The argentiniform *Surlykus longigracilis* gen. et sp. nov., the most abundant fish from the Eocene Fur Formation of Denmark

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Bony fishes are among the best represented macrofossils from the earliest Eocene Fur Formation, northern Denmark. The most abundant fish of the formation has never been formally described, in spite of its abundance throughout the formation, and only referred to as an 'argentinoid'. This work provides a taxonomic study of this argentinoid taxon, which is described herein as *Surlykus longigracilis* gen. et sp. nov. The caudal skeleton shows separated first preural and first ural centra, a unique condition within the Argentiniformes. In addition, it is characterised by having a large mouth and a single supramaxilla, which suggest that *Surlykus* gen. nov. occupies a basal position within the Argentiniformes, representing the sister-group to all the other lineages of this clade ([Argentinidae + Opisthoproctidae] + [Bathylagidae + Microstomatidae]), and, consequently, a stem-group Argentiniformes. Mass-mortality assemblages may indicate that *Surlykus longigracilis* gen. et sp. nov. formed large schools in the ancient North Sea Basin, where it probably represented the trophic nucleus of the fish communities.

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Marine smelts of the order Argentiniformes represent a small group of broadly distributed oceanic fishes usually characterised by a silvery colour. This group is commonly regarded as monophyletic (Ahlstrom *et al.* 1984; Begle 1992; Johnson & Patterson 1996) and is considered to comprise less than 90 extant species in 21 genera arranged in four families, Argentinidae, Bathylagidae, Microstomatidae and Opisthoproctidae (see e.g., Chapman 1942, 1948; Hubbs 1953; Bertelsen 1958; Cohen 1958, 1964; Greenwood & Rosen 1971; Ahlstrom *et al.* 1984; Johnson & Patterson 1996; Nelson *et al.* 2016).

The fossil record of the argentiniforms is relatively poor. While the earliest otoliths referred to the argentiniforms date back to the Albian (Schwarzhans *et al.* 2022), articulated skeletal remains referred to the family Argentinidae (*Nybelinoides brevis*) have been reported from the Barremian-Aptian locality of Bernissart, Belgium (Taverne 1982). Argentinids are also known from the Oligocene of Caucasus and Polish and Romanian Carpathians (Jerzmańska 1967; Prokofiev 2005) as well as the Miocene of Azerbaijan (Prokofiev 2005). Fossils belonging to the family Bathylagidae are known from the Oligocene – early Miocene of the Czech Carpathians (Přikryl 2021) and the Miocene of California, Japan and Sakhalin and Urup islands (e.g., David 1943; Sato 1962; Yabumoto & Uyeno 1994; Nazarkin 2018) and a representative of the family Opisthoproctidae has been reported from the Miocene Kurasi Formation of Sakhalin Island (Nazarkin 2016).

Undescribed fossil argentiniforms are also known from the Eocene of the Fur Formation, Denmark.

These fishes, traditionally known as 'argentinoids' are well-known and abundant throughout the formation's three main lithologies, i.e., carbonate concretions, soft diatomite and silicified diatomite (e.g., Ussing 1904; Bonde 1973, 1979, 1982, 1997; Pedersen *et al.* 2012; Schrøder *et al.* submitted), being also reported from the underlying Stolleklint clay unit of the Ølst Formation (Schrøder *et al.* submitted). Old specimen tags of fossil individuals, especially those kept in the Vertebrate Palaeontology collection of the Natural History Museum of Denmark, Copenhagen University, are often labeled 'Guldlaks' or 'Strømsild' (i.e., the Danish names of *Argentina silus* and *Argentina sphyreana*, respectively), 'clupavid' or 'salmonid'. However, in spite of its renowned status, it has never been formally described, and traditionally referred to the argentinoids (Bonde 1979, 1982). This argentinoid is unquestionably the most abundant taxon of the fish fauna. Large collections of fossil material from the Fur Formation housed in the Natural History Museum of Denmark, Museum Mors and Fur Museum support the earlier observations (e.g., Bonde 1997) that fish specimens pertaining to this taxon represent the vast majority of the vertebrate remains of the Fur Formation assemblage.

As mentioned above, three main lithologies are recognised within the Fur Formation, i.e., carbonate concretions, soft diatomite and silicified diatomite (see Fig. 1), all of which contain fish remains (see Schrøder *et al.* submitted for an overview). Invertebrates, turtles and birds originating from the distinct carbonate concretion horizons (see Pedersen & Buchardt 1996; Pedersen *et al.* 2004) of the formation are often preserved in pristine conditions, i.e., they are often articulated, near-complete and occasionally three-dimensionally preserved (Rasmussen 1972; Dyke & Lindow 2009; Karl & Madsen 2012; Lindgren *et al.* 2017). The majority of the fish skeletons originating from the concretions are similarly exquisitely preserved, without significant disarticulation, with the bones partially maintaining their three-dimensional shape, most obvious in the skeletal elements of the head and the body axis (Schrøder *et al.* 2022; Schrøder *et al.* submitted). This also applies to the 'argentinoid fish', especially for the specimens preserved in the carbonate concretions close to the ash layers +25 to +30 (Fig. 1C). The specimens from the soft diatomite are commonly poorly preserved as flattened or moderately three-dimensional, extremely fragile impressions. However, specimens from certain soft diatomite levels, e.g., laminated layers close to ash layer –19, may contain minute and delicate skeletal elements as well (Schrøder *et al.* submitted). Specimens within the silicified horizons are relatively uncommon, usually being slightly flattened, with a preservation comparable to

that of the specimens from the carbonate concretions, in terms of preserved anatomical details (Schrøder *et al.* submitted). The 'argentinoid fish' is also known to occur in large 'schools' from bedding planes of carbonate concretion and soft diatomite horizons, and occasionally found as stomach contents of larger fish species (observations by the authors, see also Pedersen *et al.* 2012 and in one instance also in a single specimen of coraciiform bird (see Bourdon *et al.* 2016).

Therefore, the aim of the present study is to provide a taxonomic study of the 'argentinoid fish' from the Eocene Fur Formation. The fish is described as a new genus and species of the order Argentiniformes, *Surlykus longigracilis* gen. et sp. nov.

