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The putative lampridiform *Iratusichthys ulrikii* gen. et sp. nov. from the Stolleklint clay unit of the Ølst Formation, Denmark

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The early Eocene Fur and Ølst formations are globally renowned for their exceptionally well-preserved ichthyofaunas. Until now, only one lampridiform genus and species, *Palæocentrotus böggildi*, has been described from these, exclusively known from the Fur Formation. Here, we describe a new genus and species of lampridiform fish, *Iratusichthys ulrikii* gen. et sp. nov. from the earliest Eocene Ølst Formation. The single available specimen consists of moderately well-preserved and largely incomplete articulated skeletal remains, lacking most of the axial skeleton. It exhibits a unique set of morphological features that support its recognition as a new lampridiform genus, including a deep anterior concavity of the ethmoid region, orbitosphenoid lacking a ventral keel, presence of tiny, conical teeth in the lower and upper jaws, beryciform foramen piercing the anterior ceratohyal, unique predorsal formula (/0/0/?+1/1/), and absence of parapophyses. Moreover, these characters, especially the presence of tiny conical teeth in the lower and upper jaws might suggest that it should be regarded as a putative stem-lampridiform. However, additional comparative information would be necessary to properly define its phylogenetic position within the lampridiform fishes.

Keywords: Lampridiformes, Ypresian, Eocene, Lampridomorpha, stem-lampridiform.

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Understanding the impact of the Eocene climate in the diversification of the modern groups of teleosts may provide relevant information for investigating possible impacts of current climate changes on marine communities. The Eocene European ichthyofaunas, especially those from Denmark, England, Italy and Russia, are of global interest to understand climatic hazards today's oceans are facing. As far as concerns the Danish ichthyofaunas, the abundance of exquisitely preserved fish fossils from the earliest Eocene Ølst and Fur formations, have been largely neglected. However, over the last few years several papers on the fishes from the Ølst and Fur formations have been published, primarily dealing with taxonomy, palaeoecological interpretations and modes of preservation (Schrøder *et al*. 2022; Schrøder and Carnevale 2023; Schrøder *et al*. 2023a; Schrøder *et al*. 2023b).

Lampridiforms are a well-defined clade within the acanthomorphs. Here, we use the term Lampridiformes, rather than Lampriformes, as endorsed by Colin Patterson (see Olney *et al*. 1993), which has been widely accepted and applied in the majority of taxonomic and phylogenetic studies (e.g. Oelschläger 1983; Patterson 1993; Wiley *et al*. 1998; Sorbini & Sorbini 1999; Wiley and Johnson 2010; Betancur *et al*. 2013; Bannikov 1991, 1999, 2014; Davesne *et al.* 2014, 2016, 2017; Delbarre *et al.* 2016, Carnevale

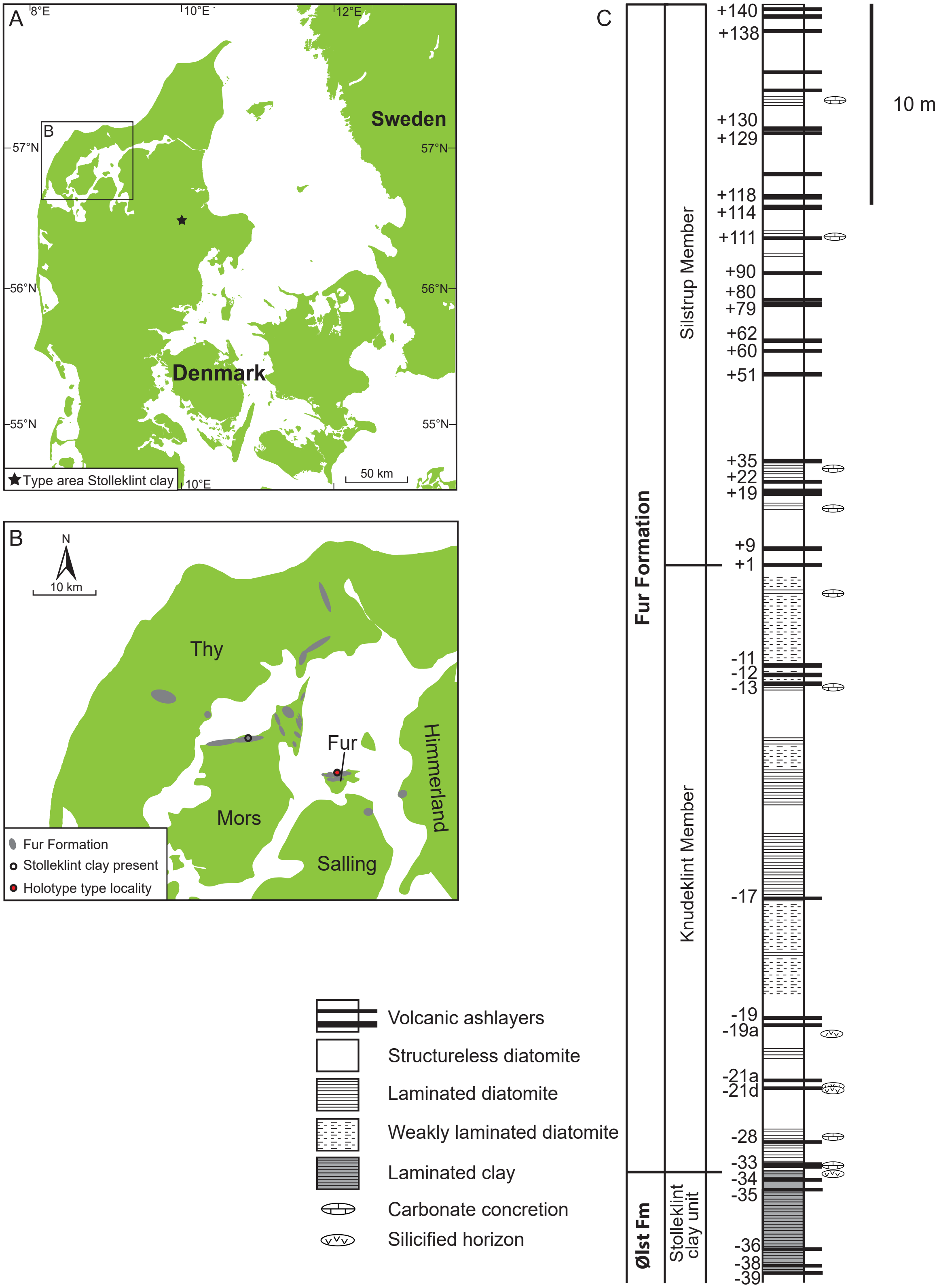

Fig. 1. A: Map of Denmark with the type area of the Stolleklint clay, located between the hills of Ølst and Hinge, marked by a star. **B:** Outcrop localities and near-surface occurrences of the Fur Formation overlying the lowermost part of the Ølst Formation, marked in grey. Circles mark locations where the underlying Stolleklint clay unit is occasionally exposed. **C:** Sedimentological log portraying the ash-series throughout the Stolleklint clay unit of the Ølst Formation, and the Fur Formation. The silicified clay slab containing the holotype specimen originates from a stratigraphic level between -39 to -34, possibly closest to -34. Modified from Schrøder & Carnevale 2023.

and Bannikov 2018; Micklich & Bannikov 2022). The phylogenetic position of Lampridiformes is still debated, as molecular and morphological evidence often provide conflicting results (e.g. Davesne 2014, 2016; Brownstein & Near 2024). Molecular studies have thus 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 (Dettaï & Lecointre 2005), and as sister to the Euacanthopterygii (Near *et al*. 2012). In addition, molecular studies based on mtDNA places Lampridiformes as sister to either Ateleopodiformes or Myctophiformes (for overviews on mitochondrial DNA-studies, see Miya *et al*. 2005, 2007; Poulsen *et al*. 2013). Conversely, the majority of the morphological studies have placed 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).

