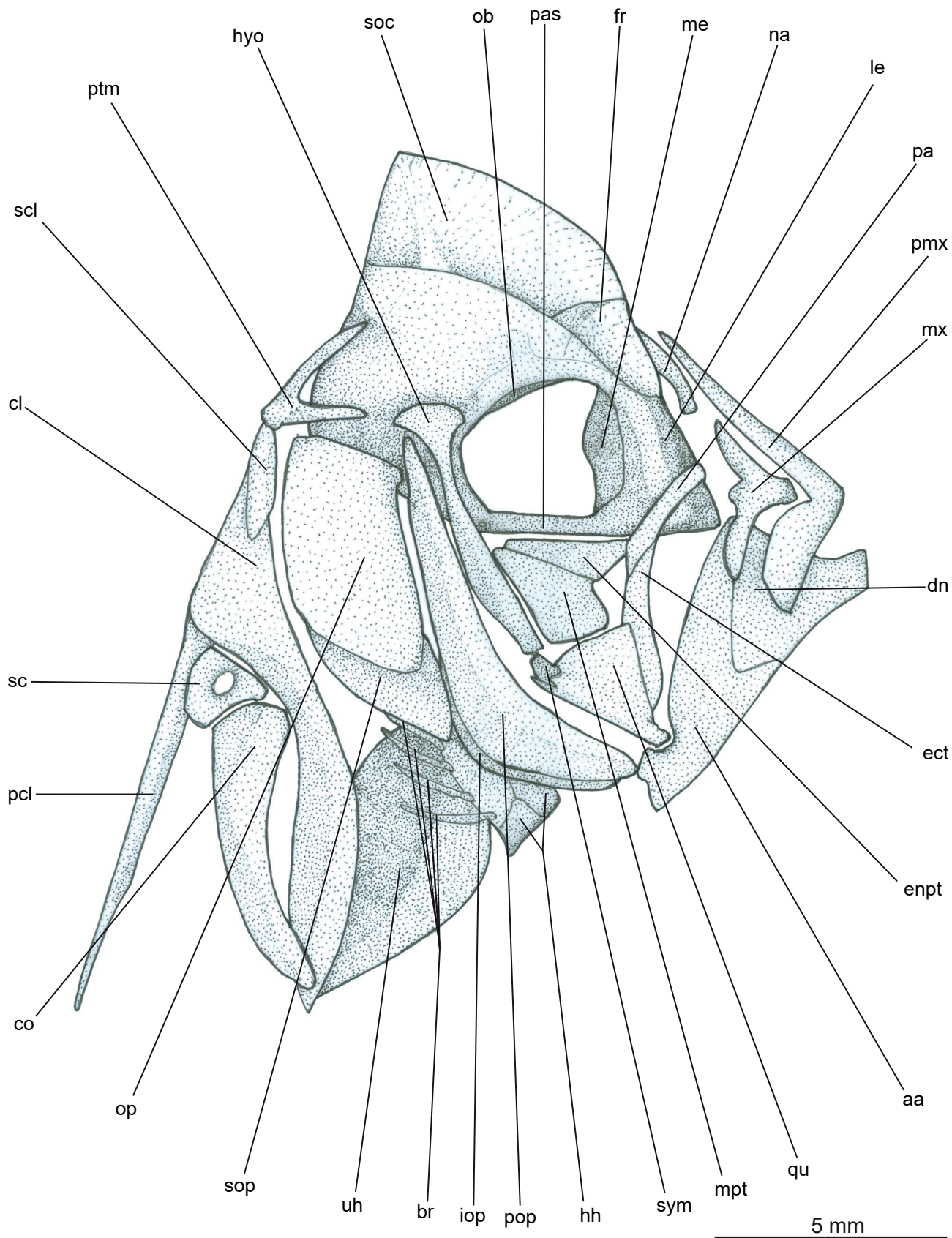


Fig. 5. *Palaeocentrotus boggildi* Kühne, 1941. Reconstruction of the head skeleton, primarily based on MM-11959, right lateral view.

MM-108, nearly complete well-preserved articulated skeleton in a small carbonate concretion, 14 mm SL; MM-11959, impression of nearly complete, well-preserved articulated skeleton in soft diatomite, in part and counterpart, 29 mm SL; NHMD-624663 (DK-79), impression of nearly complete, well-preserved articulated skeleton in soft diatomite, in part and counterpart, 35 mm SL; NHMD-625274 (DK-1067), impression of well-preserved articulated skeleton in soft diatomite, including small patches of overlapping scales, in part and counterpart, about 178 mm SL; NHMD-2002586, incomplete, articulated skeleton lacking the caudal fin, and most the of anal- and dorsal fins preserved mostly as impressions, in soft diatomite, preserved length 26 mm.

Description. The body is rather deep, discoid and laterally compressed. The head is higher than long, its depth contained about two times in SL. The body depth ranges between about 60% to more than 72% SL. The dorsal profile of the body is almost straight from the nape to the posterior end of the spinous portion of the dorsal-fin, becoming oblique for the entire length of the soft-rayed portion of the dorsal fin. The caudal peduncle is short and deep, its maximum depth contained about seven times in SL. The orbit is moderately large its diameter being contained between three and more than five times in SL.

Neurocranium. The neurocranium is large and roughly triangular in outline. There is a broad, relatively high and triangular supraoccipital crest; laterally, at the base of both sides of the crest there is a thick and expanded shelf that also involves the

frontals, the parietals, and other neurocranial bones. The supraoccipital crest is relatively low and inconspicuous in juveniles (Fig. 3A–D, MM-108), becoming much more prominent in larger specimens (Figs 2 and 3E–F). The lateral surface of the crest is ornamented with numerous almost parallel delicate ridges; a larger and thickened ridge radiates from the base of the crest to its posterodorsal corner. A large ovoid hole is visible on the ventral portion of the crest on the holotype; this was misinterpreted and illustrated as an actual anatomical structure by Kühne (1941: p. 382 “spacious hole”; figure 1 and 3) and Bannikov (1999: p. 68 “a foramen between the frontal and supraoccipital crests”), but later identified as an artifact of preservation by Bannikov (2014). A similar preservational feature is visible in MM-94 and FUM-N-16193 (Fig. 3F, and 3G–H, respectively). The supraoccipital articulates anteroventrally with the dorsally expanded frontals that are arched anteromedially to form a vault for the insertion of the ascending process of the premaxilla (see Olney *et al.* 1993). The frontals are the largest bones of the skull roof; the central portion of the supraorbital lateral-line canal is well-exposed along the dorsal border of the orbit; a tubule emerges dorsally from the supraorbital canal at the level of the mid-length of the orbit, possibly corresponding to the so-called epiphyseal branch (see Arratia & Huaquín 1995; Di Dario 2004). The ethmoid region is thickened and compact. The lateral ethmoid is massive, robust and columnar; the irregularly curved posterior rim of the lateral ethmoid forms the anterior wall of the orbit. The mesethmoid is located posteriorly and medially to the lateral ethmoids and is exposed in the anterior