Geological setting

The world-renowned Ypresian Fur Formation crops out in the north-western Limfjord region of Jylland, Denmark (Fig. 1A–B). The formation, which reaches an approximate thickness of 60 m, comprises a fossil-rich, marine diatomite, interbedded with approximately 200 official recognised ash layers. A total of 179 layers have been given official numbers, whereas certain distinctive ash layers not included in the original sequence, since have been assigned numbers and added letters (Fig. 1C; Bøggild 1918; Gry 1940; Pedersen & Surlyk 1983; Pedersen & Buchardt 1996; Larsen *et al.* 2003; Pedersen *et al.* 2004). The ash layers originate from volcanic eruptions connected to the opening of the northeast Atlantic (Bøggild 1918; Andersen 1937; Pedersen & Surlyk 1983; Danielsen & Thomsen 1997; Storey *et al.* 2007), and the age of the formation has been determined by radiometric dating of locally numbered ash layers –17 and +19, yielding $^{39}Ar/^{40}Ar$ age determinations of *c.* 55.6 Ma and *c.* 54.4 Ma, respectively (Storey *et al.* 2007; Westerhold *et al.* 2009; Stokke *et al.* 2020). The Fur Formation is divided into the lower Knudeklint Member, defined by laminated beds and relatively few ash layers, and the upper Silstrup Member, which is dominated by structureless beds and an abundancy of often thick ash layers; sequences reflecting the alternating conditions of slight dysoxia and anoxia (Fig. 1C; Pedersen & Surlyk 1983; Heilmann-Clausen *et al.* 1985). The fossil representatives of the otherwise scarce benthic fauna (see Pedersen *et al.* 2012) also correlates with the structureless or weakly laminated beds suggesting a fluctuating oxygen level. Sediments of the Fur Formation were deposited below storm wave base in the North Sea Basin, and possibly in a locally nutrient-rich area, where massive diatom blooms occurred periodically (Bonde 1979; Pedersen & Surlyk 1983). Another indicator of recurring anoxic
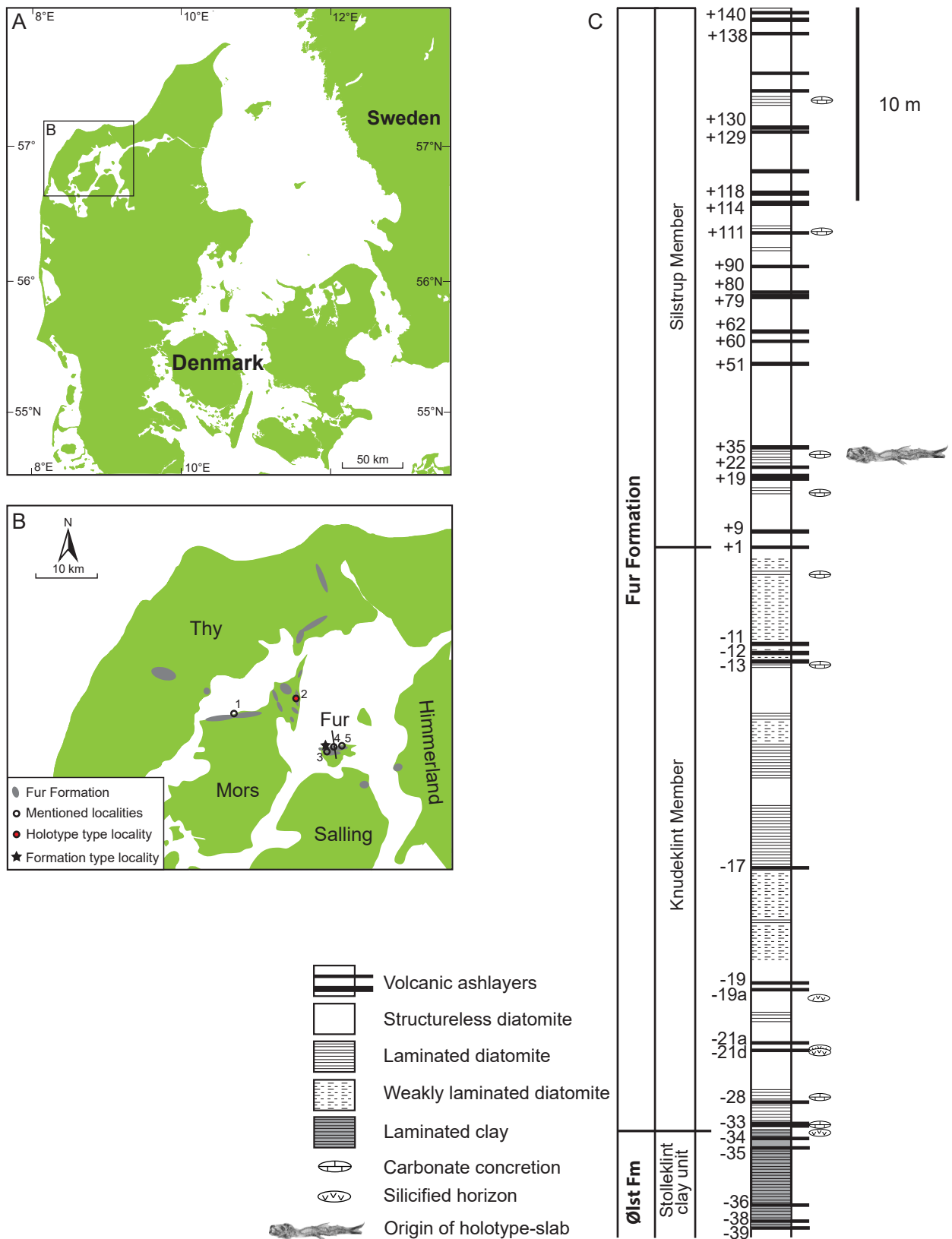
Fig. 1. A: map of the western Limfjord region in Denmark. **B**: outcrop localities and near surface occurrences of the Fur Formation. Circles mark locations of selected outcrops and old digging pits where specimens of the present study were collected (see Table 1). Ejerslev mo-clay pit is the type locality of the slab containing the holotype and five paratypes. The Fur Formation type locality is indicated by a star. **C**: sedimentological log of the Fur Formation and uppermost part of the Ølst Formation. The slab containing the holotype was collected from carbonate concreted horizons from a stratigraphic level between +25 to +30. Modified from Schrøder *et al*. (2022; submitted).

conditions is evident from several of the magnificent preserved acanthomorph fossils. For instance, many of the specimens of the recently described *Polyspinatus fluere* exhibit clear evidence of muscular contractions usually brought on by respiratory stress caused by anoxia (Elder & Smith 1988; Ferber & Wells 1995), including tetany of the jaws, and erect and fan-spread fins (see Schrøder *et al*. 2022, figs 2 and 4).

Material and methods

Despite the remarkable number of available material, we focused this study on 20 very well-preserved specimens, collected from the Silstrup and Knudeklint members of the earliest Eocene Fur Formation. The material comprises specimens originating from the carbonate concretions, soft diatomite and silicified diatomite.

The carbonate concreted slab containing the holotype, five paratypes and a referred specimen (designated herein, MM-13564) was collected by Henrik Madsen (Museum Mors), and mechanically and acid-prepared with Paraloid B72 by conservator Franck Osbæk (Fur Museum). The slab is reposited in the collection of Fossil- and Mo-clay Museum, Museum Mors. The specimens in this study were examined by applying the *µ*XRF method following Schrøder *et al*. submitted (see also Schrøder *et al*. 2022) using bench-top *µ*XRF devices for element-mapping of strontium, phosphorous and calcium in order to expose intricate anatomical details, commonly not readily available directly from the fossils. *µ*XRF analyses were supplemented by conventional stereomicroscopy, applying a Leica MS5 and a Leica M80. We used a Bruker M4 Tornado Plus Amics (Department of Geosciences and Natural Resource Management, Copenhagen University), with maximum acceleration voltage of 50 kV and a current of 600 *µ*A for the slab containing the type material (plus a referred specimen), whereas the prototype model, Bruker M4 Tornado (Quadlab, Natural History Museum of Denmark, Copenhagen University), was used for the remaining specimens, using an anode current of 230 *µ*A (see Schrøder *et al*. submitted).

Counts and measurements follow Hubbs & Lagler (1958). Due to the delicate nature of the fossil bones of the investigated specimens, measurements were obtained with ImageJ (Rasband 2018) in order to not damage the specimens.

Anatomical abbreviations: aa, anguloarticular; ach, anterior ceratohyal; ant, antorbital; ba, basipterygium; br, branchiostegal rays; crc, cranial condyle; dn, dentary; ds, dermosphenotic; ect, ectopterygoid; endt, endopterygoid; ep, epural; fepa, foramen for the efferent pseudobranchial artery; fr, frontal; hh, hypohyal; hspu, haemal spine of preural vertebra; hyo, hyomandibula; hyp, hypural; io, infraorbitals; iop, interopercle; la, lachrymal; lpmx, left premaxilla; me, mesethmoid; mtp, metapterygoid; mx, maxilla; na, nasal; op, opercle; pa, palatine; pac, palatine condyle; par, parietal; pas, parasphenoid; pch, posterior ceratohyal; pfr, pelvic-fin radials; phy, parhypural; pmx, premaxilla; pop, preopercle; ptm, posttemporal; pto, pterotic; pu, preural centrum; qu, quadrate; ra, retroarticular; rmx, right maxilla; rpmx, right premaxilla; rsmx, right supramaxilla; smx, supramaxilla; snl, supraneural laminae of pu1 and u; so, supraorbital; sop, subopercle; sph, sphenotic; sym, symplectic; u, ural centrum; uh, urohyal; un, uroneural; vo, vomer.

Morphometric abbreviations: AFB, anal-fin base; CPD, caudal peduncle depth; CPL, caudal peduncle length; DFB, dorsal-fin base; HD, head depth; HL, head length; MBD, maximum body depth; ML, mandible length; MXL, maxillary length; OD, orbit diameter (measured horizontally); PAD, preanal distance; PDD, predorsal distance; PMXL, premaxillary length; POD, preorbital distance; PoOD, postorbital distance; PPD, prepectoral distance; PPeD, prepelvic distance; SL, standard length.

Institutional abbreviations: FUM-N, Fur Museum (a division of Museum Salling), Denmark; MM, Fossil- and Mo-clay Museum (a division of Museum Mors) Denmark; NHMD, Natural History Museum of Denmark (department within Copenhagen University).

Systematic palaeontology

Order Argentiniformes Bertelsen, 1958

Genus *Surlykus* gen nov.

Type species. Surlykus longigracilis gen et sp. nov.

Etymology. Named in honour of professor emeritus Finn Surlyk, a remarkable mentor to the first author, in recognition of his exceptional contributions across geological disciplines, counting palaeontology, sedimentology and stratigraphy.

Stratigraphic and geographic range. Ypresian (earliest Eocene), Ølst and Fur formations, north-western Denmark (Fig. 1).