Davesne *et al.* (2014) incorporated osteological datasets from both extant and fossil relatives in their phylogenetic study of Lampridiformes and found that Lampridiformes + *Pharmacichthys* Woodward, 1942 + Aipichthyoidea + *Pycnosteroides* Woodward, 1942 form the clade Lampridomorpha, which forms the sister group to the Euacanthomorpha, with the oldest representatives of Lampridomorpha being of Cenomanian age. This hypothesis was subsequently corroborated by Delbarre *et al*. (2016). Extant lampridiforms are strictly marine, pelagic fishes, comprising an astonishing morphological diversity considering their relatively low number, being represented by 26 extant species, arranged into six families grouped into the deep-bodied bathysomes (Veliferidae and Lamprididae) and the long-bodied taeniosomes (Lophotidae, Radiicephalidae, Regalecidae, Trachipteridae) (Olney *et al.* 1993; Davesne *et al*. 2014, 2016; Brownstein & Near 2024). At least 15 different genera of fossil Lampridiformes have been described to date (e.g. Sorbini & Sorbini 1999; Bannikov 1991, 1999, 2014; Carnevale 2004; Delbarre *et al*. 2016; Micklich & Bannikov 2022; Davesne *et al*. 2023). The oldest undisputable lampridiform *Nardovelifer altipinnis* Sorbini & Sorbini, 1999 (Campanian), was resolved as a stem-lampridiform due to the presence of a set of plesiomorphies not present in the crown group (Davesne *et al*. 2014; Delbarre *et al*. 2016; see also Brownstein & Near 2024). Morphologically, it is the most advanced Cretaceous lampridomorph taxon, with closest resemblance to extant veliferids (Sorbini & Sorbini 1999). All other Cretaceous lampridomorh taxa are morphologically similar, characterised by small, deep bodies, high and long-based dorsal fins, and moderately protrusible premaxilla (see Delbarre *et al*. 2016, figure 12). *Bathysoma lutkeni* Davis, 1890, from the Paleocene of Denmark and Sweden is currently considered the oldest Cenozoic lampridiform (Patterson 1964, 1968; Davesne *et al.* 2014; Adolfssen *et al*. 2017). The latest combined morphological and molecular phylogeny supports that the origin of extant lampridiform morphotypes took place about 10 myr after the K/Pg-mass extinction event (Brownstein & Near 2024), which roughly corresponds with the age of the earliest Eocene Ølst and Fur formations of Denmark (Storey *et al.* 2007; Westerhold *et al*. 2009, Stokke *et al*. 2020) and the onset of the Paleocene-Eocene Thermal Maximum (Stokke *et al*. 2021).

To date, only a single lampridiform species, *Palæocentrotus böggildi*, Kühne, 1941, has been reported from the early Eocene of Denmark. It was the first fish from the Fur Formation to be described in detail, and to date only known from this formation (Kühne 1941; see also Patterson 1964; Bannikov 1999, 2014).

The aim of the present paper is to describe a new putative lampridiform taxon from the Stolleklint clay unit of the Ølst Formation underlying the Fur Formation in the western Limfjord region in northern Denmark.

Geological setting

The basal Eocene Ølst Formation is, contrary to the Fur Formation, present across most of the Danish Eocene, with observations from the western Limfjord area in northwestern Jutland, through eastern Jutland (Hinge, Ølst) to the Femern Bælt area (Lolland, southeastern Denmark) (e.g. Heilmann-Clausen *et al*. 1985; Sheldon *et al*. 2012). The Ølst Fm, however, is largely replaced by the Fur Formation in the northwestern Limfjord area, including on the islands of Mors and Fur (Fig. 1A–B; see also Heilmann-Clausen *et al.* 1985, figure 4 and 5). Only the lowermost part of the Ølst Formatiion, the Stolleklint clay unit, is exposed at these islands (Fig 1C). This informal unit (for overviews see Heilmann-Clausen 1995 and Schrøder *et al.* 2023b), comprises a non-calcareous, laminated silty clay with presence of silicified beds. The beds occur just below ash layer -33 (Fig. 1C). The Carbon Isotope Excursion (CIE) at the base of the Stolleklint clay at Fur, identifies the Paleocene–Eocene boundary (e.g. Schmitz *et al*. 2004; Stokke *et al.* 2020, Stokke *et al.* 2021). Most fossils uncovered from the Ølst Fm originate from these silicified beds exposed at Mors and Fur, between ash layers -34 to -39 (e.g. Pedersen *et al.* 2012). The type area of the Ølst Fm comprises the clay-pits situated on each side of Ølst Bakker (bakke = hill), close to the two cities Ølst and Hinge in Jutland (Fig. 1A). The Stolleklint clay reaches a thickness of approx. 15 m at the type area (Heilmann-Clausen 1995). One of the most important localities exposing the Stolleklint clay unit is found on the island of Fur close to Stolleklint (klint = cliff), where the estimated thickness is 10 m, but difficult to determine due to the glacial reworking (Heilmann-Clausen 1995; Pe-dersen *et al*. 2012). The ash layers evident throughout the Ølst and Fur formations in the western Limfjord area, originate from the volcanic activity related to the opening of the Northeast Atlantic (e.g. Bøggild 1918; Pedersen & Surlyk 1983; Storey *et al*. 2007; Baumann *et al*. 2024). The ash layers were assigned official numbers by Bøggild (1918), encompassing a negative and a positive series from -39 to +140, respectively (Fig. 1C). However, as more distinctive layers are continuously identified, not included the original ash series, letters are assigned alongside the number of the original designated ash layer, e.g. 21a, 21d (e.g. Pedersen & Surlyk 1983; Pedersen & Buchardt 1996; Larsen *et al*. 2003; Pedersen *et al*. 2004).

Material and methods

The material of the present study is focused on a single, moderately well-preserved specimen, NHMD-625089, comprising the head skeleton and the posteriormost part of the body, including the pectoral and pelvic girdles and fins. The specimen is preserved in silicified, hardened clay of the Stolleklint clay unit, Haslund Member, Ølst Formation. It was collected to the left of Stolleklint on the island of Fur (Fig. 1B). The holotype, NHMD-625089 (designated herein) was declared Danekræ fossil trove in 2008 (fossil trove no. DK-551). It is therefore part of the Danekræ collection housed at the Natural History Museum of Denmark (University of Copenhagen, Denmark). However, this specimen is on permanent loan for Fur Museum, and hence kept in their collections, but not registered as a FUM-N-specimen.

The specimen was examined by both conventional methods applying a Leica M80, and by applying the µXRF-element mapping method described by Schrøder *et al*. (2023b) (see also Schrøder & Carnevale 2023) using 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 a current of 600 µA. Measurements were obtained directly on the specimen with a digital caliper.

Institutional Abbreviations: NHMD, acronym for specimens housed in the collections of the Natural History Museum of Denmark; DK, acronym for specimens declared Danekræ fossil trove, and housed in the Danekræ collection of the Natural History Museum of Denmark; FUM-N, acronym for specimens housed in the collections of Fur Museum, Museum Salling, Denmark.

Anatomical abbreviations: aa, anguloarticular; ach, anterior ceratohyal; bs, basisphenoid; dn, dentary; ect, ectopterygoid; enpt, endopterygoid; fr, frontal; hyo, hyomandibula; inth, interhyal; iop, interopercle; le, lateral ethmoid; me, mesethmoid; mtp, metapterygoid; mx, maxilla; na, nasal: ob, orbitosphenoid; op, opercle; pa, palatine; par, parietal; pas, parasphenoid; pch, posterior ceratohyal; pmx, premaxilla; pop, preopercle; pts, pterosphenoid; qu, quadrate; ra, retroarticular; sop, subopercle; soc, supraoccipital; sym, symplectic; uh, urohyal;

Morphometric abbreviations: ASL, ascending process length; HD, head depth; HL, head length; ML, mandible length; MXL, maxillary length; OD, orbit diameter (measured horizontally); PMXL, premaxillary length; POD, preorbital distance; PoOD, postorbital distance; PDD, predorsal distance; PPD, prepectoral distance; SPL1, length of first supraneural; SPL2, length of second supraneural.