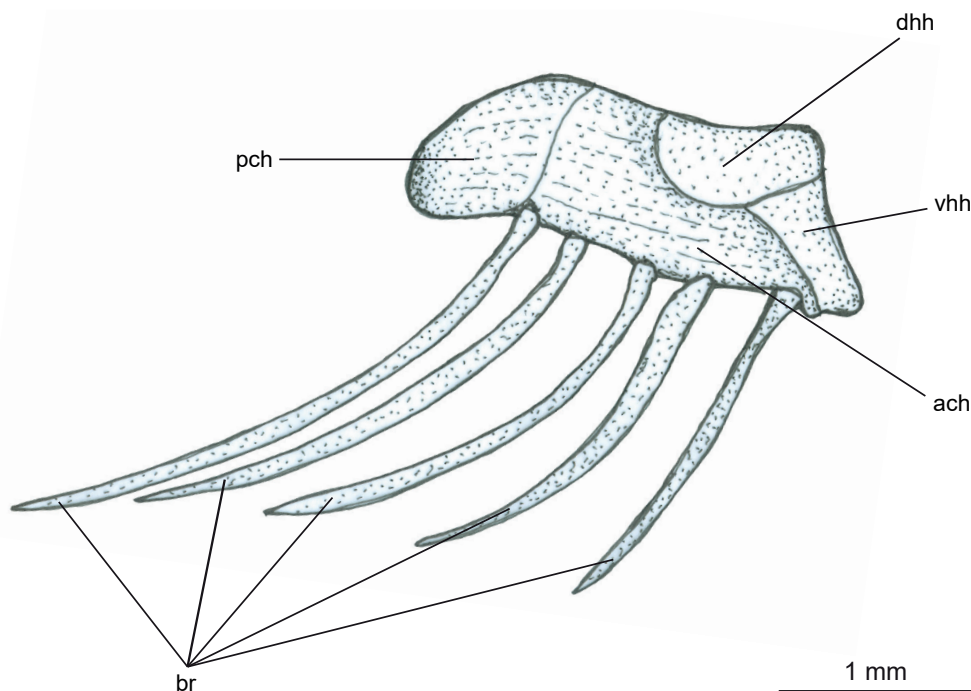


Fig. 6. *Palaeocentrotus boggildi* Kühne, 1941. MM-11959, Reconstruction of the hyoid bar, right lateral view.

one-third of the orbit. The mesethmoid is posterior to the lateral ethmoid being well exposed in the anterior part of the orbit. The mesethmoid together with the orbitosphenoid possibly form part of the floor of the frontal vault. The vomer is stout, toothless and almost triangular in lateral view. The parasphenoid is almost straight and thick, and exposed in the lower part of the orbit, showing a curvature just behind the orbit; an ovoid foramen pierces the parasphenoid at the level of the posterior wall of the orbit and is tentatively interpreted herein as the foramen for the internal carotid artery. The orbitosphenoid has a smooth outer surface and lacks a ventrally directed process. There is no clear evidence of the presence of the basisphenoid. The sphenotic and pterotic are recognisable in the holotype; both these bones articulate dorsally with the frontal. Although the limits of the other bones of the otic and occipital regions are difficult to recognise, the basioccipital is partially exposed in the holotype. The nasal is rather large, tubular, and curved.

Circumorbital bones. Of the infraorbital series, only the lachrymal is preserved in the holotype. It appears to be subquadrangular, with a slightly curved anteroventral margin; at least two pores of the infraorbital lateral-line canal are recognisable.

Jaws. The mouth is terminal, and the lower jaw articulation is in front of the anterior margin of the orbit. The premaxilla is large, toothless and bears a remarkably elongate and robust ascending process, measuring about 43% of head length; the outer surface of the premaxilla is ornamented with short and moderately deep striations. The maxilla is relatively large, thick, and L-shaped, resembling that of veliferid fishes (Oelschläger 1983; Olney *et al.* 1993; Carnevale & Bannikov 2018); it has a prominent articular process and a distally spatulate main shaft similar in size and form to the ascending process. The outer surface of the maxilla is ornamented with thin ridges radiating towards the angle formed by the main shaft of the bone and its ascending process. There are no supramaxillae. The mandible is very large, its length is about 57% of head length; it is approximately triangular, with a thick and vertically oriented symphysis and a gently sigmoid anteroventral margin. The toothless alveolar process of the dentary is relatively short and slightly concave. The anguloarticular is large and has a prominent posteroventral corner.

Suspensorium. The suspensorium is relatively well-preserved in the holotype, MM-108 and MM-11959 (Figs 2, 3A–D, 4A–B, 5). The hyomandibula is obliquely oriented and has a moderately expanded dorsal articular head and a thick vertical shaft that

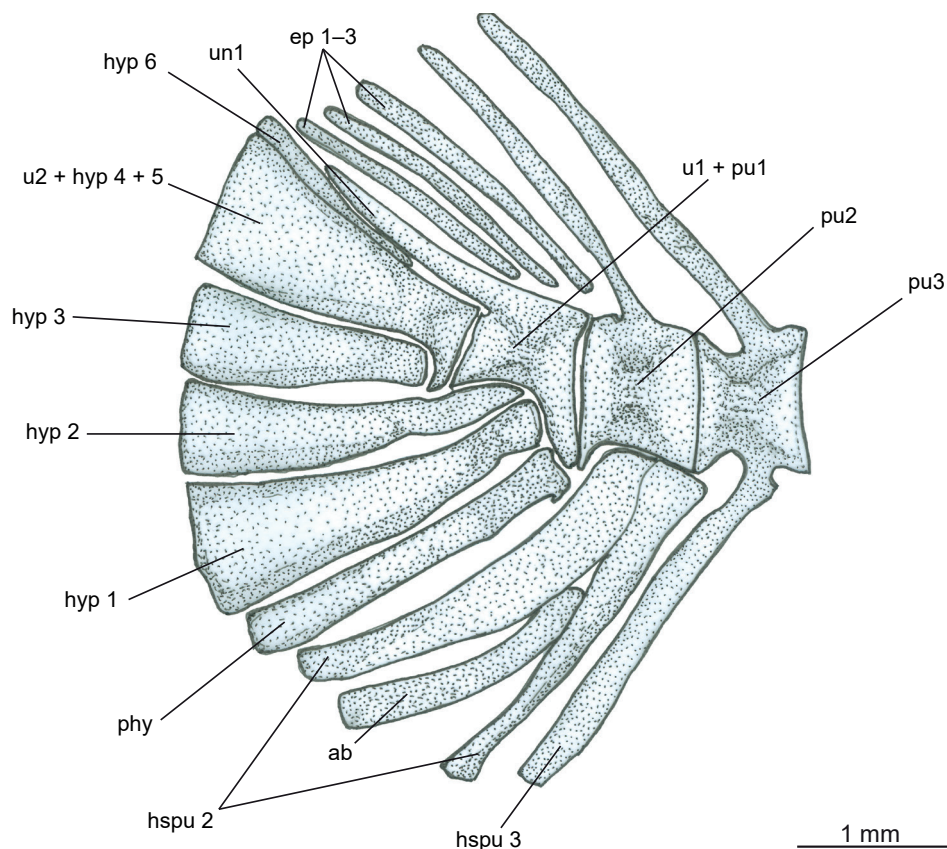


Fig. 7. *Palaeocentrotus boggildi* Kühne, 1941. MM-11959, reconstruction of the caudal-fin skeleton, right lateral view.

