

A new beardfish (Teleostei, Polymixiiformes) from the Eocene Fur Formation,
Denmark

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ANE ELISE SCHRØDER–JAN AUDUN RASMUSSEN–PETER RASK MØLLER– GIORGIO
CARNEVALE–*POLYSPINATUS FLUERE*, A NEW BEARDFISH FROM THE FUR
FORMATION

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A B S T R A C T—The earliest Eocene (Ypresian) Fur Formation (Denmark) is globally renowned for its exceptionally well-preserved fossils, including birds, sea turtles, insects, plants, and fishes. Fishes, albeit abundant and diverse, however, are only superficially known and very few detailed, taxonomic studies have been realized to date. A new polymixiiform fish, *Polyspinatus fluere* gen. et sp. nov., from the Fur Formation is described based on seven well-preserved, nearly complete specimens. All the specimens were studied by traditional stereomicroscopy, and by micro-X-ray fluorescence-element mapping. Digital 2D-element images of strontium-, phosphorous- and calcium distributions of each specimen were directly applied for the taxonomic descriptions presented herein. *Polyspinatus fluere* gen. et sp. nov. is the first known Eocene record of the family Polymixiidae based on articulated skeletal remains. *Polyspinatus* gen. nov. exhibits a unique combination of characters that support its recognition as a new genus of the Polymixiidae. Its specialized hyoid apparatus with the first and second branchiostegal rays being sinuous and parallel to each other, and the third being wide and plate-like, followed by four saber-like elements, is strikingly similar to that of *Polymixia* supporting a possible sister-group relationship with extant beardfishes.

INTRODUCTION

Polymixiiform fishes appeared during the Cenomanian, Late Cretaceous (around 94 Mya) and comprise several Cretaceous and Paleogene families, namely the Boreiohydriidae, Dalmatichthyidae, Digoriidae, Dinopterygidae, Polymixiidae, and Pycnosteroididae (Patterson, 1964, 1968; Rosen and Patterson, 1969; Murray and Wilson, 2014; Murray, 2016). One of these families, the Polymixiidae, dates back to the Cretaceous and is today represented by a single genus, the beardfish *Polymixia*. Seven fossil genera have been referred to the Polymixiidae, including

Apricenaichthys, *Berycopsis*, *Berycopsia*, *Homonotichthys*, *Omosoma*, *Omosomopsis*, and *Pycnosterinx* (see Patterson, 1964, 1993; Radovčić, 1975; Gaudant, 1978; Patterson and Rosen, 1989; Taverne, 2011; Murray, 2016).

The family Polymixiidae was formerly aligned with the Beryciformes (Patterson, 1964; Zehren, 1979; Kotlyar, 1984, 1993), but is currently placed within its own order, the Polymixiiformes (e.g., Wiley and Johnson, 2010). The phylogenetic relationships of polymixiiforms has been extensively debated during the past decades (Johnson and Patterson, 1993; Near et al., 2012, 2013; Borden et al., 2013, 2019; Grande et al., 2013; Chen et al., 2014; Betancur-R et al., 2017). *Polymixia* has long been considered pivotal to resolve the interrelationships of the acanthomorph (spiny-rayed fishes) radiation, often referred to as the ‘bush of the top’ of the phylogenetic tree of the Teleostei (Nelson, 1989; Betancur-R. et al., 2013, 2017). Spiny-rayed fishes constitute approximately one third of all living vertebrate species (Helfman et al., 2009; Nelson et al., 2016). Near et al. (2013) provided the first comprehensive, time-calibrated phylogeny to resolve the acanthomorph relationships, which placed *Polymixia* and Percopsiformes as two separate clades at the base of Paracanthopterygii; this study also suggested that acanthomorphs originated in the Early Cretaceous. Subsequent morphological and molecular-based phylogenies resulted in similar placements of *Polymixia* at or near the base of Paracanthopterygii (Paracanthopterygii sensu Miya et al., 2005; Grande et al., 2013; Ghezelayagh et al., 2022), e.g., polymixiids plus paracanthopterygians as sister to the acanthopterygians (Grande et al., 2013), *Polymixia* as a paracanthopterygian being sister to all the other members of the group (Chen et al., 2014), or as sister to the Paracanthopterygii (Betancur-R et al., 2017). The most recent molecular studies support the placement of *Polymixia* within the Paracanthopterygii as sister-group to the Percopsiformes, Gadiformes, Stylephoriformes, and Zeiformes (Hughes et al., 2018; Borden et al., 2019).

The species of the genus *Polymixia* are characterised by a prominent pair of fleshy hyoid barbels protruding from their lower jaws and giving them their common name ‘beardfishes’. The barbels act as a sensory organ and individuals have been observed swimming with the barbels in continuous contact with the substrate (Ono, 1982; Moore, 2002). *Polymixia* comprises 11 species, exhibiting a wide geographic distribution in subtropical to tropical oceans, inhabiting environments ranging from the vicinity of islands over the outer continental shelf and slope, in the Atlantic, Pacific, and Indian Oceans (Kotlyar, 1984, 1986, 1991, 1993, 2002; Borden et al., 2019; Grande and Wilson, 2021; Fricke et al., 2022). Representatives of the genus predominantly occupy the rariphotic and apophotic zones, with depths ranging from 150 to 800 m (Kotlyar, 1986, 1993; Borden et al., 2019; Grande and Wilson, 2021); however, there are records of specimens, e.g. individuals of the recently described *Polymixia hollisterae*, caught from the mesophotic zone between ~40 and 129 m (Grande and Wilson, 2021). *Polymixia* species are demersal and feed on a variety of benthic invertebrates, small fishes, and occasionally octopuses and squids (e.g. Kotlyar, 1986, 1993; Moore, 2002; García-Mederos et al., 2010).