Systematic palaeontology

Clade Lampridomorpha *sensu* Davesne *et al*., 2014

Order Lampridiformes Goodrich, 1909

Genus *Iratusichthys* gen. nov.

Type species. *Iratusichthys ulrikii* gen. et sp. nov.

Etymology. The name is derived from the latin word ‘iratus’, meaning angry, and the greek word ‘ichthys’ (ikhthýs) meaning fish.

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

Diagnosis. A lampridiform genus unique in having the following combination of characters: Ethmoid region of the neurocranium with a deep anterior concavity; ventral keel of orbitosphenoid absent; premaxilla and dentary bearing numerous tiny, conical teeth arranged in multiple rows; beryciform foramen piercing the anterior ceratohyal; two straight supraneurals, the first one inserting in the first interneural space; anteriormost two dorsal fin-pterygiophores inserting in the third interneural space; parapophyses absent; four pectoral-fin radials; pectoral fin with 14 rays; pelvic fin with six rays; squamation represented by small and rounded cycloid scales.

Table 1. Measurements of *Iratusichthys ulrikii* gen. et sp. nov., as percentage of HL

Morphometric characters	Measurements (mm)	% of HL
HL	40.2	100.0
HD	32.0	79.6
PPD	37.0	92.0
PDD	40.6	100.9
POD	21.0	52.3
PoOD	8.9	22.0
OD	8.0	19.9
ASL	12.0	29.9
PMXL	6.2	15.3
MXL	11.2	27.8
ML	13.7	34.1
SPL1	11.7	29.1
SPL2	11.8	29.4

Iratusichthys ulrikii sp. nov.

Figs 2, 3, 4, 5, 6, Table 1

Holotype. NHMD-625089. Moderately well-preserved articulated head skeleton with associated pectoral and pelvic fins and girdles, preserved on a single slab of silicified clay, 40.22 mm in HL. The specimen is exposed in left lateral view. However, some of the skeletal structures originating from the left side are exposed in lateral view, while some others originate from the right side and are exposed in medial view.

Etymology. Named in honour of the retired chief editor, Ulrik Schrøder, who has a profound interest in Danish geology and is an avid amateur geologist. Ulrik has been a great inspiration to the first author. The ‘facial expression’ of the species bears an uncanny resemblance to a certain expression exhibited by Ulrik Schrøder. ‘Ulriki’ is the Latinization of the masculine name Ulrik, prevalent particularly in the Nordic countries. The second ‘i’ denominates the genitive case. The complete binomen means “the angry fish of Ulrik”.

Type locality of holotype. Ølst Formation, lowermost Eocene. Collected from the Stolleklint locality on the island of Fur, northwestern Limfjord area, Denmark. The holotype, and only specimen, originates from a stratigraphic level between ash series -39 to -34 from the Stolleklint clay unit (Fig. 1).

Referred material. None

Diagnosis. As for the genus.

Description. The specimen is moderately well-preserved. Based on the relative size of the bones of the head and pectoral girdle skeleton, it is reasonable to assume that *Iratusichthys ulrikii* gen. et sp. nov. was a deep-bodied fish. The bones of the jaws and suspensorium are slightly displaced anteroventrally due to taphonomic processes. The head is moderately elongate. The head depth is approximately 80% of HL. The snout is contained about two times in HL. The mouth is terminal. The orbit is almost circular and relatively large, its diameter is nearly 20% of HL. The mandible length is about 34% of HL. The pectoral fin inserts obliquely, approximately in the lower half of the cleithrum. The pelvic fin-origin is located just below the pectoral fin.

Neurocranium. The neurocranium is almost triangular, exhibiting a distinctive appearance with a large sagittal crest formed by the convergence of the supraoccipital and frontal crests, the latter protruding anteriorly well beyond the ethmoid region, and a deep anterior concavity located just below the anterior protruding portion of the frontal crest. The lateral surface of the supraoccipital is ornamented with ridges, which are most prominent in its anterior half. The supraoccipital largely contributes to the rear portion of the neurocranium forming a broad laminar blade with a gently curved profile that almost contacts the anterior supraneural; this laminar blade is separated from the anterior portion of the supraoccipital crest by a strong ridge that emerges obliquely from the parietal region of the skull roof and reaches the posterior vertex of the neurocranium. As described above, the supraoccipital and frontal crests articulate with each other forming a continuous structure that occupies the entire length of the skull roof. The anterior portion of the two contralateral frontals form a vault to accommodate the elongated ascending process of the premaxilla. The outline of the parietals is difficult to recognise. The lateral ethmoid is robust, nearly sigmoid in outline, and forms part of the anterior wall of the orbit. The mesethmoid is partly median and partly posterior to the lateral ethmoids and is moderately thick (Figs 2, 3A–C); it articulates dorsally with the frontals. What appears to be the orbitosphenoid forms the dorsal wall to the orbit. The parasphenoid is almost straight extending through most of the basicranial length, exhibiting a minor curvature just behind the orbit. Anteriorly, the parasphenoid articulates with the thick vomer; no vomerine teeth can be observed. The basisphenoid is short, small, thin and rod-like, and does not articulate with the parasphenoid ventrally. The bones of the otic region are difficult to recognise due to inadequate preservation in this part of the neurocranium. The nasals are short, narrow and tubular.

Infraorbital series. The bones of the infraorbital series are feebly preserved, solely represented by fragments of two infraorbitals that can be recognised immediately ventrally to the parasphenoid, and just above the metapterygoid.

Jaws. The mouth is terminal. The upper jaws comprise the premaxilla and maxilla, while the supramaxilla is absent. The premaxilla has a large ascending process, whose length represents almost one third of the head length, also being 1.9 times the length of the alveolar process. The dorsal anterior half of the ascending process is finely sculptured. The distal portion of the alveolar portion is spatulate. There are closely spaced, small and numerous tooth sockets arranged into multiple rows along the alveolar process of the premaxilla (Figs 3D, 4A–B, 5). The maxilla is oblong with a well-developed posterior laminar portion characterised by a gently curved ventral profile, and a moderately preserved anterior articular portion exhibiting an irregular morphology. The mandible is compact and thick with an overall ovoid outline. Tiny conical teeth, apparently arranged in multiple rows, are present on the dentary (Figs 3D, 4C, 5). The anguloarticular is massive, bearing a broad articular facet for the condyle of the quadrate. The thick and compact retroarticular forms the posteroventral corner of the mandible.

Suspensorium. The hyomandibula is slender and appears almost straight, running parallel to the anterior edge of the preopercle; the outline of the articular head is difficult to recognise. The quadrate, endopterygoid and metapterygoid are all large. The quadrate, originating from the left side, is triangular and bears a relatively small condyle that articulates with the anguloarticular. The endopterygoid is oblong and appears to be toothless. The metapterygoid is trapezoid in outline. Both the left and right ectopterygoids are present. They are stout and feebly curved. The palatine is thick, ovoid in outline and lacks an anterior process and palatine teeth.