Table 2. Measurements (as percentage of SL) of *Palaeocentrotus boggildi* Kühne, 1941

	NHMMUK PV P 22956–22957	FUM-N- 16193a+b	NHMD-625274 / / DK-1067	NHMD-624663 / / DK-79	MM-108	MM-11959
Standard Length (mm)	84.6*	20.1	178	35.2	14.1	28.9
Head length	33.8	40.3	43.1	41.2	37.6	42.2
Head depth	49.6	N/A	45.3	52.6	50.4	42.9
Maximum body depth	72.5	64.2	71.9	64.2	68.8	60.2
Snout length	N/A	14.4	19.7	21.9	15.6	17.3
Orbit diameter	11.7	10.0	7.5	9.9	12.1	8.3
Mandible length	N/A	N/A	17.6	25.9	20.6	23.2
Dorsal-fin base	N/A	48.8	53.8	47.4	54.6	47.1
Anal-fin base	N/A	41.8	N/A	48.9	46.1	39.8
Caudal peduncle length	N/A	7.5	7.4	7.7	8.5	10.5
Caudal peduncle depth	N/A	16.9	N/A	16.8	17.7	15.7
Prepectoral distance	N/A	34.3	42.1	40.6	41.8	38.1
Predorsal distance	N/A	51.7	49.4	52.0	34.0	45.3
Prepelvic distance	N/A	41.3	48.2	39.2	44.0	47.1
Preanal distance	N/A	49.8	N/A	58.2	56.7	56.1

*Estimated Standard Length.

bears a long and laterally protruding flange. The quadrate is compact and triangular in outline, with a notably thickened anterior margin. The symplectic is rod-like. The metapterygoid is quadrangular in outline; it is weakly ossified and laminar in adult individuals and mostly cartilaginous in juveniles. The endopterygoid is toothless and appears to be roughly triangular in outline. The ectopterygoid is slightly arched. The anterior palatine process (=palatine prong; Olney *et al.* 1993) seems to be absent.

Opercular series. The preopercle is crescent-shaped, its horizontal limb is more than half of the length of the vertical one; the posterior margin of the preopercle is smooth and its outer surface is ornamented with delicate longitudinally oriented striations. The interopercle is thin and scarcely recognisable in the available specimens. The opercle is quadrangular in outline and laminar, with a straight and moderately thickened anterior margin and a gently curved posterior margin. The subopercle is partially exposed just below the opercle in MM-11959 (Figs 4A–B, 5).

Hyoid apparatus and branchial skeleton. The hyoid bar is compact and resembles those of other lampridiforms in having the dorsal hypohyal that overlaps the anterior dorsal half of the anterior ceratohyal. The articulation between the anterior ceratohyal and ventral hypohyal is difficult to interpret. The anterior and posterior ceratohyals are ornamented with delicate transversal striations. There is no evidence of a beryciform foramen in the anterior ceratohyal (Figs 4A–B, 6). At least five sabre-like branchiostegal rays can be recognised. The urohyal is well-developed and ventrally expanded, leaf-shaped, with curved anterior and posterior margins. The branchial skeleton is not recognisable in the available specimens due to inadequate preservation.

Vertebral column and intermuscular bones. The

vertebral column consists of 10 abdominal and 19 caudal (including the second ural centrum) vertebrae (Figs 3A–D, 4C). The abdominal portion represents slightly more than one third of the length of the entire vertebral column. The first abdominal vertebra is often laterally displaced from its original position, overlapping the posterior portion of the basicranium; such a displacement might indicate that the articulation between neurocranium and vertebral column was relatively weak in origin. The centra are subrectangular, longer than high, their lateral surface being ornamented with thick horizontal ridges and deep irregular pits and fossae. Dorsal prezygapophyses are moderately developed throughout the vertebral column. The posterior four abdominal vertebrae bear thick and distally pointed parapophyses gradually increasing in size backward. The neural arches are triangular in lateral view. The neural spines are thin and slender. The neural spines of the abdominal vertebrae are nearly vertically oriented except the three posterior that are slightly bent forward; the length of the neural spines gradually increases up to the third caudal vertebra, and then gradually decreases. The haemal spines are similar to their neural counterparts except for those of the first two caudal vertebrae that are anteroposteriorly expanded and spatulate. There are seven pairs of thin ribs that articulate with the basal portion of the centra or the parapophyses of the posterior abdominal vertebrae; the ribs are rather short, extending ventrally into the upper third of the abdominal cavity. Epineural fragments associated with the second abdominal vertebra can be recognised.

Caudal skeleton and fin. The caudal fin is rounded and contains 13 principal rays, plus two to four dorsal and two or three ventral procurent rays. The caudal skeleton consists of the hypurals 1 and 2 that articulate with the compound centrum (fused first ural and

first preural centrum) together with the parhypural, and autogenous hypural 3 that articulates with hypurals 4 and 5 fused with the second ural centrum; the hypural 6 is autogenous, the uroneural appears to be fused with the compound centrum, and there are three elongate and slender epurals. There is no evidence of the parhypurapophysis. The neural spine of the second preural vertebra is completely developed and its opposite haemal spine is autogenous; the autogenous haemal spine of the second preural vertebrae is bifid in MM-11959 (Fig. 4A–B, 7). There is an autogenous accessory bone that lies anterior to the haemal spine of the second preural vertebra (Figs 2, 4, 7).

Median fins. There are two slender supraneurals with an expanded distal end that insert in the preneural space. The predorsal formula is difficult to determine in the holotype and MM-108 due to the displacement of the anterior part of the vertebral column discussed above that has modified the mutual relationships between dorsal fin (and supraneurals) and the interneural spaces; for this reason, the formula indicated by Patterson (1993) should be regarded as not correct. In FUM-N-16193a+b and MM-11959 (Figs 3G–H, 4A–B) the anterior portion of the vertebral column is not displaced from its original position and the predorsal formula is 0+0/2/1+1/1/.

There is a single long-based dorsal fin that ex-

tends backward up to the neural spine of the 15th caudal vertebra. The dorsal fin can be subdivided into three portions, of which the first one forms a well-developed crescent lobe. The first portion consist of six elongate, filamentous and segmented rays, whose length gradually decreases backward (Figs 2, 4D); the anterior dorsal-fin ray is supernumerary on the first pterygiophore; the lateral surface of these filamentous rays is ornamented with irregular striations. The central portion of the dorsal fin contains eight or nine thick and short spines similar in length and characterised by lateral ornamentations represented by oblong and shallow pits (Figs 2, 3E, 8). The posterior portion of the dorsal fin consists of 21 to 24 segmented and distally bifurcated rays that are much more elongated than the preceding spines. Overall, the dorsal-fin spines and rays are supported by 35 to 38 pterygiophores; the pterygiophores of the anterior and central portions of the fin are much thicker and ossified, and anteroposteriorly expanded compared to those of the posterior soft-rayed portion; however, the morphological transition between the pterygiophores of the spinous portion and those of the posterior portion of the dorsal fin is gradual. The length of the base of the spinous portion of the dorsal fin is about three times longer than that of the anterior (soft-rayed) crescent-shaped portion, and only slightly shorter than that of the posterior portion.