Diagnosis. An argentiniform genus unique in having the following combination of morphological characters: Head length contained less than four times in SL; cranial fontanelle present; parietals meeting on the midline; vomer toothless; basipterygoid process absent, basisphenoid absent; circumorbital series with supraorbital, antorbital and six infraorbitals; mouth terminal and large; jaws edentulous; premaxilla with ascending and articular processes and low postmaxillary process; maxilla oblanceolate in outline; a single supramaxilla present; six branchiostegal rays; ecto- and endopterygoids long and toothless; palatine toothless; basihyal toothless; 53–56 (30–32+23–24) vertebrae; three series of intermuscular bones; epineurals from the first through to the 29th vertebra; epicentrals and epipleurals from the fifth through the 23rd vertebrae; ribs from the second to the ultimate abdominal vertebrae; short parapophyses on the two or three posteriormost abdominal centra; neural spines of the majority of abdominal vertebrae not fused medially; caudal skeleton with six autogenous hypurals, autogenous parhypural, two epurals, three uroneurals, and a single urodermal; first preural centrum usually separated from the first ural centrum; second ural centrum free; caudal fin with 19 (10+9) principal rays plus 10–11+9–10 procurrent rays; supraneurals tubular and rod-like; dorsal fin with 12–14 rays; anal fin with 14–15 rays; pectoral fin with 18–20 rays; pelvic fin with nine or ten rays; body covered by small, deciduous cycloid scales.

Surlykus longigracilis sp. nov.

Figs 2–8; Table 1, Table 2, Table 3

Holotype. MM-13564_5, *Surlykus longigracilis* gen. et sp. nov. Nearly complete, well-preserved articulated, acid-prepared specimen on a single slab of carbonate concretion, bordered by five designated paratypes (MM-13564, no 1, 2, 3, 4, and 6). 47.6 mm SL (Fig. 2)

Etymology. The name is derived from the Latin words 'longus' (long) and 'gracilis' (slender) referring to the body shape of the species.

Type locality of holotype. Fur Formation, lowermost Eocene. Collected from Ejerslev mo-clay pit, on the island of Mors, north-western Limfjord area, Denmark. The holotype originates from a stratigraphic level between ash series +25 to +30, Silstrup Member (Fig. 1; Table 1).

Paratypes. Five paratypes are associated with the holotype into a single slab of carbonate concretion, MM-13564, which also contain a single referred specimen (MM-13564_7; Fig. 2): MM-13564_1, the largest nearly complete, well-preserved articulated specimen on the slab, 83.7 mm SL (Fig. 2A, 1); MM-13564_2; well-preserved, almost complete specimen, 64.4 mm SL (Fig. 2A, 2); MM-13564_3, well-preserved, nearly complete specimen, however, most of the squamation and neural spines in the precaudal region are not

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

Catalog number	Formation	Member	Lithology	Ash-series	Locality
MM-13564_1 Paratype	Fur	Silstrup	Carbonate concretion	+25 to +30	Ejerslev mo-clay pit, Mors
MM-13564_2 Paratype	Fur	Silstrup	Carbonate concretion	+25 to +30	Ejerslev mo-clay pit, Mors
MM-13564_3 Paratype	Fur	Silstrup	Carbonate concretion	+25 to +30	Ejerslev mo-clay pit, Mors
MM-13564_4 Paratype	Fur	Silstrup	Carbonate concretion	+25 to +30	Ejerslev mo-clay pit, Mors
MM-13564_5 Holotype	Fur	Silstrup	Carbonate concretion	+25 to +30	Ejerslev mo-clay pit, Mors
MM-13564_6 Paratype	Fur	Silstrup	Carbonate concretion	+25 to +30	Ejerslev mo-clay pit, Mors
MM-13564_7	Fur	Silstrup	Carbonate concretion	+25 to +30	Ejerslev mo-clay pit, Mors
FUM-N-10506 Paratype	Fur	N/A	Carbonate concretion	N/A	Ejerslev mo-clay pit, Mors
NHMD-159386	Fur	N/A	Carbonate concretion	N/A	Svaleklit, Mors
NHMD-159980	Fur	N/A	Carbonate concretion	N/A	Ejerslev mo-clay pit, Mors
NHMD-161741	Fur	N/A	Carbonate concretion	N/A	Stolleklint, Fur
NHMD-161747	Fur	N/A	Silicified diatomite	N/A	Fur
NHMD-161773	Fur	N/A	Carbonate concretion	N/A	Mors or Fur
NHMD-864870	Fur	Knudeklint	Carbonate concretion	Negative series	Ejerslev mo-clay pit, Mors
NHMD-865572	Fur	Knudeklint	Silicified diatomite	Around -21?	Fur
MM-9671	Fur	N/A	Carbonate concretion	N/A	Unknown, probably Mors
MM-9684	Fur	N/A	Carbonate concretion	N/A	Unknown, probably Mors
FUM-N-16146	Fur	N/A	Soft diatomite	N/A	N/A
FUM-N-16977	Fur	N/A	Soft diatomite	N/A	Elkegraven mo-clay pit, Fur
FUM-N-13458	Fur	N/A	Carbonate concretion	N/A	Østklinten, Fur

preserved, 54.9 mm SL (Fig. 2A, 3); MM-13564_4, well-preserved, nearly complete specimen, 66.0 mm SL (Fig. 2A, 4); MM-13564_6, well-preserved, nearly complete specimen, however, most of the squamation in the abdominal region is not preserved, 54.3 mm SL (Fig. 2A, 6); FUM-N-10506, well-preserved head skeleton, showing exquisitely preserved details of the lateral-line canal, plus pectoral girdle and anteriormost part of vertebral column (Fig. 3).

Referred material. The additional 13 articulated specimens and relevant collection information are listed together with the type-series in Table 1.

Diagnosis. As for the genus

Description. Measurements and counts are shown in Table 2 and Table 3, respectively. The body is elongate and slender, tapering slightly posteriorly. The maximum body depth measured at the dorsal-fin insertion is about 12% of SL. The head is moderately elongate and subrectangular in outline, its length is contained less than four times in SL. The snout is contained about 3.5 times in the head length. The mouth is terminal; its gape extends almost in front of the anterior border of the orbit. The orbit is rounded and relatively large; its diameter is nearly 30 % of the head length. The caudal peduncle is relatively short and deep; its length is contained about 10 times in SL, while its depth is about 9 % of SL. The dorsal fin inserts approximately at the half of SL. The anal-fin origin is located in the
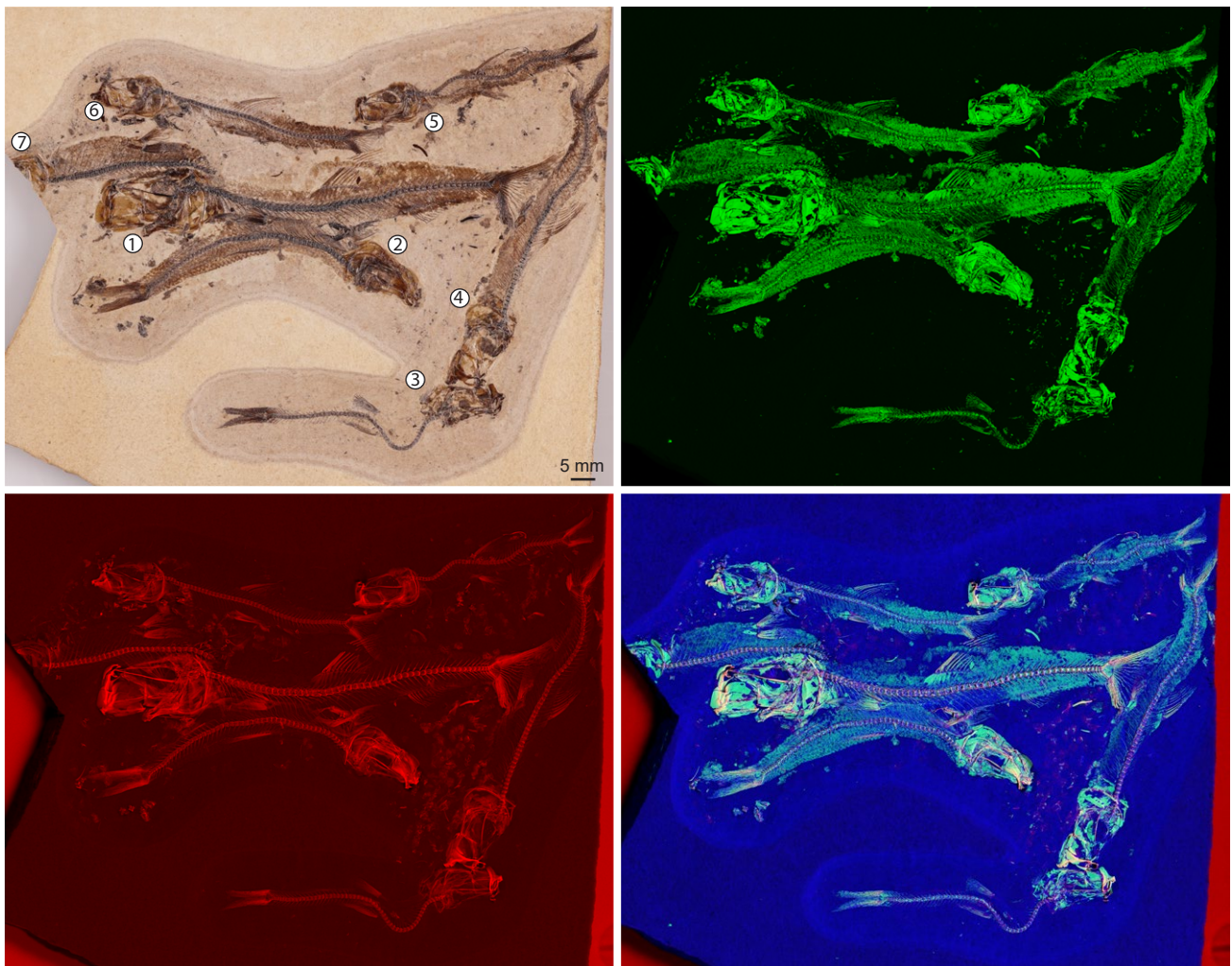