Opercular series. The right opercular series is preserved, exposed in medial view. The preopercle is crescent-shaped with a slightly rounded, smooth posterior margin; the vertical limb appears to be more than twice as long as the horizontal one and is characterised by a thickened anterior margin. Only the smooth ventral portion of the laminar interopercle is recognisable. The opercle appears to have been

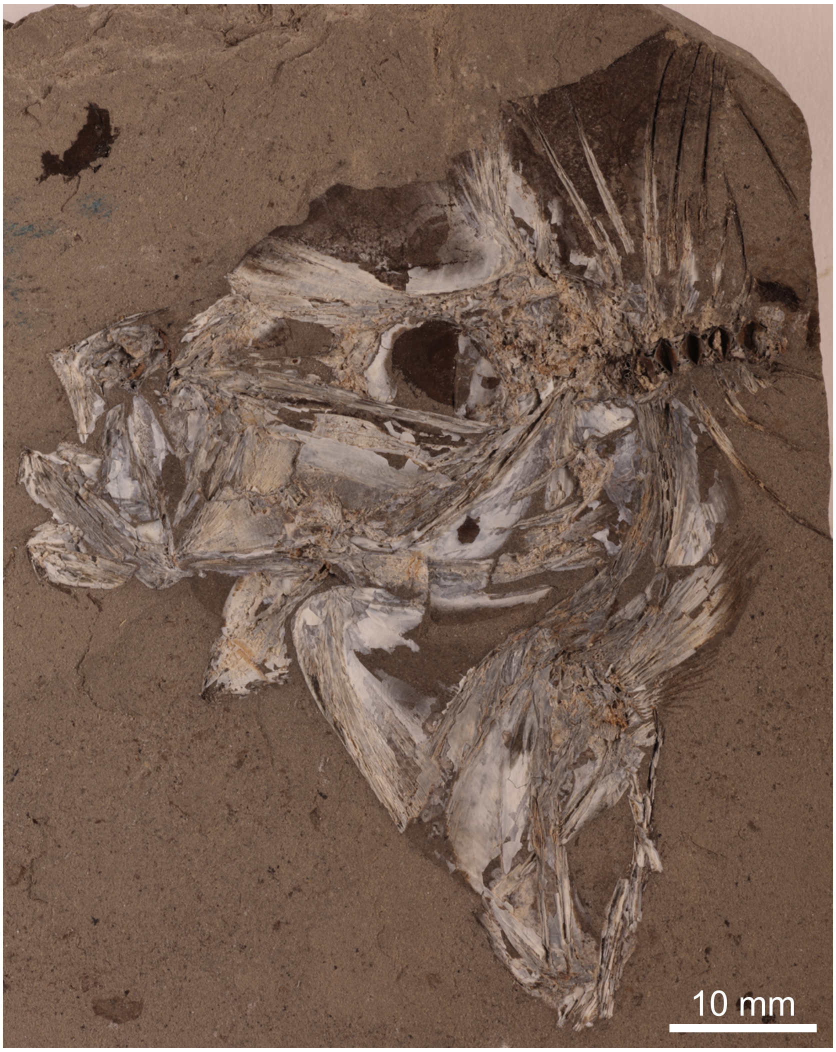

Fig. 2. High-resolution photo image of *Iratusichthys ulrikii* gen. et sp. nov., holotype NHMD-625089 (DK-551). Head skeleton and pectoral and pelvic girdles preserved on a single slab of silicified clay, collected from the Stolleklint clay between ash layer -34 to -39.

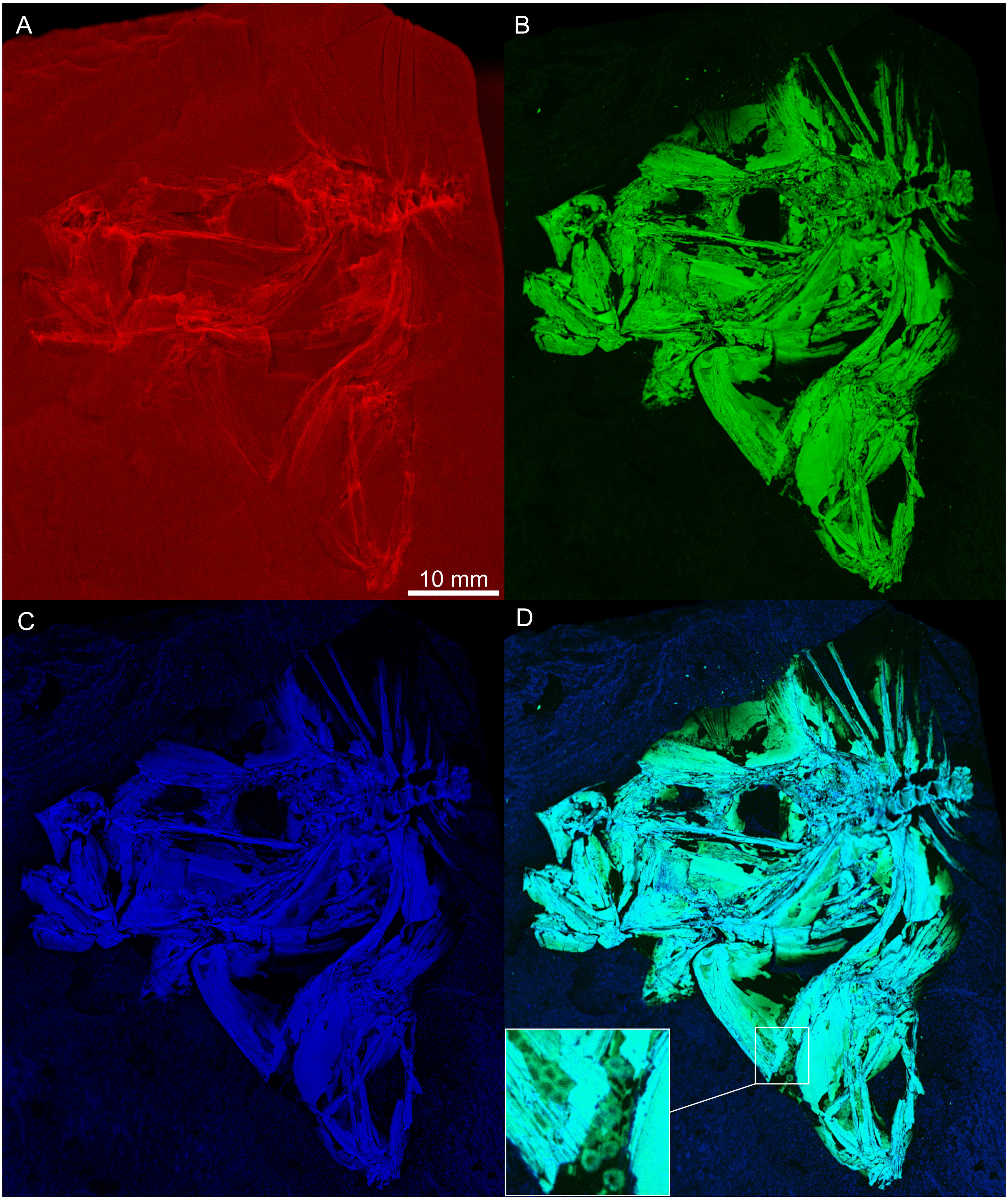

Fig. 3. µXRF-element maps of *Iratusichthys ulrikii* gen. et sp. nov., holotype NHMD-625089 (DK-551). A: Strontium element map. Stronger ossification of the bone structures is evident with regards to the Sr-signal, i.e. more intense red colour is indicative of stronger ossification. The mesethmoid is hardly visible in the Sr map, whereas it is clearly evident in the phosphorous map. B: Phosphorous element map. Laminar portions of the bones are more easily recognisable when the same bone or part of the bone is compared to the Sr or Ca maps. C: Calcium element map, compare e.g. the mesethmoid with the Sr-map in A. D: Combined phosphorous and calcium element map with enlarged insert of the area with visible scales. The small, cycloid scales originating from the right side of the body, visible in medial view behind and posteroventral to the urohyal.

relatively large in origin, but only laminar fragments of its upper portion are preserved. The dorsal border of the opercle appears to have been almost horizontal. The laminar subopercle articulates anteriorly with the interopercle.