The anal-fin is long-based, its length represents

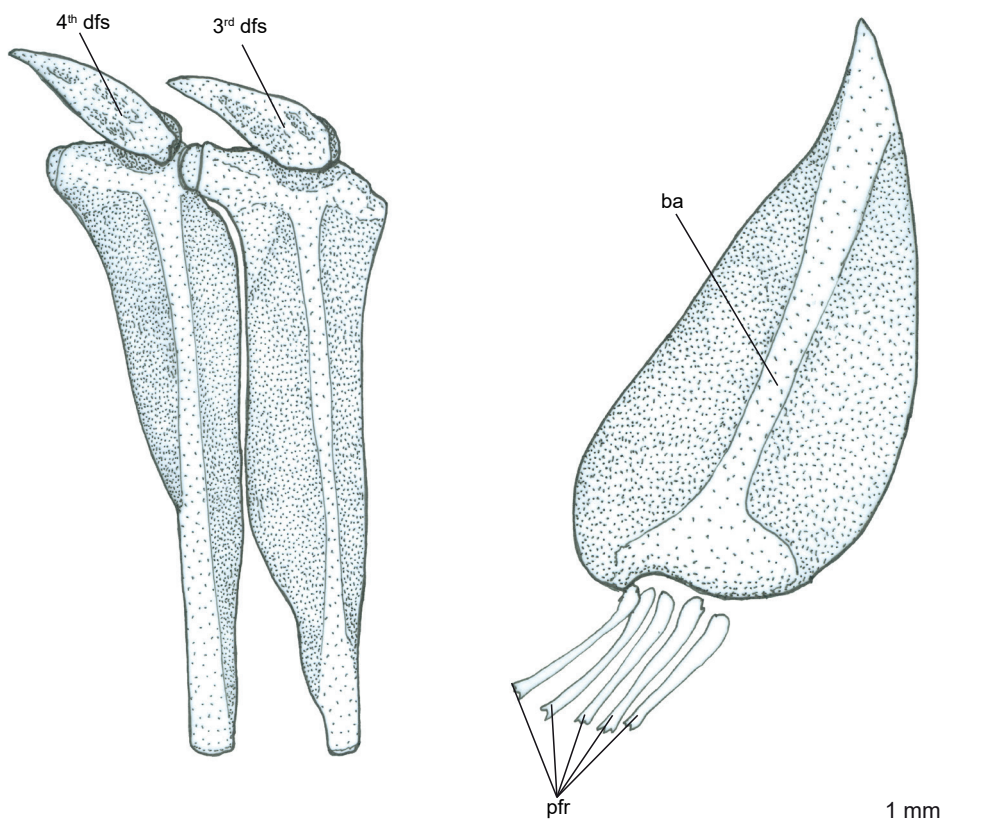


Fig. 8. *Palaeocentrotus boggildi* Kühne, 1941. MM-11959, reconstruction of the 3rd and 4th dorsal-fin spines and of the basipterygium, right lateral views.

slightly less than 70% of that of the dorsal fin. The anal fin consists of six or seven thick spines plus 21 to at least 22 segmented and distally bifurcated rays; the anal-fin rays are distinctly longer than the preceding spines. The soft-rayed portion of the anal fin is about 1.4 times longer than the spinous portion. The posterior end of the spinous portion of the anal fin is usually opposite to the posterior end of the central (spinous) portion of the dorsal fin, located at the transition between the third and fourth caudal vertebrae. The size and shape of the anal-fin spines are almost identical to those of their dorsal counterparts. The first anal-fin spine is supernumerary on the first anal-fin pterygiophore. The anal-fin is supported by at least 27 pterygiophores. The first anal-fin pterygiophore is very large and anteroposteriorly expanded, slightly bent posteriorly and characterised by a gently concave anterior profile. The pterygiophores of the spinous portion of the anal fin are thicker and strongly ossified. However, the morphological transition between the pterygiophores of the spinous and soft-rayed portions of the anal fin is gradual and the overall size of the anal-fin pterygiophores constantly decreases posteriorly in the series. The anterior three anal-fin pterygiophores insert in the first interhaemal space, and the successive interhaemal spaces are usually occupied by two (rarely one) pterygiophores.

Paired fins and girdles. The posttemporal has two large arms, of which the upper one is longer, thicker and slightly curved. The supracleithrum is oblong. The cleithrum is the largest bone of the pectoral girdle; it is distinctly sigmoid in shape and terminates ventrally into a pointed process; it shows a thickened and sigmoid anterior shaft and bears a large, triangular and laterally flattened posterior shelf, whose ventral margin articulates with the anterodorsal margin of the scapula. The coracoid is rather large and curved. The scapula is polygonal and pierced by an ovoid scapular foramen. A single postcleithrum can be recognised; it is strong and elongate, terminating ventrally in the restricted space between the pelvic-fin base and the anal-fin origin. The pectoral-fin radials are not clearly recognisable. The pectoral-fin base is almost vertically oriented being located just above the mid-length between the vertebral column and the ventral profile of the body. The pectoral fin consists of 16 segmented rays, of which the longest extends posteriorly up to the level of the last abdominal vertebra.

The basipterygia are large, obliquely oriented and teardrop-shaped, bearing laterally flattened anterior and posterior keels that emerge from a thick central shaft (Figs 2, 4, 8). The pelvic-fin origin is located just behind the pectoral-fin base. The pelvic fin seems to contain up to nine rays, of which the outer two or three are thicker and greatly elongate, almost reach-

ing posteriorly the distal end of the spinous anal fin.

Squamation. Delicate cycloid scales are rarely preserved. The squamation is partially preserved in NHMD-625274 (Fig. 3E), where small areas with cycloid scales are preserved between the dorsal-fin pterygiophores, ventral to the pectoral-fin base, and immediately above the pelvic fin and the bases of the anal-fin spines, and a few remains at the pectoral fin in NHMD-2002586 (Fig. 4D).

Comparative discussion

The systematic affinities of *Palaeocentrotus* within acanthomorph fishes have never been properly discussed. A comparative analysis of the skeletal anatomy of the genera *Cyttus* and *Zeus* was used by Kühne (1941) to support the placement of *Palaeocentrotus* within the zeiforms. He recognised that despite certain features (e.g. the caudal skeleton) are completely different from those characteristic of the zeiforms, the overall configuration of the skeleton of *Palaeocentrotus* provides unambiguous evidence of its alignment with this lineage of paracanthopterygian fishes. The monophyly of the zeiforms has been demonstrated by the recognition of a broad set of morphological synapomorphies (e.g. Johnson & Patterson 1993; Tyler *et al.* 2003; Wiley & Johnson 2010; Davesne *et al.* 2017; Grande *et al.* 2018), among which only one – second preural vertebra bearing a fully developed neural spine – can be easily recognised in *Palaeocentrotus*. This condition, however, is widespread among paracanthopterygians (Patterson & Rosen 1989; Borden *et al.* 2013) and it has been observed also in other acanthomorphs, including the pan-lampridiform *Aipichthys* (see Patterson 1968) and the elongate crown lampridiforms *Desmodema* and *Trachipterus* (see Rosen 1973; Fujita 1990). A further potential similarity between the caudal skeleton of *Palaeocentrotus* and that of Zeiformes is the autogenous accessory bone that lies between the haemal spines of the second and third preural vertebrae. The occurrence of this peculiar structure in the caudal skeleton was figured by Kühne (1941) and not reported in subsequent reconstructions of the caudal skeleton of *Palaeocentrotus* (e.g. Oelschläger 1983). This unpaired autogenous ossification lying in the mid-sagittal plane is also termed the ‘Y bone’, being common in gadiform fishes (e.g. Monod 1968; Fahay & Markle 1984; Patterson & Rosen 1989), and is also present in some zeiforms (*Cyttus*, *Xenolepidichthys*, *Zenopsis* and *Zeus*; Borden *et al.* 2013; Grande *et al.* 2013), the extinct polymixiiform *Omosomopsis* (see Patterson & Rosen 1989), and certain atheriniforms, beloniforms, and channids (Fujita 1990; Johnson & Patterson 1993; Murray 2012). There are different interpretations about the identity

of these accessory bones. Markle (1982) and Fahay & Markle (1984) regarded them as anal-fin pterygiophores that have lost their rays, while Rosen & Patterson (1969) considered them as haemal spines of centra that have been either fused or lost (see also Borden *et al.* 2013). Given the distribution of these accessory bones among acanthomorphs, it is reasonable to conclude that its presence in *Palaeocentrotus* may be interpreted as the result of convergence.