Fig. 2. *Surlykus longigracilis* gen. et sp. nov., holotype and five paratypes, contained in a single slab of carbonate concretion collected from Ejerslev mo-clay pit, ash layer +25 to +30. **A**: photo image, 1, the largest paratype, MM-13564_1; 2, paratype MM-13564_2; 3, paratype MM-13564_3; 4, paratype MM-13564_4; 5, the holotype MM-13564_5; 6, paratype MM-13564_6; 7, referred specimen MM-13564_7. **B**: phosphorous element image. **C**: strontium element map. **D**: combined element map of phosphorous, strontium and calcium. Scale bar equals 5 mm.

posterior fourth of the body. The pectoral fin inserts ventrolaterally along the flanks; the prepectoral distance is contained slightly more than three times in SL. The pelvic-fin origin is located just behind the insertion of the dorsal fin. The caudal fin is deeply forked.

Table 2. Measurements of *Surlykus longigracilis* gen. et sp. nov. as % of SL

Morphometric characters	Range % of SL	Mean % of SL
HL	24.6–29.4	27.0
HD	13.7–18.9	16.4
MBD	10.9–14.0	12.3
DFB	7.6–12.9	10.4
AFB	9.5–13.7	11.7
CPL	9.5–12.9	11.0
CPD	7.2–9.7	8.5
PPD	25.6–31.8	28.8
PDD	50.2–57.4	53.7
PPeD	51.3–58.0	55.5
PAD	74.5–80.7	76.1
POD	8.3–13.6	11.1
PoOD	8.4–10.6	9.7
OD	5.9–8.9	7.7
PMXL	4.5–7.3	5.8
MXL	9.5–11.9	11.9
ML	9.3–12.6	10.6

Several specimens exhibit a dark organic matter in the abdominal cavity, which possibly represents the peritonerum or, alternatively, part of the digestive tract.

Neurocranium. The neurocranium is almost triangular in lateral view, longer than high. The frontals are the largest bones of the skull roof; they are triangular in outline, sharply tapering anteriorly. An elongate fontanelle can be observed medially between the two contralateral frontals. The outer surface of the frontals

Table 3. Counts for *Surlykus longigracilis* gen. et sp. nov.

| Meristic characters	Counts
Branchiostegal rays	6
Vertebrae (precaudal+caudal)	53–56 (30–32+23–24)
Hypurals	6
Epurals	2
Uroneurals	3
Caudal fin, principal rays	19 (10+9)
Caudal procurrent rays (dorsal+ventral)	10–11+9–10
Supraneurals	8–10
Dorsal-fin rays	12–14
Dorsal-fin pterygiophores	11–13
Anal-fin rays	14–15
Anal-fin pterygiophores	13–14
Postcleithra	3
Pectoral-fin rays	18–20
Pelvic-fin rays	9–10
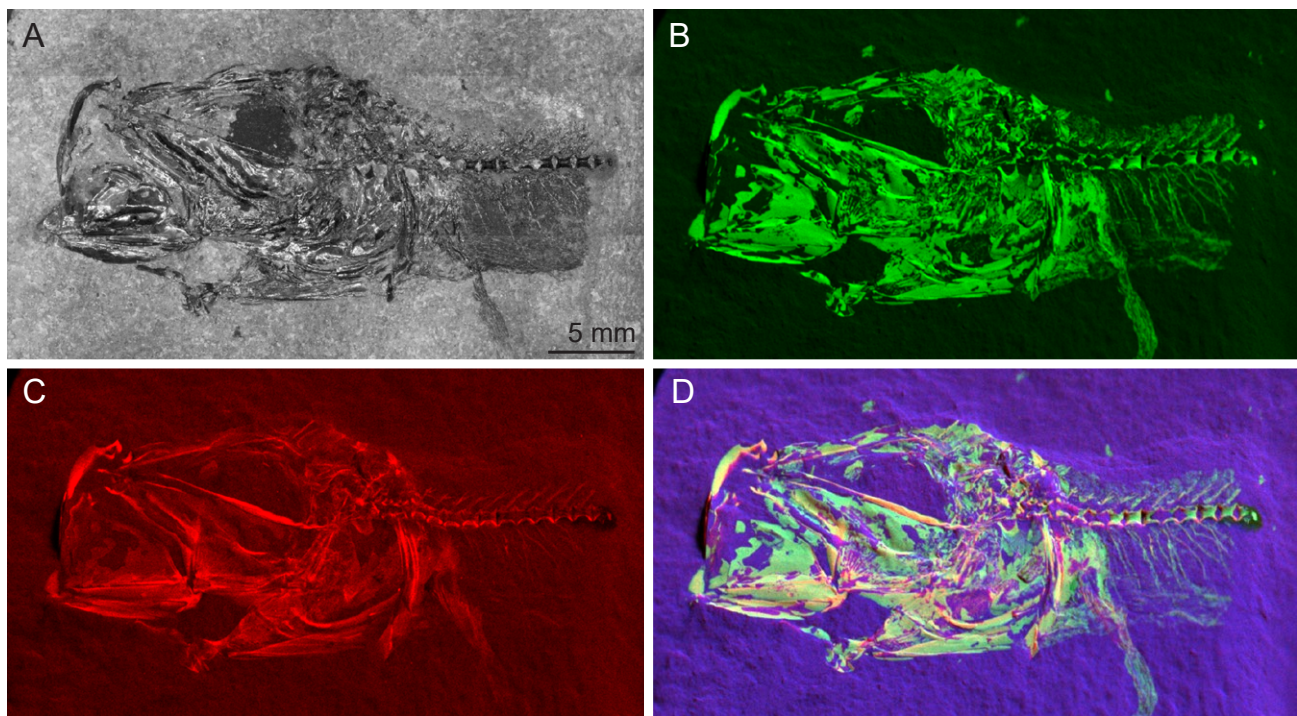
Fig. 3. *Surlykus longigracilis* gen. et sp. nov., paratype FUM-N-10506, collected from Ejerslev mo-clay pit. **A**: mosaic image. **B**: phosphorous element map. **C**: strontium element map. **D**: combined element map of phosphorous, strontium and calcium. Scale bar equals 5 mm.
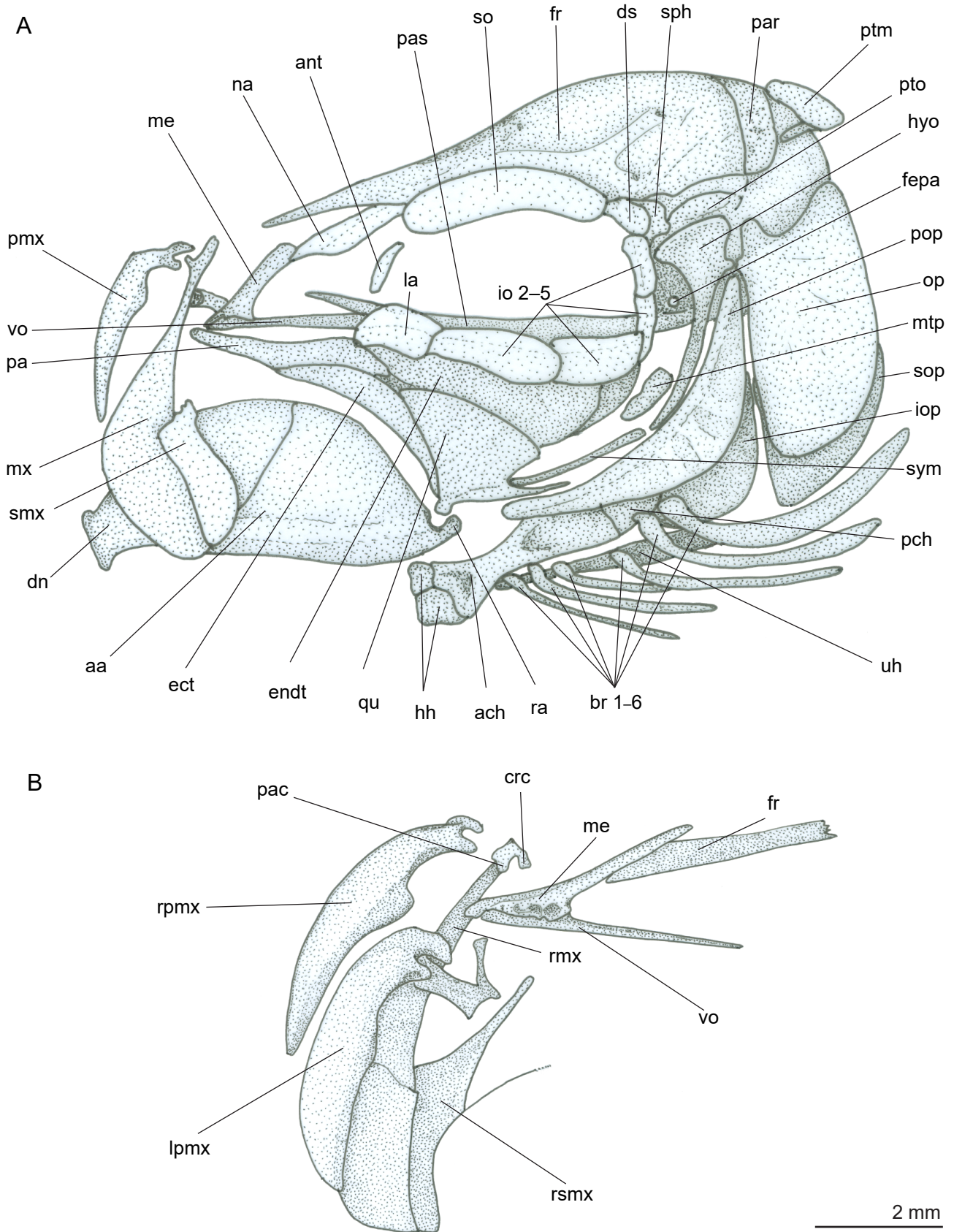
Fig. 4. *Surlykus longigracilis* gen. et sp. nov. **A**: interpretive reconstruction of the head of the holotype, MM-13564_5 (see Fig. 2A, 5). **B**: upper jaws and ethmoid region of the neurocranium, based on paratype MM-13564_1 (Fig. 2A, 1). Scale bar equals 2 mm.