Hyoid apparatus and branchial skeleton. The hyoid bar is displaced from its original position and rotated clockwise so that the posterior ceratohyal is exposed anterior to the anterior ceratohyal. The dorsal margin of the anterior ceratohyal is concave and a depressed ovoid 'beryciform' foramen (see Davesne *et al.* 2014) pierces the central part (Figs 2, 6). The partially recognisable anterior end of the anterior ceratohyal seems to form a condylar structure that likely articulated with the ventral hypohyal in origin. The posterior ceratohyal is triangular and articulates dorsally with a small incompletely preserved interhyal (Fig. 6). There is no clear evidence of the hypohyals, which are likely hidden by the suspensorium and opercular bones. There is no evidence of the branchiostegal rays in the specimen. The urohyal is massive and ventrally expanded, almost triangular in outline, with slightly curved dorsal and anterior margins (Fig. 6). Of the branchial skeleton, what appear to be slender ceratobranchials are visible in the opercular region (Figs 2, 3).

Vertebral column and intermuscular bones. Only the six anterior vertebrae are preserved in the specimen. The first and second vertebrae are compressed anteroposteriorly compared to the succeeding ones. The centra of the other vertebrae are subrectangular in outline, slightly higher than long. The neural spine of the first vertebra is broad and shortened. Both the first and second neural spines are slightly inclined forward, while those of the third to sixth vertebrae are anteroposteriorly expanded, bearing a posterior laminar outgrowth with a rounded profile. Parapophyses are absent on all preserved vertebrae

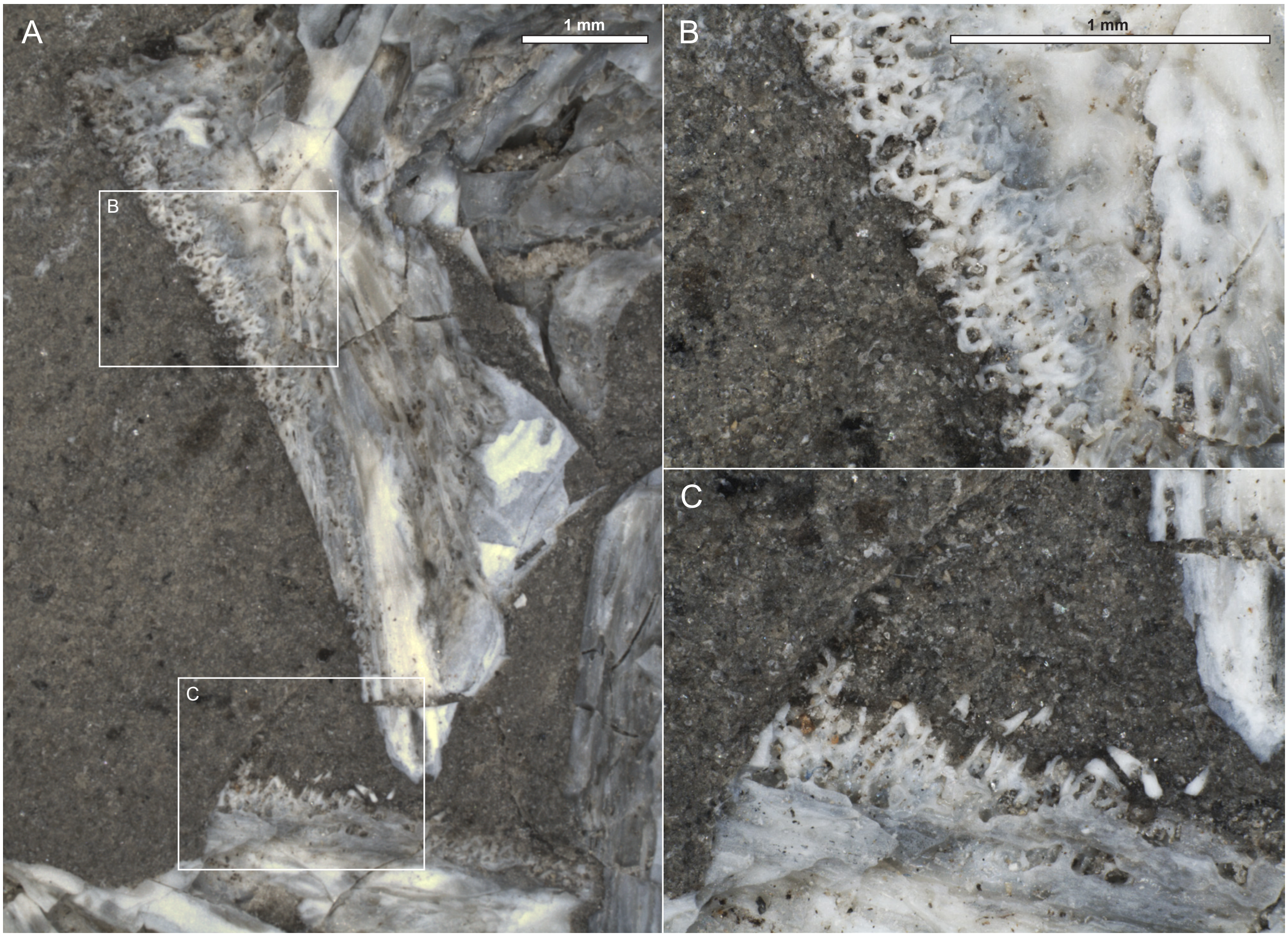

Fig. 4. *Iratusichthys ulrikii* gen. et sp. nov, holotype NHMD-625089 (DK-551). Micrographs of the tiny tooth sockets and conical teeth, arranged in multiple rows. A: Section showing the premaxilla and dentary. B: Ten times magnification of the insert of the premaxilla indicated in A, showing numerous tooth sockets arranged into multiple rows along the alveolar process of the premaxilla. C: Ten times magnification of the insert of the dentary indicated in A, showing the anterior half of the dentary with tiny conical teeth arranged in multiple rows. Several detached teeth are also visible. Scale bars = 1 mm. The scale bar in B also applies to C.

(Figs 2, 3A). The dorsal portion of three pairs of ribs is preserved, the first articulating with the third vertebra.

Median fins and supports. The dorsal fin, which is not preserved, is preceded by two slender, nearly straight and elongate supraneurals, which are almost equal in length (29% of HL). They are slightly expanded dorsally, forming the shape of a flat nail-head; the expanded parts are mostly preserved as impressions (Fig. 2, Fig. 3A, D). The supraneurals are closely spaced, but the first ends ventrally just above the boundary between the neural spines of the first and second vertebrae, possibly representing the first interneural space; the second supraneural inserts in the second interneural space. The dorsal-fin pterygiophores are mostly preserved as impressions. The first pterygiophore bears a horizontal limb that follows the dorsal profile of the nape. The first two dorsal-fin pterygiophores insert in the third interneural space, while the third pterygiophore inserts in the fourth interneural space. The fourth pterygiophore is displaced from its original position. There are no dorsal-fin spines or rays preserved. However, it is reasonable to hypothesize that the predorsal formula was /0/0/?+1/1/.

Paired fins and girdles. The posttemporal is poorly preserved, with only the dorsal, slightly curved limb being discernible. The rest of the pectoral girdle is displaced ventrally from its original position as indicated by the separation of the posttemporal and supracleithrum. The supracleithrum is oblong with a ventral, broad laminar expansion and a thickened anterior edge. The cleithrum is large and sigmoid-shaped; its ventral part is inflated and paddle-like and terminates ventrally abruptly into a small pungent process. The distal portion of the elongate postcleithrum is closely associated with the basipterygium. The scapula is relatively small and rounded, centrally pierced by a scapular foramen. The coracoid is narrow and terminates at the same level as the cleithrum. Four pectoral-fin radials appear to be present, of which the two posteriormost can easily be recognised; the three anterior radials articulate with the scapula and the fourth only with the coracoid. A total of 14 pectoral-fin rays are identified, of which the two dorsalmost articulate directly with the scapula.