Bonde (1966) was the first that recognised the lampridiform affinities of *Palaeocentrotus*. However, this hypothesis was not supported by a discussion of the relevant features that can justify a possible relationship with the Lampridiformes. The anatomical survey of the known material of *Palaeocentrotus boggildi* presented herein resulted in the identification of a suite of features that are regarded as diagnostic of the Lampridiformes (e.g. Olney *et al.* 1993; Wiley & Johnson 2010; Davesne *et al.* 2014; Delbarre *et al.* 2016), including anterior palatine process absent, mesethmoid posterior to lateral ethmoids, elongate ascending premaxillary process longer than the alveolar process and inserting into the frontal vault, premaxilla and dentary edentulous, endopterygoid teeth absent, urohyal bearing a large ventral laminar expansion, second ural centrum free from fused first ural and preural centra and fused posteriorly to the upper hypural plate, and presence of two supraneurals and of a single postcleithrum. According to Olney *et al.* (1993), lampridiforms are also characterised by the insertion of the first dorsal-fin pterygiophore in the preneural space. As described above, the first dorsal-fin pterygiophore of *Palaeocentrotus boggildi* is allocated in the first interneural space between the first and second neural spines. This condition is shared with the Oligocene palaeocentrotid *Natgeosocus sorini*, thereby representing a diagnostic feature at the family level (Bannikov 2014). Other fossil lampridiforms diverge from the condition reported by Olney *et al.* (1993), including the turkmenid *Analectis pala* from the Upper Eocene and Lower Oligocene of Caucasus, whose first dorsal-fin pterygiophore inserts in the second interneural space (e.g. Bannikov 1999), and the putative stem-lampridiform *Iratuschichthys ulirikii* from the Lower Eocene of Denmark (Schröder & Carnevale 2025a), which is unique by having the first dorsal-fin pterygiophore inserting in the third interneural space. The pattern of dorsal-fin insertion, therefore, is not stable within the lampridiform lineage and should not be regarded as an unambiguous lampridiform synapomorphy.

Deep-bodied (bathysomous) lampridiforms have traditionally been recognised as non-monophyletic with the Lamprididae representing the sister group to the long-bodied (taeniosomous) families (e.g. Olney *et al.* 1993; Davesne *et al.* 2014, 2016; Delbarre *et*

al. 2016). Recent studies, however, have recovered a monophyletic clade formed by veliferids plus lampridids (Grande *et al.* 2013; Wang *et al.* 2023; Brownstein & Near 2024). The peculiar configuration of the caudal skeleton (with elongate neural spine of the second preural vertebra and an autogenous accessory bone between the haemal spines of the second and third preural vertebrae) and of the dorsal fin (with spines restricted to its central portion) of *Palaeocentrotus*, allows the exclusion of any possible attribution to the Veliferidae or Lamprididae, as well as to the other Paleogene deep-bodied lampridiforms (Oelschläger 1983; Olney *et al.* 1993). A unique combination of character states further rules out the attribution of *Palaeocentrotus* to the Veliferidae and Lamprididae, including a reduced number of vertebrae (29 vs. 33–46; Olney 1984) and principal caudal-fin rays (13 vs. 19; Olney *et al.* 1993), basisphenoid absent, and ventral keel of the orbitosphenoid absent (see Oelschläger 1983). The alignment of *Palaeocentrotus* with the Veliferidae can be also excluded due to a set of reductive features (see Oelschläger 1983), including the infraorbital series solely represented by the lachrymal, anterior ceratohyal lacking a beryciform foramen, parapophyses absent on the anteriormost abdominal vertebrae, and absence of scaly sheaths along the dorsal- and anal-fin bases. Finally, a distinct separation from the Lamprididae is also justified by the possession of two (vs. one) supraneurals and almost vertical (vs. horizontal) pectoral-fin insertion.

Bannikov (1999, 2014) suggested that *Palaeocentrotus* should be regarded as closely related to the veliferid fishes and based on this hypothesis, Near & Thacker (2024) considered it as a pan-veliferid. The descriptive analysis of *Palaeocentrotus* presented herein does not provide a clear support for this hypothesis for which additional comparative information about Paleogene bathysomous lampridiforms would be necessary (see Davesne *et al.* 2023).

Concluding remarks

The most salient feature of palaeocentrotids is the unique structure of the dorsal fin that contains true spines only in its central portion. Bonde (1966) used this very peculiar feature to assign *Palaeocentrotus* to a separate family within the Lampridiformes. The uniqueness of the dorsal fin of *Palaeocentrotus* was also mentioned by Rosen (1964) in the context of an extensive discussion on the variable structure and position of paired and median fins in certain acanthomorph groups.

The evolutionary origin of this unique condition is difficult to interpret. The dorsal-fin spines of palaeocentrotids seem to exhibit the chain-link support

(see Bridge 1896) and are therefore different from the spinous rays present in certain veliferids (see Bannikov 1991; Olney *et al.* 1993). Overall, the ‘first’ spinous dorsal fin of acanthomorphs seems to represent a new module, which is independent from the other median fins (first dorsal fin module of Mabee *et al.* 2002), being positioned anteriorly along the trunk. According to Mabee *et al.* (2002), the evolution of a regionalised (spinous) and spatially separated anterior dorsal fin is an example of duplication and divergence (e.g. Raff 1996), facilitated by modular organisation. Duplication allows the formation of redundant structures, and divergence allows them to assume new roles (Gilbert 2013). Following this perspective, the dorsal fin is essentially duplicated anteriorly in acanthomorphs. True spines are solid bony structures resulting from the fusion of two contralateral hemitrichia, which lack proximo-distal segmentation and are usually rounded in cross-section. Recent studies by Miyamoto *et al.* (2025) revealed that actinotrichia do not play a relevant role in the development of fin spines in acanthomorphs, whereas mesenchymal cell condensation surrounded by a thick layer composed by basement membrane and basal lamella appears to be crucial for the morphogenesis of developing spines. Höch *et al.* (2021) demonstrated that the positioning of the dorsal and anal fins into spinous and soft-rayed portions is established through canonical developmental mechanisms responsible for the anteroposterior patterning of the appendages. Höch *et al.* (2021) also suggested that homeotic transformations of spines into rays and vice versa can be induced by modulation of BMP signalling. As repeatedly mentioned above, the spines of palaeocentrotids are placed in the central portion of the dorsal fin, preceded and followed by rays. However, what actually produces the unique configuration of the dorsal fin in palaeocentrotids are the elongate and filamentous rays that precede the dorsal-fin spines, which form an additional distinct module positioned in front of the ‘spinous’ dorsal-fin module (see Mabee *et al.* 2002). In this context, it is reasonable to suggest that the evolution of a further regionalised anterior portion of the dorsal fin in *Palaeocentrotus* and *Natgeosocus* could represent the result of an additional duplication event. In any case, regardless of the possible evolutionary interpretation of its origin, the peculiar configuration of the dorsal fin of palaeocentrotids represents another spectacular example of the remarkable plasticity of the acanthomorph median fins.