is feeble ornamented and also bears the ridges of the tubes that contain the lateral-line canals. The supraorbital lateral-line canal is tubular and well-developed and bifurcates posteriorly, showing a well-developed and posteromedially directed epiphyseal branch. The nasal is a tubular trough-like bone that carries the supraorbital lateral-line canal. The outline of the parietals is difficult to define. The two contralateral parietals seem to contact each other medially. There is a small supraoccipital showing a very short and low posterior median crest. The mesethmoid is strongly ossified, not showing a separate rostral portion. The lateral ethmoids are laminar and usually not exposed hidden below the large supraorbital. The vomer has a long posterior shaft that extends below the anterior portion of the parasphenoid. There is no evidence of the vomerine teeth. The parasphenoid is slender; in the posteroventral corner of the orbit it is expanded dorsally and shows a large circular foramen for the efferent pseudobranchial artery. There is no basipterygoid process. The sphenotic is usually covered by the dermosphenotic. The pterotic is relatively large and carries a short and tubular otic lateral-line canal. The articular facet for the hyomandibular is large and almost ventrally directed. The morphology of the prootic, intercalar, exoccipital, basioccipital and epioccipital is difficult to determine due to inadequate preservation of this part of the neurocranium. The pterosphenoids are partially exposed in the posterodorsal corner of the orbit. It is not possible to clearly recognise the morphology of the orbitosphenoid.

Circumorbital bones. The circumorbital series consist of a large supraorbital, a small tubular and poorly ossified antorbital, and six infraorbitals, including the dermosphenotic. The supraorbital is a large and ovoid bone that partly covers the lateral supraorbital flange of the frontal. The lachrymal is thin and scarcely ossified. The infraorbital two and three are laminar, ovoid and expanded dorsally. The fourth and fifth infraorbitals are short and tubular. The dermosphenotic is roughly triangular in outline. It covers most of the lateral fossa. The infraorbital lateral-line canal can be traced in the infraorbitals two to five and in the dermosphenotic. In the dermosphenotic there is a posterior branch that is connected to the otic canal of the pterotic (especially evident paratype FUM-N-10506, Fig. 3).

Jaws. The upper jaws consist of premaxilla, maxilla, and a single supramaxilla. The premaxilla is curved and toothless; its upper border is thickened and terminates anteriorly into short and stout ascending and articular processes. There is a low postmaxillary process, which is separated from the articular process by a shallow concave depression approximately extending for one third of the premaxillary length. The maxilla is large oblanceolate and toothless, extending posteriorly up to the mid-length of the orbit. The anterior head of the maxilla is bifurcated, with an anterior cranial condyle, which possibly articulated with the mesethmoid in origin, and a thickened palatine condyle, which likely articulated with the head of the palatine (Figs 2, 4). There is a single supramaxilla, corresponding to the posterior one of other teleosts; it is ovoid in outline bearing a long and slender anterior process, obliquely emerging from its anterodorsal corner of its. The lower jaw is very large with the dentary occupying the vast majority of it. The dentary has a straight and moderately deep symphysis followed by a toothless and gently concave oral boarder that rises sharply into a very deep coronoid process. The anguloarticular is quadrangular in outline and bears a robust articular facet for the quadrate condyle. The retroarticular is very small and can be recognised in several specimens in the posteroventral corner of the mandibular. The mandibular lateral-line canal passes through the anguloarticular entering the dentary anteriorly.

Suspensorium. The hyomandibula has a slender vertical shaft bearing a very short opercular process; the articular head has an almost straight dorsal border. The symplectic is long and rod-like. The quadrate is inclined forward, with its posteroventral border being almost horizontal; the outer surface is characterised by low and delicate undulations, radiating from the articular condyle. The quadrate condyle is located just in front of the anterior border of the orbit. The metapterygoid is strongly reduced in size. Ecto- and endopterygoids are thin and long, evidently toothless. The palatine is almost straight, thick and toothless

Opercular series. The preopercle is crescent-shaped with the horizontal limb being slightly longer than the vertical one. The vertical limb ends dorsally just below the pterotic. The preopercular lateral-line canal passes in a closed tube, located close to the anterior border of the bone. The opercle has an almost straight anterior border, gently curved posterior border, and an anteriorly concave upper border. The interopercle and subopercle are usually thin, laminar and oblong.

Hyoid apparatus and branchial skeleton. The anterior ceratohyal is rather thick and constricted in the middle. The posterior ceratohyal seems to be subtriangular in outline. There are six branchiostegal rays of which four articulates along the ventral margin of the anterior ceratohyal and two, saber-like, articulate with the posterior ceratohyal. The third and fourth branchiostegal rays appear to be separated by a large diastema. The hypohyals are compact and closely associated with each other. The urohyal is long and triangular in outline. The basihyal plate is partly preserved in some specimens (e.g., FUM-N-10506, Fig. 3) and appears to be toothless.

The gill arches can be partially observed in the holotype and certain paratypes (e.g., MM-13564_1, MM-13564_4; Fig. 2C). Long and slender ceratobranchials and epibranchials bearing closely spaced gill rakers can be easily recognised in several specimens.

Vertebral column and intermuscular bones. The vertebral column comprises 53–56 (30–32+23–24) vertebrae, including the two usually free ural centra. The abdominal region represents about 57 % of the entire vertebral column. The centra are subrectangular, slightly longer than high. Their lateral surface is ornamented with longitudinal ridges alternated with irregular fossae. Short parapophyses emerge lateroventrally close to the posteroventral corner of the two or three posteriormost abdominal centra. The neural spines of the majority of the abdominal vertebrae are not fused medially. The two contralateral neural spines became fused medially in the posterior three to six abdominal vertebrae, and in all the vertebrae of the caudal region where they are stiffened and obliquely oriented. The haemal spines are similar in length and morphology to their opposite neural spines. The accessory neural arch is absent in all the examined specimens.

The complement of ossified intermuscular bones consists of slender epineurals, epicentrals and epipleurals. The epineurals seem to be associated with the abdominal vertebrae with medially unfused neural spines, where they originate dorsolaterally close to the anterior border of the centra. The epicentrals and epipleurals can be observed from the fifth through the 23rd vertebrae. The epicentrals insert centrally on the flanks of the centra, whereas the epipleurals insert slightly below the epicentrals. Ribs occur from the second to the ultimate abdominal vertebrae. The ribs extend ventrally to the ventral border of the abdominal cavity.