The prominent basipterygium is dorsally inclined and attached to the pectoral girdle; the central axis of the basipterygium is almost vertical and articulates with the cleithrum, while the internal wing is associated with the ventral end of both cleithrum and coracoid. The pelvic fin appears to include at least six rays of which the outer one is thicker and apparently unsegmented; these are rotated dorsally around the articular surface of the basipterygium.

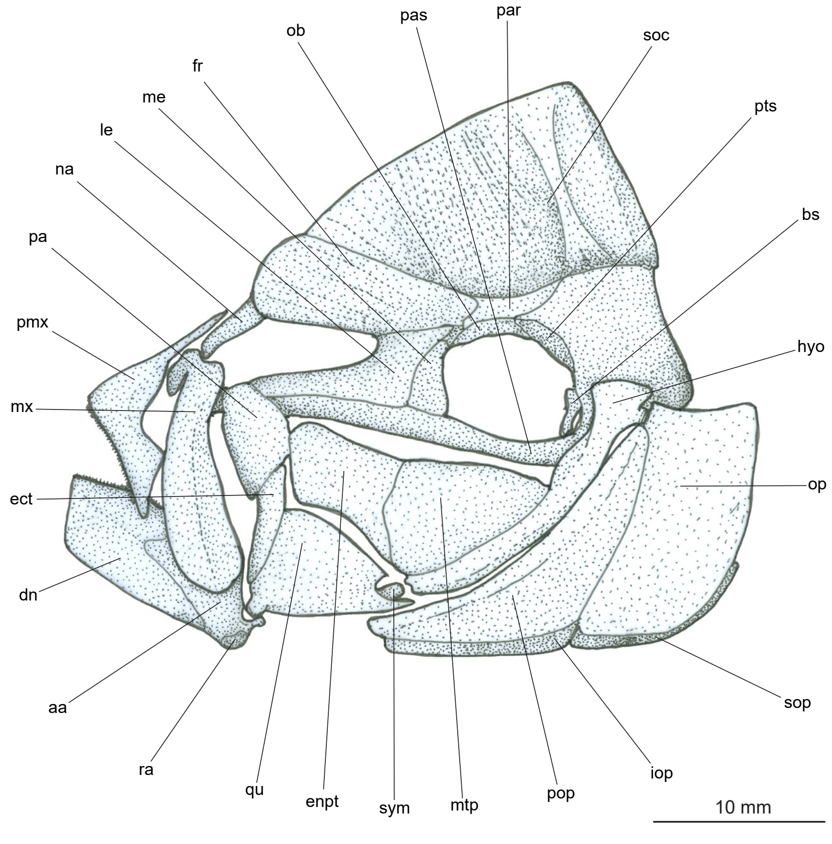

Fig. 5. *Iratusichthys ulrikii* gen. et sp. nov. Reconstruction of the head.

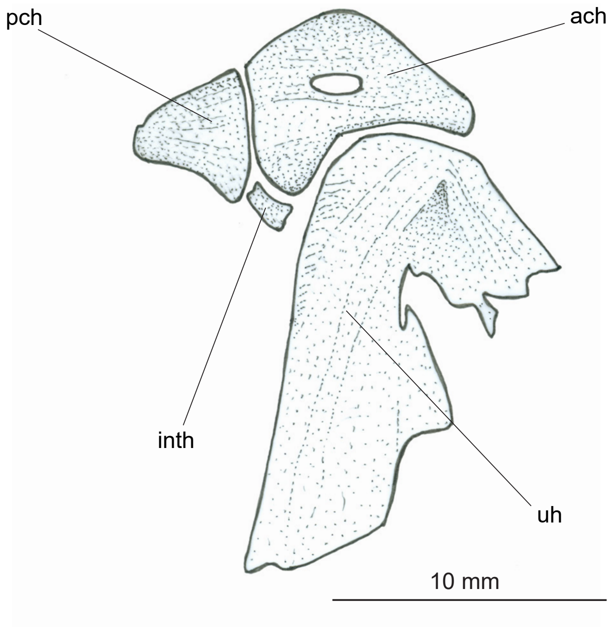

Fig. 6. *Iratusichthys ulrikii* gen. et sp. nov. Interpretive reconstruction of the hyoid apparatus.

Squamation. Small and rounded cycloid scales, originating from the right side of the body, are visible behind and posteroventral to the urohyal in medial view (Fig. 3D).

The nomenclatural acts of this paper are registered on ZooBank. LSID of the new genus Iratusichthys:
https://zoobank.org/NomenclaturalActs/E1EBCB81-B81B-40EF-914C-26ABC83D607B
and the LSID of the new species Iratusichthys ulrikii:
https://zoobank.org/NomenclaturalActs/C870AD54-3609-48E6-B652-D0AF7074FF32

Comparative discussion

The phylogenetic relationships of lampridiform fishes have been extensively discussed in the last decades, based on morphological and molecular data (e.g. Oelschläger 1983; Olney *et al.* 1993; Wiley *et al*. 1998; Miya *et al.* 2007; Wiley and Johnson 2010; Davesne *et al.* 2014, 2016, 2017; Delbarre *et al.* 2016; Brownstein & Near 2024). Olney *et al*. (1993) proposed four main synapomorphies to support the monophyletic status of the crown Lampridiformes, including: 1) absence of the anterior palatine process (referred to as the palatine 'prong' by Olney *et al*. 1993); 2) mesethmoid posterior to the lateral ethmoids; 3) premaxillae with greatly elongate ascending processes associated with frontals elevated forming a vault to accommodate them; 4) first dorsal-fin pterygiophore (and, therefore, the preceding supraneurals) inserting in the preneural space. As described above, the first three of these features can be observed in the new taxon described herein, *Iratusichthys ulrikii* gen. et sp. nov. As far as concerns the fourth of these features, as pointed out by Bannikov (1999), the pattern regarding the preneural insertion of the supraneurals and first dorsal-fin pterygiophore may diverge in certain fossil lampridiforms, including *Palæocentrotus böggildi* from earliest Eocene of Denmark (predorsal formula 0/0+2/1+1+1; Patterson 1993), and the turkmenid *Analectis pala* Daniltshenko, 1980 from the Upper Eocene and Lower Oligocene of northern Caucasus (predorsal formula 0/0+0/1; Bannikov 1999). In particular, *Analectis* Daniltshenko, 1980 is unique within lampridiforms by having three supraneurals and the first dorsal-fin pterygiophore that inserts in the second interneural space. The list of lampridiform synapomorphies was recently expanded by Davesne *et al*. (2014) by including additional features of the hyoid apparatus, intermusculars and caudal skeleton. While some of these characters refer to structures not accessible in the single available specimen described herein, at least three lampridiform synapomorphic features, absence of supramaxillae, urohyal expanded ventrally, and possession of two supraneurals, can be observed in *Iratusichthys* gen. nov., thereby reinforcing its alignment with the Lampridiformes.

Long-bodied (taeniosomous) lampridiforms have traditionally been recognised as a monophyletic assemblage (e.g. Oelschläger 1983, Olney *et al*. 1993), while the deep-bodied (bathysomous) lampridiforms are commonly not recognised as monophyletic because the Lamprididae is regarded as the sister group to the elongate families (e.g. Olney *et al*. 1993; Davesne *et al*. 2014, 2016; Delbarre *et al*. 2016). However, several studies recurrently recovered a monophyletic clade formed by lamprids plus veliferids as sister group to the taeniosomes (Grande *et al*. 2013; Wang *et al*. 2023; Brownstein & Near 2024). Therefore, due to the presence of these two contrasting phylogenetic hypotheses, it is difficult to interpret the phylogenetic relationships of fossil lampridiform taxa.