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References

- Arratia, G. & Huaquín L. 1995: Morphology of the lateral line system and of the skin of diplomystid and certain primitive loricarioid catfishes and systematic and ecological considerations. *Bonner Zoologische Monographien* 36, 1–110.
- Bøggild, O.B. 1918: Den vulkanske Aske i Moleret samt en Oversigt over Danmarks ældre Tertiærbjærgarter. *Danmarks Geologiske Undersøgelse II. Række* 33, 159 pp. <https://doi.org/10.34194/raekke2.v33.6818>
- Baumann, N.B., Regelous, M., Adatte, T., Thibault, N., Regelous, A., Schultz, B.P., Fantasia, A., Madsen, H. & Haase, K.M. 2024: Linking the PETM and North Atlantic volcanism using tellurium in sediments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 656, 112575. <https://doi.org/10.1016/j.palaeo.2024.112575>
- Bannikov, A.F. 1991: An Eocene veliferoid (Teleostei, Lampridiformes) from Bolca. *Studi e Ricerche sui Giacimenti Terziari di Bolca* 6, 161–174.
- Bannikov, A.F. 1999: A review of fossil Lampridiformes (Teleostei) finds with a description of a new Lophotidae genus and species from the Oligocene of the Northern Caucasus. *Paleontological Journal* 33, 68–76.
- Bannikov, A.F. 2014: A new genus of the family Palaeocentrot-

- idae (Teleostei, Lampridiformes) from the Oligocene of the Northern Caucasus and comments on other fossil Veliferoidae. *Paleontological Journal* 48, 625–632.
- Betancur-R., R. et al. 2013: The tree of life and a new classification of bony fishes. *PLOS Currents Tree of Life* 2013; Apr 18 Edition 1, 1–45.
- Betancur-R., R., Wiley, E.O., Arratia, G., Acero, A., Bailly, N., Miya, M., Lecointre, G. & Ortí, G. 2017: Phylogenetic classification of bony fishes. *BMC Evolutionary Biology* 17, 1–40. <https://doi.org/10.1186/s12862-017-0958-3>
- Bonde, N. 1966: The fishes of the Mo-clay Formation (Lower Eocene). *Meddelelser fra Dansk Geologisk Forening* 16, 198–202.
- Bonde, N. 1992: Flint-fisk, moler-fisk, tropefisk og danekræ. *Varv* 1992(2), 35–36.
- Bonde, N. 1995: Tidligt tertiære fisk - flere danekræ. *Varv* 1995 (1), p. 1–2, 24–30.
- Bonde, N. 1997: A distinctive fish fauna in the basal Ash-series of the Fur/Ølst Formation (U. Paleocene, Denmark). *Aarhus Geosciences* 6, 33–48.
- Bonde, N., Andersen, S., Hald, N. & Jakobsen, S.L. 2008: Danekræ - Danmarks bedste fossiler, 255 pp. Copenhagen: Gyldendal.
- Bonde, N., Madsen, H., Schultz, B., Sylvestersen, R. & Jakobsen, S.L. 2010: Moléret i Nordjylland – diatomitten og fossilerne. *Dansk Naturhistorisk Forenings Årsskrift* 19 and 20, 25–40.
- Borden, W.C., Grande, T. & Smith, W.L. 2013: Comparative osteology and myology of the caudal fin in the Paracanthopterygii. In: Arratia G., Schultze H.-P. & Wilson M.V.H. (eds): *Mesozoic Fishes 5 – Global Diversity and Evolution*, 419–455. München: Verlag Dr. Friedrich Pfeil.
- Bridge, T.W. 1896: The mesial fins of ganoids and teleosts. *Journal of the Linnean Society of London, Zoology* 25, 530–602.
- Brownstein, C.D. & Near, T.J. 2024: Evolutionary origins of the lampriform pelagic radiation. *Zoological Journal of the Linnean Society* 201, 422–430. <https://doi.org/10.1093/zoolinnean/zlad142>
- Carnevale, G. 2004: The first fossil ribbonfish (Teleostei, Lampridiformes, Trachipteridae). *Geological Magazine* 141, 573–582. <https://doi.org/10.1017/s0016756804009598>
- Carnevale, G. & Bannikov, A.F. 2018: A sailfin velifer (Lampridiformes, Veliferidae) fish from the Eocene of Monte Bolca, Italy. *Bollettino della Società Paleontologica Italiana* 57, 157–186.
- Christensen, E.F. & Hald, N. 1990: Danekræ – a new concept in Danish Museum legislation. *Arkæologiske Udgravninger i Danmark* 1990, 7–16.
- Davesne, D., Carnevale, G. & Friedman, M. 2017: †*Bajaichthys elegans* from the Eocene of Bolca (Italy) and the overlooked morphological diversity of Zeiformes (Teleostei, Acanthomorpha). *Palaeontology* 60, 255–268. <https://doi.org/10.1111/pala.12280>
- Davesne, D., Friedman, M., Barriel, V., Lecointre, G., Janvier, P., Gallut, C. & Otero, O. 2014: Early fossils illuminate character evolution and interrelationships of Lampridiformes (Teleostei, Acanthomorpha). *Zoological Journal of the Linnean Society* 172, 475–498. <https://doi.org/10.1111/zoj.12166>
- Davesne, D., Gallut, C., Barriel, V., Janvier, P., Lecointre, G. & Otero, O. 2016: The Phylogenetic Intrarelations of spiny-rayed fishes (Acanthomorpha, Teleostei, Actinopterygii): Fossil taxa increase the congruence of morphology with molecular data. *Frontiers in Ecology and Evolution* 4, 1–20. <https://doi.org/10.7934/p2349>
- Davesne, D., Andrews, J. V., Beckett, H.T., Giles, S. & Friedman, M. 2023: Three-dimensional anatomy of the early Eocene *Whitehippus* (Teleostei, Lampriformes) documents parallel conquests of the pelagic environment by multiple teleost lineages. *Journal of Vertebrate Paleontology* 43, e2284998. <https://doi.org/10.1101/2023.06.13.544748>
- Delbarre, D.J., Davesne, D. & Friedman, M. 2016: Anatomy and relationships of †*Aipichthys pretiosus* and †*Aipichthys nuchalis* (Acanthomorpha: Lampridiformes), with a review of Late Cretaceous relatives of oarfishes and their allies. *Journal of Systematic Palaeontology* 14, 545–567. <https://doi.org/10.1080/14772019.2015.1078538>
- Dettaï, A. & Lecointre, G. 2005: Further support for the clades obtained by multiple molecular phylogenies in the acanthomorph bush. *Comptes Rendus Biologies* 328, 674–689. <https://doi.org/10.1016/j.crv.2005.04.002>
- Di Dario, F. 2004: Homology between the *recessus lateralis* and cephalic sensory canals, with the proposition of additional synapomorphies for the Clupeiformes and the Clupeoidei. *Zoological Journal of the Linnean Society* 141, 257–270. <https://doi.org/10.1111/j.1096-3642.2004.00122.x>
- Fahay, M.P. & Markle, D.F. 1984: Gadiformes: Development and relationships. In: Moser, H.G. et al. (eds): *Ontogeny and systematics of fishes*, 265–283. American Society of Ichthyology and Herpetology, Special Publication. <https://doi.org/10.2307/1444873>
- Fujita, K. 1990: *The Caudal Skeleton of Teleostean Fishes*, 897 pp. Tokyo: Tokai University Press.
- Gilbert, S.F. 2013: *Developmental Biology*, 719 pp. 10th Edition. Sinauer Associates Inc.
- Goodrich, E.S. 1909: *Vertebrata Craniata, first fascicle, cyclostomes and fishes. Part 9.* In: Lankester E.R. (ed.): *A Treatise on Zoology*, 518 pp. Edinburgh: Adam and Charles Black.
- Grande, T.C., Borden, W.C. & Smith, W.L. 2013: Limits and relationships of Paracanthopterygii: A molecular framework for evaluating past morphological hypotheses. In: Arratia, G., Schultze, H.-P. & Wilson, M.V.H. (eds): *Mesozoic Fishes 5 – Global diversity and evolution*, 385–418. München: Verlag Dr. Friedrich Pfeil.
- Grande, T.C., Borden, W.C., Wilson, M.V.H. & Scarpitta L. 2018: Phylogenetic relationships among fishes in the order Zeiformes based on molecular and morphological data. *Copeia* 106, 20–48.
- Gry, H. 1940: De istektoniske Forhold i Moleromraadet. Med bemærkninger om vore dislocerede klinters dannelse og om den negative askeserie: *Meddelelser Fra Dansk Geologisk Forening*, 586–627.
- Heilmann-Clausen, C. 1995: *Palæogene aflejringer over danskekalken*, 70–113. Danmarks Geologi fra Kridt til i dag. Aarhus Geoscience.
- Heilmann-Clausen, C., Nielsen, O.B. & Gersner, F. 1985: Lithostratigraphy and depositional environments in the Upper Paleocene and Eocene of Denmark. *Bulletin of the*