Caudal skeleton and fin. The caudal skeleton consists of an autogenous parhypural, six autogenous hypurals, two epurals, and three uroneurals. Usually, the first ural and first preural centra are separated from each other (Fig. 5), although in some cases they appear almost fused (paratype MM-13564_1, Fig. 6). The first uroneural lacks a membranous anterodorsal outgrowth. A small urodermal seems to be present. Distinct laminar plates (supraneural laminae *sensu* Greenwood and Rosen, 1971) emerges dorsally from the rudimentary neural arches of both the first preural and the first ural centra. The neural spine of the second preural vertebra is fully developed in most specimens. In the paratype MM-13564_1 the neural spine of the second preural centrum is shortened, not fully developed (Fig. 6). The haemal spines of the second and third preural vertebrae are autogenous. The caudal fin contains 19 (10+9) principal rays plus 10–11+9–10 procurrent rays.

Median fins and supports. The dorsal fin is preceded by a series of thin, rod-like, tubular supraneurals, whose number is difficult to determine. Eight supraneurals could be recognised in paratype MM-13564_1 (Fig. 2A, 1). In the same paratype (MM-13564_1, Fig. 2A, 1), the first supraneural seems to occur just above the anterior border of the eighth vertebra.

The dorsal fin originates above the 21st or 22nd abdominal vertebrae, occupying a length of about seven vertebrae. The dorsal fin contains 12–14 rays; all but the first, are distally branched. The third ray is the longest. The length of the rays gradually decreases backward from the third. The dorsal fin rays are supported by 11–13 pterygiophores. The first dorsal-fin pterygiophore is large and almost triangular in outline being characterised by two thickened ridges. All the pterygiophores, except the first one, have a separate medial element. A few distal pterygiophores can be observed between the hemitrichs in some specimens, including the largest paratype (MM-13564_1, Fig. 2A, 4).

The anal fin originates just below the third or fourth caudal vertebrae, occupying a length of approximately eight vertebrae. It contains 14–15 rays supported by 13–14 pterygiophores. All the anal-fin rays, but the first two, are distally branched. The fourth ray is the longest. Separate medial pterygiophores are recognisable in all the elements, except for the first one.

Paired fins and girdles. A single T-shaped extrascapula can be observed in paratype MM-13564_6 (Fig. 2A, 6), where it appears to be associated to the pterotic. The posttemporal has a large ovoid and laminar dorsal limb, and a short and slender ventral (internal) limb. The supracleithrum is oblong. The cleithrum is crescent-shaped. There are three postcleithra of which the second is the largest. In some specimens it is possible to recognise the coracoid, a short mesocoracoid and the scapula (e.g., MM-13564_4, Fig. 2A, 4). There are four hourglass-shaped pectoral-fin radials, the ventralmost being the largest. The pectoral fin contains 18–20 rays.

The pelvic fin originates below the 22nd or 23rd vertebrae and contains nine or, rarely, ten rays, of which the external one is the shorter. Three small quadrangular pelvic-fin radials can be observed along the posterior margin of the basipterygia in the paratype MM-13564_4 (Fig. 2A, 4; Fig. 5B). The basipterygia are subrectangular, robust and reinforced by an outer thickened ridge. The basipterygium bears a short, medial pelvic process, which appears to articulate with its antimere.

Squamation. The body is covered by thin, deciduous scales, arranged into eight to ten transverse series in the trunk. The scales are relatively small and cycloid, with continuous and well separated circuli. The lateral-line scales are difficult to recognise in the examined material. There is no trace of an adipose fin.
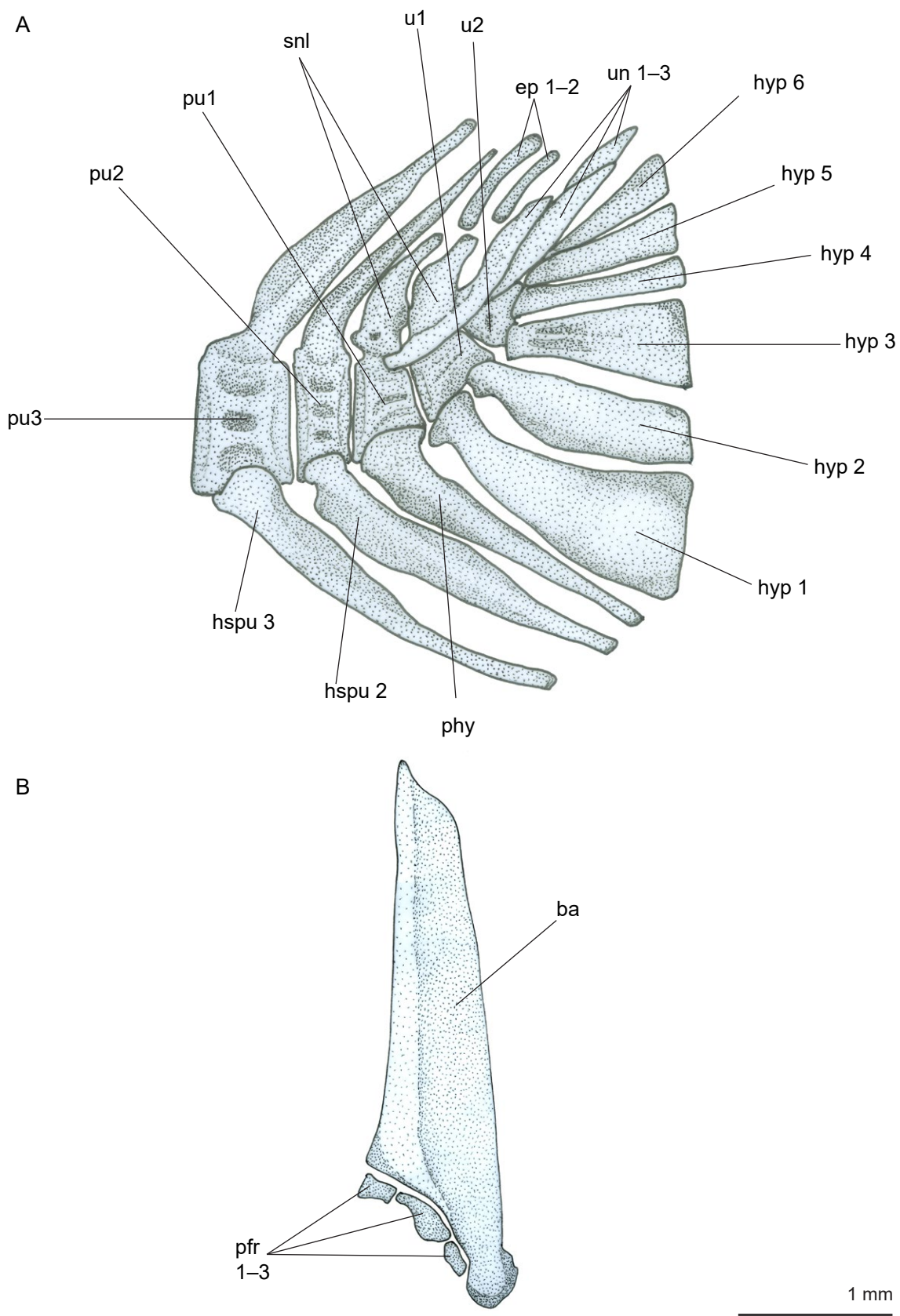
Fig. 5. *Surlykus longigracilis* gen. et sp. nov. **A**: reconstruction of the caudal skeleton in left lateral view of the holotype, MM-13564_5 (see Fig. 2A, 5). **B**: reconstruction of the right basipterygium with the associated pelvic-fin radials in ventral view, based on paratype MM-13564_4 (see Fig. 2A, 4). Scale bar equals 1 mm.
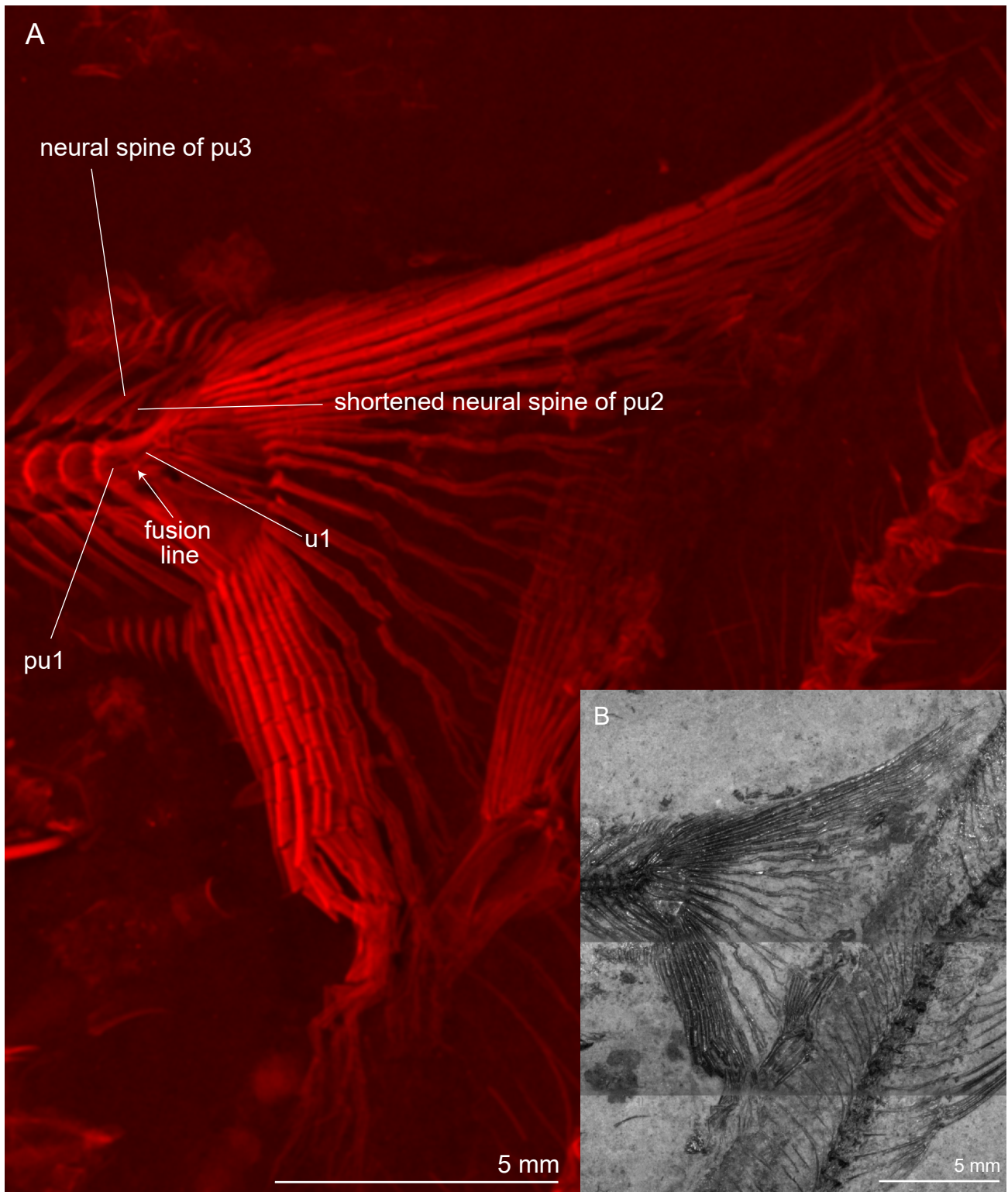
Fig. 6. *Surlykus longigracilis* gen. et sp. nov. Unusual caudal skeleton of the largest paratype (MM-13564_1), where pu1 and u1 are almost completely fused, and the neural spine of pu2 is shortened, not fully developed (compare with the other types in Fig. 2 and Fig. 5A). **A**: enlarged strontium element map; the neural spine of pu3 and the shortened neural spine of pu2 are indicated with labels, the arrow points to the weak fusion line of pu1 and u1. **B**: mosaic image of the fossil. Scale bar equals 5 mm.