As discussed above, despite the incompleteness of the available material, *Iratusichthys ulrikii* gen. et sp. nov. should be regarded as a deep-bodied fish. In addition, *Iratusichthys ulrikii* gen. et sp. nov. has two supraneurals and a well-developed supraoccipital crest, thereby excluding any possible affinity with the long-bodied taeniosomous lampridiforms (see Olney *et al*. 1993). However, it is interesting to note that the two anterior vertebrae of *Iratusichthys ulrikii* gen. et sp. nov. are in some ways reminiscent of the first vertebra of taeniosomous lampridiforms, being characterised by an anteroposteriorly compressed centra and anteriorly inclined neural spines (see Oelschläger 1983, Olney *et al*. 1993).

Among deep-bodied bathysomous lampridiforms, *Iratusichthys ulrikii* gen. et sp. nov. is characterised by having a unique set of features, including numerous tiny conical teeth in both upper and lower jaws, a peculiar configuration of the ethmoid region of the neurocranium that exhibits a deep anterior concavity and lacks a ventral keel of the orbitosphenoid, and two supraneurals inserting in the first two interneural spaces followed by dorsal-fin pterygiophores inserting in the third and successive interneural spaces. Moreover, the attribution of *Iratusichthys ulrikii* gen. et sp. nov. to the Veliferidae can also be ruled out since it lacks parapophyses on the abdominal vertebrae and the dorsal-fin base is not covered by a scaly sheath (see Reagan 1907a, b; Olney *et al*. 1993; Carnevale & Bannikov 2018). Likewise, *Iratusichthys ulrikii* gen. et sp. nov. cannot be referred to Lampridae as it exhibits a beryciform foramen piercing the anterior ceratohyal, presence of at least two infraorbitals, obliquely inserting pectoral fins, and four autogenous pectoral-fin radials (e.g. Olney *et al*. 1993; Davesne *et al*. 2023). The possession of a beryciform foramen in the anterior ceratohyal, of more than one infraorbital, and of obliquely inserting pectoral fins allows to exclude any possible alignment between *Iratusichthys ulrikii* gen. et sp. nov. and the Eocene *Whitephippus tamensis* Casier, 1966 (see Davesne *et al*. 2023). *Iratusichthys ulrikii* gen. et sp. nov. further differs from the Paleocene *Bathysoma lutkeni* by lacking a fenestration in the supraoccipital crest as well as a tubular snout resulting from the remarkable elongation of the jaw bones (Patterson 1964; Adolfssen *et al.* 2017). The Paleogene bathysomous family Turkmenidae comprises three species, including *Analectis pala*, *Danatinia casca* Daniltshenko, 1968 and *Turkmene finitimus* Daniltshenko, 1968 which are characterised by subhorizontally inserting pectoral fins (Daniltshenko 1968, 1980; Bannikov 1999). *Iratusichthys ulrikii* gen. et sp. nov. exhibits some similarities with the turkmenids. For example, it shares the possession of two supraneurals and absence of parapophyses with *Turkmene finitimus;* however, both the supraneurals of *Turkemene* insert in the preneural space. Finally, as far as concerns the Paleogene bathysomous family Palaeocentrotidae, both the known species *Natgeosocus sorini* Bannikov, 2014 and *Palæocentrotus böggildi* differ from *Iratusichthys ulrikii* gen. et sp. nov. by having heads strongly compressed antero-posteriorly, and large orbits occupying at least 30% of HL (e.g. Kühne 1941; Bannikov 2014).

One of the most salient morphological features exhibited by *Iratusichthys ulrikii* gen. et sp. nov. is the presence of tiny conical teeth in both upper and lower jaws. Extant lampridiforms as well as all the other Cenozoic taxa are characterised by toothless jaws. The Cretaceous *Nardovelifer altipinnis* recently resolved as a stem-lampridiform (e.g. Delbarre *et al*. 2016; Brownstein & Near 2024), also has small teeth on both the premaxilla and dentary (Sorbini & Sorbini 1999). Other than in *Nardovelifer* Sorbini & Sorbini, 1999 and *Iratusichthys* gen et. sp. nov. the presence of jaw teeth has been reported in the Cretaceous lampridomorph *Aipichthys*, Steindachner, 1860 (Delbarre *et al.* 2016). Whether the presence of teeth in *Iratusichthys ulrikii* gen. et sp. nov. represents a genuine plesiomorphic condition or is an example of character reversal (i.e. taxic atavism; see Stiassny 1992) cannot be determined. The configuration of the predorsal formula of *Iratusichthys ulrikii* gen. et sp. nov. also diverges from that of all the other extant and fossil lampridiform taxa. These characters might suggest that *Iratusichthys ulrikii* gen. et sp. nov. should be tentatively regarded as a stem-lampridiform. However, additional and more complete specimens would be necessary to properly define its phylogenetic position within this lineage of basal acanthomorphs.

As a final comment to this taxonomic discussion, it is interesting to note that some of the morphological features of *Iratusichthys ulrikii* gen. et sp. nov. are reminiscent of those observed in the species of the percomorph family Menidae, which were especially abundant in the earliest portion of the Paleogene (see, e.g. Blot 1969; Friedman & Johnson 2005). In particular, the overall configuration of the neurocranium, characterized by a frontal vault, a prominent supraoccipital crest ornamented with ridges, as well as the presence of tiny teeth in the oral jaws are in some ways similar to those of the menids. However, the fossil described herein lacks numerous characters diagnostic of the Menidae, (e.g. robust scleral ossicles; large series of narrow infraorbitals and a broad lachrymal with a large, depressed area on its lateral surface; diamond-shaped palatine prong; large metapterygoid foramen; massive postcleithrum; three supraneurals; Blot 1969; Friedman & Johnson 2005), thereby suggesting that the similar cranial features might be regarded as the result of convergent evolution.

Concluding remarks

The fossil record of lampridiform skeletal remains in Denmark is restricted to the earliest part of the Paleogene. As reported by Adolfssen *et al.* (2017), articulated skeletal remains of *Bathysoma lundensis* have been collected from the Selandian erratic boulders near Klint. *Iratusichthys ulrikii* gen. et sp. nov. is the oldest known Eocene lampridiform, dating back to about 55 Ma. *Palæocentrotus böggildi* also known from the earliest Eocene of Denmark, is slightly younger, exclusively known from the overlying Fur Formation. In addition, incomplete material tentatively referred to the genus *Palæocentrotus* has been reported from the middle Danian deposits, preserved in a flint nodule from a loose boulder at Endelave Strand (e.g. Adolfssen *et al.* 2017). Bonde (1987) pictured a possible new turkmenid species from the Fur Formation in his popular scientific Skamol-booklet (Bonde 1987, p. 38). However, it has been impossible to locate this or other similar specimens in the museums' collections in Denmark, including in the Vertebrate Palaeontology and Danekræ collections of the Natural History Museum of Denmark (Copenhagen University), and in the collections of the Fossil- and Moclay Museum (Museum Mors) and in the Fur Museum collections (Museum Salling). The collections of the Natural History Museum, London (UK), that also house material of the ichthyofauna from the Fur Formation were also checked for possible turkmenid specimens in November 2024, but no specimens were located.

Extant bathysomous lampridiforms are characterised by epipelagic or demersal habits. According to Delbarre *et al*. (2016), some extinct deep-bodied lampridiforms (e.g. *Nardovelifer*) are reminiscent of extant veliferids and were probably characterised by a similar demersal and neritic ecological lifestyle. The Paleogene taxa, except for those from the shallow tropical biotopes of Bolca (see Marramà *et al*. 2016; Carnevale & Bannikov 2018; Friedman & Carnevale 2018), appear to be associated with open oceanic environments (Davesne *et al*. 2023). This was probably also the case for *Iratusichthys ulrikii* gen. et sp. nov. The depositional environment of the basal Ølst Formation is poorly defined, although it is assumed that the climate conditions were subtropical to tropical, the bottom waters strongly anoxic, and the palaeo-North Sea may have been restricted to form an inland sea at this time (Heilmann-Clausen *et al*. 1985; Heilman-Clausen 1995).