- Geological Society of Denmark 33, 287–323.
<https://doi.org/10.37570/bgsd-1984-33-26>
- Hughes, L.C. *et al.* 2018: Comprehensive phylogeny of ray-finned fishes (Actinopterygii) based on transcriptomic and genomic data. *Proceedings of the National Academy of Sciences of the United States of America* 115, 6249–6254.
- Hösch R., Scheider, R.F., Kikuth, A., Meyer, A. & Woltering, J.M. 2021: Spiny and soft-rayed fin domains in acanthomorph fish are established through a BMP-gremlin-shh signaling network. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e2101783118. <https://doi.org/10.1073/pnas.2101783118>
- Johnson, G.D. & Patterson, C. 1993: Percomorph phylogeny: a survey of acanthomorphs and a new proposal. *Bulletin of Marine Science* 52, 554–626.
- Kühne, W. 1941: A new Zeomorph fish from the Paleocene Moler of Denmark. *The Annals and Magazine of Natural History* 7, 374–386.
<https://doi.org/10.1080/03745481.1941.9727939>
- Larsen, L.M., Fitton, J.G. & Pedersen, A.K. 2003: Paleogene volcanic ash layers in the Danish Basin: compositions and source areas in the North Atlantic Igneous Province. *Lithos* 71, 47–80.
<https://doi.org/10.1016/j.lithos.2003.07.001>
- Li, B., Dettai, A., Cruaud, C., Couloux, A., Desoutter-Meniger, M. & Lecointre, G. 2009: RNF213, a new nuclear marker for acanthomorph phylogeny. *Molecular Phylogenetics and Evolution* 50, 345–363.
<https://doi.org/10.1016/j.ympev.2008.11.013>
- Mabee, P.M., Crotwell, P.L., Bird, N.C. & Burke, A.C. 2002: Evolution of median fin modules in the axial skeleton of fishes. *Journal of Experimental Zoology (Mol Dev Evol)* 294, 77–90. <https://doi.org/10.1002/jez.10076>
- Markle, D.F. 1982: Identification of larval and juvenile Canadian Atlantic gadoids with comments on the systematics of gadid subfamilies. *Canadian Journal of Zoology* 60, 3420–3438.
- Micklich, N. & Bannikov, A.F. 2022: *Oechsleria unterfeldensis*, gen. et sp. nov., a sailfin velifer fish (Lampridiformes, Veliferidae) from the Oligocene of the Unterfeld (“Frauenweiler”) clay pit. *PalZ* 97, 81–104.
<https://doi.org/10.1007/s12542-022-00633-7>
- Miya, M., Satoh, T.P. & Nishida, M. 2005: The phylogenetic position of toadfishes (order Batrachoidiformes) in the higher ray-finned fish as inferred from partitioned Bayesian analysis of 102 whole mitochondrial genome sequences. *Biological Journal of the Linnean Society* 85, 289–306. <https://doi.org/10.1111/j.1095-8312.2005.00483.x>
- Miya M, Holcroft N.I., Satoh, T.P., Yamaguchi, M., Nishida, M. & Wiley, E.O. 2007: Mitochondrial genome and a nuclear gene indicate a novel phylogenetic position of deep-sea tube-eye fish (Stylephoridae). *Ichthyological Research* 54, 323–332. <https://doi.org/10.1007/s10228-007-0408-0>
- Miyamoto, K., Kuroda, J., Kamimura, S., Sasano, Y., Abe, G., Ansai, S., Funayama, N., Uesaka, M. & Tamura, K. 2025: Actinotrichia-independent developmental mechanisms of spiny rays facilitate the morphological diversification of Acanthomorpha fish fins. *bioRxiv*.
<https://doi.org/10.1101/2025.03.01.640274>
- Monod, T. 1968: Le complexe urophore des poissons téléostéens. *Mémoires de l'Institut Fondamental d'Afrique Noire* 81, 1–705.
- Murray, A.M. 2012: Relationships and biogeography of the fossil and living African snakehead fishes (Percomorpha, Channidae, *Parachanna*). *Journal of Vertebrate Paleontology* 32, 820–835.
<https://doi.org/10.1080/02724634.2012.664595>
- Near, T.J., Eytan, R.I., Dornburg, A., Kuhn, K.L., Moore, J.A., Davis, M.P., Wainwright, P.C., Friedman, M. & Smith, W.L. 2012: Resolution of ray-finned fish phylogeny and timing of diversification. *Proceedings of the National Academy of Sciences of the United States of America* 109, 13698–13703.
<https://doi.org/10.1073/pnas.1206625109>
- Near, T.J. & Thacker, C.E. 2024: Phylogenetic classification of living and fossil ray-finned fishes (Actinopterygii). *Bulletin of the Peabody Museum of Natural History* 65, 3–302.
<https://doi.org/10.3374/014.065.0101>
- Oelschläger, H.A. 1983: Vergleichende und funktionelle Anatomie der Allotriognathi (=Lampridiformes), ein Beitrag zur Evolutionsmorphologie der Knochenfische. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 541, 1–127.
- Olney, J.E. 1984: Lampriformes: Development and relationships. In: Moser, H.G. *et al.* (eds): *Ontogeny and systematics of fishes*, 368–379. American Society of Ichthyology and Herpetology, Special Publication.
- Olney, J.E., Johnson, G.D. & Baldwin, C.C. 1993: Phylogeny of lampridiform fishes. *Bulletin of Marine Science* 52, 137–169.
- Patterson, C. 1964: A review of Mesozoic acanthopterygian Fishes, with special reference to those of the English Chalk. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 247, 213–482.
- Patterson, C. 1968: The caudal skeleton in Mesozoic acanthopterygian fishes. *Bulletin of the British Museum (Natural History) Geology* 17, 5–102.
- Patterson, C. 1993: An overview of the early fossil record of acanthomorphs. *Bulletin of Marine Science* 52, 29–59.
- Patterson, C. & Rosen, D.E. 1989: The Paracanthopterygii revisited: order and disorder. In: Cohen D.M. (ed.): *Papers on the Systematics of Gadiform Fishes*. Science Series, Natural History Museum of the Los Angeles County 32, 5–36.
- Pedersen, G.K. 1981: Anoxic events during sedimentation of a Palaeogene diatomite in Denmark. *Sedimentology* 28, 487–504. <https://doi.org/10.1111/j.1365-3091.1981.tb01697.x>
- Pedersen, G.K. & Surlyk, F. 1983: The Fur Formation, a late Paleocene ash-bearing diatomite from northern Denmark. *Bulletin of the Geological Society of Denmark* 32, 43–65.
<https://doi.org/10.37570/bgsd-1983-32-03>
- Pedersen, G.K. & Buchardt, B. 1996: The calcareous concretions (cementsten) in the Fur Formation (Paleogene, Denmark): isotopic evidence of early diagenetic growth. *Bulletin of the Geological Society of Denmark* 43, 78–86.
<https://doi.org/10.37570/bgsd-1996-43-09>
- Pedersen, G.K., Pedersen, S.A.S., Steffensen, J. & Pedersen, C.S. 2004: Clay content of a clayey diatomite, the Early Eocene Fur Formation, Denmark. *Bulletin of the Geological Society of Denmark* 51, 159–177.
<https://doi.org/10.37570/bgsd-2004-51-11>
- Pedersen, G.K. *et al.* 2012: Molerområdets geologi – sediment-