Comparative discussion

The phylogenetic relationships of argentiniform fishes have been largely discussed in the past decades. Following the classification proposed by Gosline (1960), these fishes were included within the protacanthopterygian order Salmoniformes by Greenwood *et al.* (1966). A few years later, Greenwood & Rosen (1971) hypothesised a sister-group relationship between argentiniforms and alepocephaloids primarily based on the shared possession of the so-called crumenal organ, a posterior branchial structure that differs from the epibranchial organ for the presence of an accessory cartilage possibly resulted from the segmentation of the posterior articular surface of the fifth ceratobranchial (see also Nelson 1967). The relevance of this feature in supporting the close relationships between these two lineages was also emphasised by Begle (1992), who recognised five additional potential synapomorphies (reduction in endopterygoid teeth, loss of nuptial tubercles, loss of uncinate process on the fourth epibranchial, and loss of maxillary

and basihyal teeth), none of which was regarded by Johnson & Patterson (1996) as valid to potentially characterise a group formed by argentiniforms and alepocephaloids. On the other hand, Johnson & Patterson (1996) offered two additional characters in order to characterise this pair, the ventral displacement of the distal parts of the first two to four epineurals (see also Patterson & Johnson 1995) and the caudal median cartilages supporting the lowermost ray of the upper caudal lobe (see also Wiley & Johnson 2010). Arratia (2018) evidenced the controversial nature of these features, especially of the accessory cartilage that connects the fifth ceratobranchial to the fifth epibranchial, which represents the novel element of the crumenal organ, whose occurrence has been reported by De Pinna & Di Dario (2010) also in the African freshwater clupeomorph *Denticeps clupeoides*. Ontogenetic (Ahlstrom *et al.* 1984) and molecular (e.g., Ishiguro *et al.* 2003; Lavoué *et al.* 2008; Near *et al.* 2012; Betancur-R *et al.* 2017) evidences do not support a relationship with the alepocephaloids, and the argentiniforms are currently regarded as protacanthopterygians, pos-
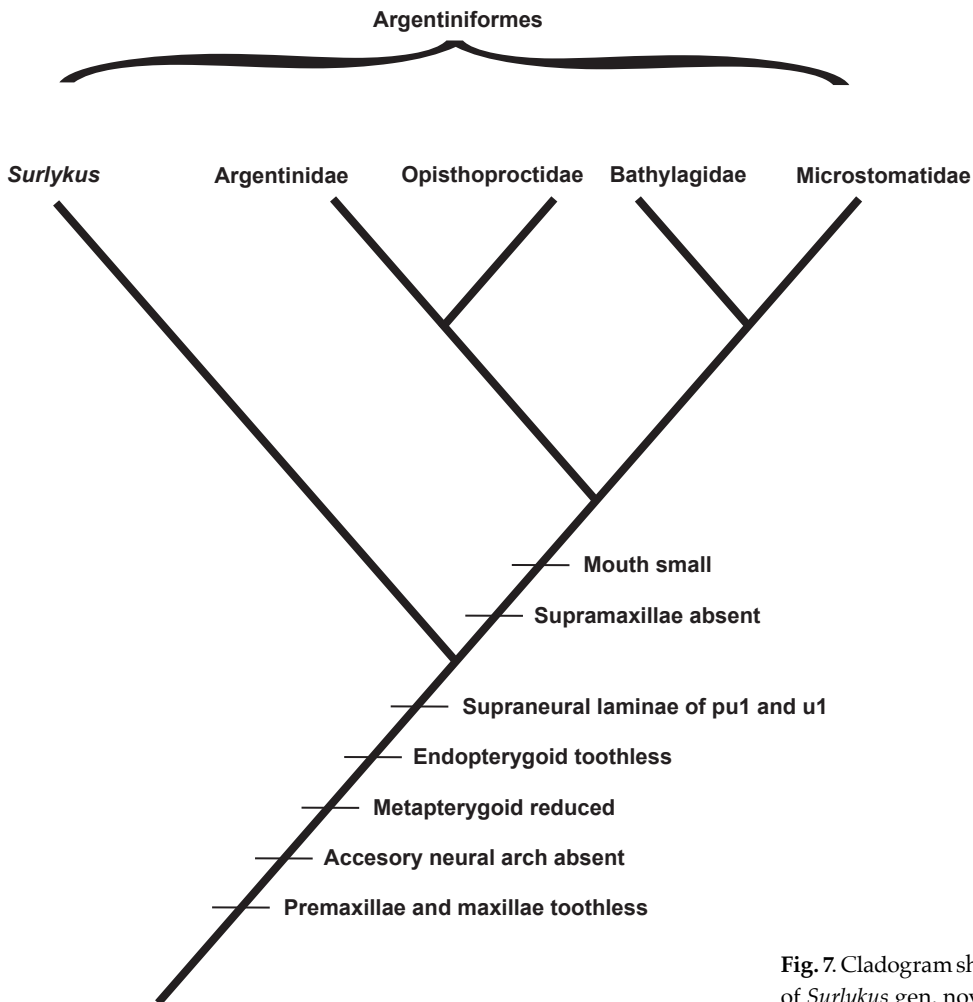

Fig. 7. Cladogram showing hypothetical relationships of *Surlykus* gen. nov. within the Argentiniformes.