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References

Adolfssen, J.S., Milan, J. & Friedman, M. 2017: Review of the Danian vertebrate fauna of southern Scandinavia. Bulletin of the Geological Society of Denmark 65, 1–23. https://doi.org/10.37570/bgsd-2017-65-01

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. https://doi.org/10.1134/s0031030114060021

Bannikov, A.F. 2014: A new genus of the family Palaeocentrotidae (Teleostei, Lampridiformes) from the Oligocene of the Northern Caucasus and comments on other fossil Veliferoidei. Paleontological Journal 48 (6), 624–632. https://doi.org/10.1134/S0031030114060021

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 (2024), https://doi.org/10.1016/j.palaeo.2024.112575

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. https://doi.org/10.1371/currents.tol.53ba26640df0ccaee75bb165c8c26288

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

Blot, J. 1969: Les poissons fossiles du Monte Bolca, classés jusu'ici dans les familles des Carangidae, Menidae, Ephippidae, Scatophagidae. Studi e Ricerche sui Giacimenti Terziari di Bolca 1, 1–540.

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

Bonde, N. 1987: Moler - its origin and its fossils especially fishes, 53 pp. Published by Skamol Skarrehage Molerværk A/S, on the occasion of the company's 75th anniversary.

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, C. & Bannikov, A.F. 2018: A sailfin velifer (Lampridiformes, Veliferidae) fish from the Eocene of Monte Bolca, Italy. Bollettino della Società Paleontologica Italiana 57 (3), 175–186. https://doi.org/10.1007/s12542-022-00633-7

Casier, E. 1966: Faune ichthyologique du London Clay. British Museum Natural History London, 1966, 1–496.

Daniltschenko, P.G. 1968: Fishes from the Upper Paleocene of Turkmenia. In: Obruchev, D.V. (ed.): Ocherki po filogenii i sistematike iskopayemykh ryb i beschelyustnykh, 113–156.

[In Russian: Essays on the Phylogeny and Systematics of Fossil Fishes and Agnathans. Moscow: Nauka.

Daniltschenko, P.G. 1980: The order Lampridiformes. Trudy Paleontologicheskogo Instituta Nauk SSSR 178, 91–96 [in Russian].

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): Fossils and Lampridiformes Interrelationships. 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 Intrarelationships of Spiny-Rayed Fishes (Acanthomorpha, Teleostei, Actinopterygii): Fossil taxa increase the congruence of morphology with molecular data. Frontiers in Ecology and Evolution 4 (129), 1–20. https://doi.org/10.3389/fevo.2016.00129

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., Andrews, J. V., Beckett, H.T., Giles, S. & Friedman, M. 2023: Three-dimensional anatomy of the early Eocene *Whitephippus* (Teleostei, Lampriformes) documents parallel conquests of the pelagic environment by multiple teleost lineages. Journal of Vertebrate Paleontology 43, e2284998. https://doi.org/10.1080/02724634.2023.2284998

Davis, J.W. 1890: On the fossil fish of the Cretaceous formations of Scandinavia. Scientific Transactions of the Royal Dublin Society 4, 363–434.

Delbarre, D.J., Davesne, D. & Friedman, M. 2016: Anatomy and relationships of †*Aipichthys pretiosus* and †*'Aipichthys' nuchalis* (Acanthomorpha: Lampridomorpha), 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.crvi.2005.04.002

Friedman, M. & Carnevale, G. 2018: The Bolca Lagerstätten: shallow marine life in the Eocene. Journal of the Geological Society 175, 569–579. https://doi.org/10.1144/jgs2017-164

Friedman, M. & Johnson, G.D. 2005: A new species of *Mene* (Perciformes: Menidae) from the Paleocene of South America, with notes on paleoenvironment and a brief review of menid fishes. Journal of Vertebrate Paleontology 25, 770–783. https://doi.org/10.1671/0272-4634(2005)025[0770:ansomp]2.0.co;2

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.

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

Heilmann-Clausen, C. 1995: Palæogene aflejringer over danskekalken, 70–113. Danmarks Geologi fra Kridt til i dag. Aarhus Geoscience.

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, 115, 6249–6254. https://doi.org/10.1073/pnas.1719358115

Johnson, D.G. & 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 Molerof Denmark. The Annals and Magazine of Natural History 7, 374–386

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., Dettaï, 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

Marramà, G., Bannikov, A.F., Tyler, J.C., Zorzin, R. & Carnevale, G. 2016: Controlled excavations in the Pesciara and Monte Postale sites provide new insights about the palaeoecology and taphonomy of the fish assemblages of the Eocene Bolca Konservat-Lagerstätte, Italy. Palaeogeography, Palaeoclimatology, Palaeoecology 454, 228–245. https://doi.org/10.1016/j.palaeo.2016.04.021

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

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 109, 13698–13703. https://doi.org/10.1073/pnas.1206625109

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., 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, 49–102.

Patterson, C. 1993: An overview of the early fossil record of acanthomorphs. Bulletin of Marine Science 52, 29–59.

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 – sedimenter, 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.

Regan C.T. 1907a: Descriptions of the teleostean fish *Velifer hypselopterus* and of a new species of the genus *Velifer*. Proceedings of the Zoological Society of London 1907, 633–634.

Regan C.T. 1907b: On the anatomy, classification and systematic position of the teleostean fishes of the suborder Allotriognathi. Proceedings of the Zoological Society of London 1907, 634–643.

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

Schrøder, A.E. and Carnevale, G. 2023: The argentiniform *Surlykus 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/bgsd2023-72-01

Schrøder, 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(2), e2142914. https://doi.org/10.1080/02724634.2022.2142914

Schrøder, 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(3), e2171798. https://doi.org/10.1080/02724634.2023.2171798

Schrøder, A.E., Wielandt, D.K.P., Rasmussen, J.A., Carnevale, G. & Storey, M. 2023b: Benchtop micro–X-ray fluorescence, μXRF: an exciting tool for anatomical studies of fossil bony fishes. Lethaia 56, 1–29. https://doi.org/10.18261/let.56.2.3

Sheldon, E., Gravesen, P. & Nohr-Hansen, H. 2012: Geology of the Femern Bælt area between Denmark and Germany. Geological Survey of Denmark and Greenland (GEUS) Bulletin 26, 13–16. https://doi.org/10.34194/geusb.v26.4740

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.

Steindachner, V.F. 1860: Beiträge zur Kenntniss de fossilen Fische, Österreichs. II Folge. I. Ueber einen neuen Vomerachnilichen Fisch von Comen an Karst. Sitzungsberichte der Akademie der Wissenschaften, Wien, 38, 763–777.

Stiassny, M. 1992: Atavisms, phylogenetic character reversals, and the origin of evolutionary novelties. Netherlands Journal of Zoology 42, 260–276.

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

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 lampriform fishes. International Journal of Molecular Sciences 24, 8756. https://doi.org/10.3390/ijms24108756

Wiley, E.O., Johnson, G.D. & Dimmick, W.W. 1998: The phylogenetic relationships of lampridiform fishes (Teleostei: Acanthomorpha), based on a total-evidence analysis of morphological and molecular data. Molecular Phylogenetics and Evolution 10, 417–425.

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/10.1006/mpev.1998.0532

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 Pheil, München. https://doi.org/10.1016/s0305-1978(99)00069-1

Westerhold, T., Röhl, U., McCarren, H. K. & Zachos, J.C. 2009: Latest on the absolute age of the Paleocene–Eocene Thermal

Maximum (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

Woodward, A.S. 1942: Some new and little-known Upper Cretaceous Fishes from Mount Lebanon. The Annals and Magazine of Natural History 9, 537–568.