- er, fossiler, askelag og glacialtektonik. *Geologisk Tidsskrift* 2011, 41–135.
- Poulsen, J.Y., Byrkjedal, I., Willassen, E., Rees, D., Takeshima, H., Satoh, T.P., Shinohara, G., Nishida, M. & Miya, M. 2013: Mitogenomic sequences and evidence from unique gene rearrangements corroborate evolutionary relationships of Myctophiformes (Neoteleostei). *BMC Evolutionary Biology* 13, 111. <https://doi.org/10.1186/1471-2148-13-111>
- Raff, R.A. 1996: *The Shape of Life*, 544 pp. University of Chicago Press.
- Rosen, D.E. 1964: The relationships and taxonomic position of the halfbeaks, killifishes, silversides, and their relatives. *Bulletin of the American Museum of Natural History* 127, 218–267.
- Rosen, D.E. 1973: Interrelationships of higher euteleostean fishes. In: Greenwood, P.H., Miles, R.S. & Patterson, C. (eds): *Interrelationships of Fishes*. *Zoological Journal of the Linnean Society* 53 (Supplement 1), 397–513.
- Rosen, D.E. & Patterson, C. 1969: The structure and relationships of the paracanthopterygian fishes. *Bulletin of the American Museum of Natural History* 141, 357–474.
- Schmitz, B., Peucker-Ehrenbrink, B., Heilmann-Clausen, C., Åberg, G., Asaro, F. & Lee, C.-T.A. 2004: Basaltic explosive volcanism, but no comet impact, at the Paleocene–Eocene boundary: high-resolution chemical and isotopic records from Egypt, Spain and Denmark. *Earth and Planetary Science Letters* 225, 1–17. <https://doi.org/10.1016/j.epsl.2004.06.017>
- Schröder, A.E. 2023. *The deep past of Denmark – the origin of modern teleost fishes*. Published PhD Dissertation, 315 pp. University of Copenhagen.
- Schröder, A.E. and Carnevale, G. 2023: The argentiniform *Surylkus longigracilis* gen. et sp. nov., the most abundant fish from the Eocene Fur Formation of Denmark. *Bulletin of the Geological Society of Denmark* 72, 1–18. <https://doi.org/10.37570/bgsd-2023-72-01>
- Schröder, A.E. & Carnevale, G. 2025a: The putative lampridiform *Iratusichthys ulrikii* gen. et sp. nov. from the Stollklint clay unit of the Ølst Formation. *Bulletin of the Geological Society of Denmark* 74, 33–47. <https://doi.org/10.37570/bgsd-2025-74-04>
- Schröder, A.E. & Carnevale, G. 2025b: *Gerpegezhus daniaoriundus*: a new species of centriscoid fish (Gerpegezhidae) from the Eocene Fur Formation of Denmark. *Journal of Paleontology* 99, 369–381. <https://doi.org/10.1017/jpa.2025.10123>
- Schröder, A.E., Rasmussen, J.A., Møller, P.R. & Carnevale, G. 2022: A new beardfish (Teleostei, Polymixiiformes) from the Eocene Fur Formation, Denmark. *Journal of Vertebrate Paleontology* 42, e2142914. <https://doi.org/10.1080/02724634.2022.2142914>
- Schröder, A.E., Rasmussen, J.A., Møller, P.R. & Carnevale, G. 2023a: *Butyrumichthys henricii* gen. et sp. nov.: a new stromateiform fish from the early Eocene Fur Formation, Denmark. *Journal of Vertebrate Paleontology* 42, e2171798. <https://doi.org/10.1080/02724634.2023.2171798>
- Schröder, A.E., Wielandt, D.K.P., Rasmussen, J.A., Carnevale, G. & Storey, M. 2023b: Benchtop micro-X-ray fluorescence, μ XRF: an exciting tool for anatomical studies of fossil bony fishes. *Lethaia* 56, 1–29. <https://doi.org/10.18261/let.56.2.3>
- Sorbini, C. & Sorbini, L. 1999: The Cretaceous fishes of Nardò. 10°. *Nardovelifer altipinnis*, gen. et sp. nov. (Teleostei, Lampridiformes, Veliferidae). *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 8, 11–27.
- Stokke, E., Liu, E. & Jones, M. 2020: Evidence of explosive hydromagmatic eruptions during the emplacement of the North Atlantic Igneous Province. *Volcanica* 3, 227–250. <https://doi.org/10.30909/vol.03.02.227250>
- Stokke, E.W., Jones, M.T., Riber, L., Haflidason, H., Midtkandal, I., Schultz, B.P. & Svensen, H.H. 2021: Rapid and sustained environmental responses to global warming: the Paleocene–Eocene Thermal Maximum in the eastern North Sea. *Climate of the Past* 17, 1989–2013. <https://doi.org/10.5194/cp-17-1989-2021>
- Storey, M., Duncan, R.A. & Swisher, C.C. 2007: Paleocene–Eocene Thermal Maximum and the opening of the Northeast Atlantic. *Science* 316, 587–589. <https://doi.org/10.1126/science.1135274>
- Tyler, J.C., O'Toole, B. & Winterbottom, R. 2003: Phylogeny of the genera and families of zeiform fishes, with comments on their relationships with tetraodontiforms and caproids. *Smithsonian Contributions to Zoology* 618, 1–110.
- Wang, J.-f., Yu, H.-y., Ma, S.-b., Lin, Q., Wang, D.-z. & Wang, X. 2023: Phylogenetic and evolutionary comparison of mitogenomes reveal adaptive radiation of lampridiform fishes. *International Journal of Molecular Sciences* 24, 8756. <https://doi.org/10.3390/ijms24108756>
- Westerhold, T., Röhl, U., McCarren, H. K. & Zachos, J.C. 2009: Latest on the absolute age of the Paleocene–Eocene Thermal Maximum. *Bulletin of the Geological Society of Denmark (PETM): New insights from exact stratigraphic position of key ash layers +19 and –17*. *Earth and Planetary Science Letters*, 287, 412–419. <https://doi.org/10.1016/j.epsl.2009.08.027>
- Wiley, E.O., Johnson, G.D. & Dimmick, W.W. 2000: The interrelationships of Acanthomorph fishes: a total evidence approach using molecular and morphological data. *Biochemical Systematics and Ecology* 28, 319–350. [https://doi.org/10.1016/s0305-1978\(99\)00069-1](https://doi.org/10.1016/s0305-1978(99)00069-1)
- 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*, 123–182. München: Verlag Dr. Friedrich Pfeil.