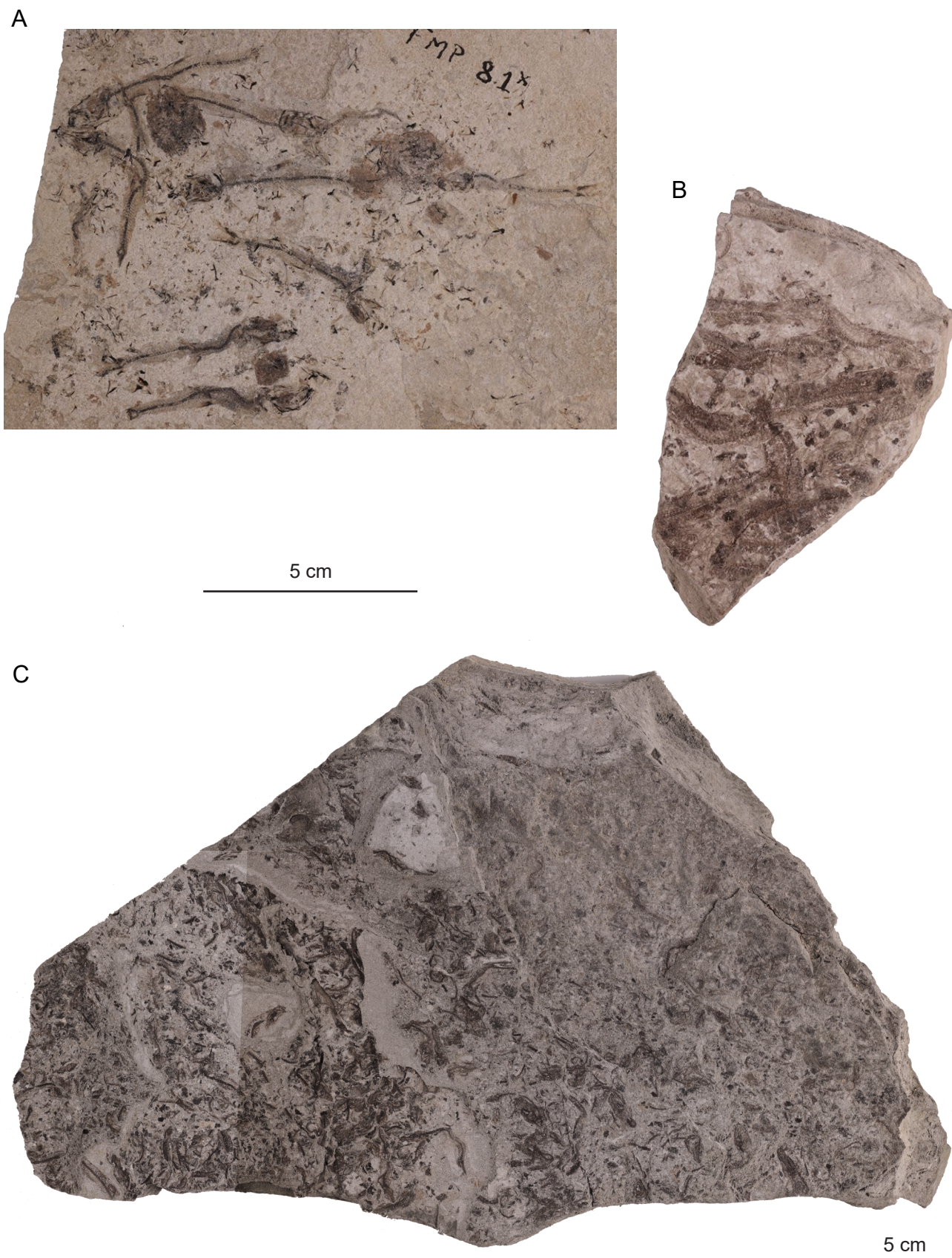*Surlykus longigracilis* gen. et sp. nov., the most abundant fish from the Fur Fm · 13

Fig. 8. Mass-mortalities of *Surlykus longigracilis* gen. et sp. nov. preserved in bedding planes. **A**: FUM-N-14093, specimens preserved in carbonate concretion. **B**: NHMD-865604, specimens preserved in soft diatomite. **C**: NHMD-191265, specimens preserved in slightly hardened diatomite. The image in C is a composite, formed by three individual photographs stitched together digitally. Both scale bars equal 5 cm; the upper applies to A and B, and the lower applies to C.

sibly representing the sister group to a pair formed by salmoniforms and esociforms (Straube *et al.* 2018).

The interrelationships between the four argentiniform families, Argentinidae, Bathylagidae, Microstomatidae and Opisthoproctidae, have been hypothesised based on morphology and molecules (e.g., Johnson & Patterson 1996; Straube *et al.* 2018).

According to Ishiguro *et al.* (2003) argentinids form a clade together with the opisthoproctids that is the sister group to a clade containing bathylagids and microstomatids (see also Poulsen *et al.* 2016).

A list of synapomorphies diagnosing the argentiniforms was provided by Johnson & Patterson (1996) and reiterated by Wiley & Johnson (2010). This includes endopterygoid teeth absent, metapterygoid reduced, premaxillae and maxillae toothless, supramaxillae absent, basibranchials 1–3 toothless, second and third pharyngobranchials toothless, accessory neural arch absent, and first uroneural without membranous anterodorsal outgrowth. In addition, as emphasised by Greenwood & Rosen (Greenwood & Rosen 1971), argentiniforms also exhibit a small and terminal mouth and bony plates (=supraneural laminae) associated with neural arches of the first ural and first preural centra (see also Patterson 1970; Kobyliansky 1990).

The anatomical analysis of *Surlykus longigracilis* gen. et sp. nov. has revealed a set of features that clearly supports its attribution within the Argentiniformes. While the absence of teeth in the branchial skeleton elements cannot be determined due to inadequate preservation, *Surlykus longigracilis* gen. et sp. nov. clearly shows toothless premaxillae and maxillae, reduced metapterygoid, toothless endopterygoid, accessory neural arch absent, first uroneural devoid of a membranous anterodorsal outgrowth, and possession of supraneural laminae associated with the neural arches of the first preural and first ural centra. *Surlykus longigracilis* gen. et sp. nov., however, is also characterised by the presence of primitive features, including a large mouth and a single supramaxilla, which may indicate a basal position within the Argentiniformes. Such a placement is also corroborated by the structure of the caudal skeleton, which shows separated first preural and first ural centra (Fig. 5), a condition unique within the Argentiniformes (see Greenwood & Rosen 1971). Overall, all of these primitive features may suggest that *Surlykus* gen. nov. should be regarded as the sister-group to all the other members of this group ([Argentinidae + Opisthoproctidae] + [Bathylagidae + Microstomatidae]), thereby representing a stem-group argentiniform (Fig. 7).

Palaeoecological remarks

As discussed above, *Surlykus longigracilis* gen. et sp. nov. is the most abundant fish species throughout the Fur formation. It is also known from the Stolleklint clay unit of the underlying Ølst Formation, and from Norwegian North Sea drillings (Bonde 1982), thereby suggesting that its distribution was not restricted to a local area of the North Sea Basin. The abundance of this argentiniform species in the lower Palaeogene sediments of the North Sea may suggest that it occupied the ecological role typical of clupeids in the almost coeval fish assemblages of Tethyan realm (see Marramà & Carnevale 2015*a*, *b*, 2018; Marramà *et al.* 2016; Friedman & Carnevale 2018). In this context, considering that skeletal remains of *Surlykus longigracilis* gen. et sp. nov. are commonly found as stomach contents of predatory fish species, it is reasonable to hypothesise that this abundant species represented the trophic nucleus of the fish communities (Carnevale *et al.* 2022) of the North Sea during the earliest Eocene.

Surlykus longigracilis gen. et sp. nov. was characterised by a schooling behavior, evident from bedding planes of both carbonate concretions and soft diatomite, documenting events of collective mortality (Fig. 8). It may be speculated that these mass-mortalities may have been caused by the emergence of anoxic events. However, death caused by a rapid onset of anoxia should be evidenced by extreme muscular contractions, i.e., tetany of the jaws, deep arching of the body, and fanned and erected fins (e.g., Carnevale *et al.* 2022), which have not been consistently observed in the examined material (Figs 2, 8) (see also Elder & Smith 1988; Ferber & Wells 1995). The specimens in the mass mortality slabs show different degrees of body distortion and jaw tetany, with some not distorted at all, a few exhibiting deeply arched bodies, and many of them exhibit closed mouths. Hence, possible chocking resulting from consistent ingestion of toxic metabolites produced by algal blooms or heavy ash fall related to the volcanic activity seems to be a much more likely cause of these collective mortalities.

Acknowledgements

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