The Eocene Fur Formation in northwestern Jutland, Denmark, contains a variety of exceptionally well-preserved fully articulated fossil fish skeletons. In terms of both abundance and variety, bony fishes are one of the most well-represented groups of macrofossils known from the Fur Formation, and thousands of well-preserved specimens are housed in museum’s collections across Denmark. Despite the many well-preserved fossils, only a few detailed, taxonomic studies of the Fur Formation fish fauna exist, including two older descriptive analyses focused on the peculiar lampridiform *Palaeocentrotus boeggildi* (Kühne, 1941) and the putative syngnathiform *Rhamphosus rosenkrantzi* (Nielsen, 1960), plus a single more recent paper on the interesting, but rather uncommon osteoglossomorphs (Bonde, 2008). None of these addresses the Fur Formation's most common fishes considering that estimates suggest that the sediments of the Fur Formation

may contain as much as 60 species of bony fishes (see Bonde, 1997, 2008; Pedersen et al., 2012). Bonde (1997) mentioned and figured a fossil fish, not deposited in a recognized institution, which he referred to as ‘Polymixiid’, but without any substantiation. He further noted that the fossil represented the third most common species of the Fur Fm fish fauna; however, additional analyses to confirm whether this is in fact the case, based on current museum material housed in Denmark, are needed.

The aim of the present study is to describe a new genus and species of polymixiiform fish, *Polyspinatus fluere* gen. et sp. nov., belonging to the family Polymixiidae, based on fossil material collected from the earliest Eocene (Ypresian) Fur Formation of northern Denmark.

GEOLOGICAL SETTING

The Eocene Fur Formation is well exposed in the western Limfjord region of northern Jutland, Denmark. The outcrop area covers a large region with several localities, particularly on the two islands of Mors and Fur. Smaller outcrop localities and near surface occurrences are found in the western part of Himmerland, Salling, and Thy (Fig. 1). The formation comprises a fossil-rich marine diatomite with an approximate thickness of 60 meters (Pedersen and Surlyk, 1983; Pedersen and Buchardt, 1996). The Fur Formation is divided into two distinct members, the lower Knudeklint Member and upper Silstrup Member, respectively. The Knudeklint Member is principally laminated with relatively few ash layers, whereas the Silstrup Member is dominated by structureless beds with numerous ash layers (Pedersen and Surlyk, 1983; Heilmann-Clausen et al., 1985). The marine diatomite sediments are interbedded with a well-preserved series of more than 180 numbered ash layers originating from volcanic eruptions during the opening of the Northeast Atlantic (Bøggild, 1918; Andersen, 1937; Pedersen and Surlyk, 1983; Danielsen and Thomsen, 1997; Storey et al.,

2007). However, as more ash layers are continuously identified and officially numbered, the sediments may contain well more than 200 distinct ash layers (Andersen, 1937; Pedersen et al., 2012). The age of the Fur Formation is based on radiometric dating of ash layers -17 and +19, yielding $^{39}\text{Ar}/^{40}\text{Ar}$ age determinations of ~55.6 Ma and ~54.4 Ma, respectively (Chambers et al., 2003; Storey et al., 2007; Westerhold et al., 2009; Stokke et al., 2020). The sediments of the Fur Formation were deposited in the North Sea Basin below the storm wave base under conditions of alternating anoxia and slight dysoxia (Pedersen and Surlyk, 1983). These conditions are reflected in the sedimentary sequences; certain sequences are finely laminated without any traces of bioturbation or microturbation, whereas others are weakly laminated or structureless (Pedersen and Surlyk, 1983; Pedersen and Buchardt, 1996; Pedersen et al., 2012). The benthic fauna is scarce and represented by approximately 24 species of crustaceans, bivalves, echinoderms, gastropods and polychaetes (see Pedersen et al., 2012 for an overview). The lack of a diverse, shell-bearing benthic fauna throughout the entire formation may indicate an overall low level of oxygen in the benthic zone. The majority of the bottom-dwelling invertebrate fossils derives from the structureless or weakly laminated sections, suggesting conditions with intermittently higher oxygen levels (Pedersen and Buchardt, 1996). Sediments of the Fur Formation were presumably deposited in a region of local nutrient-rich upwelling, leading to periodically, massive diatom blooms (Bonde, 1979; Pedersen and Surlyk, 1983). The accumulation and subsequent decay of the bloom-related organisms possibly resulted in reoccurring anoxic bottom conditions and absence of benthos (Pedersen and Surlyk, 1983; Pedersen et al., 2012). The clayey diatomite sediment consists of approximately 10% volcanic ash, 30–45% clay minerals and 45–65% diatoms (Pedersen et al., 2004). Calcareous carbonate concretions, the so-called ‘cementsten’, occur within certain stratigraphic levels of the formation. These concretions were formed in the sea-floor sediment, by precipitation of calcite into the pore space before sediment compaction. The carbonate of the

concretions is in most cases of bacterial origin (based on $\delta^{13}\text{C}$ -values) (see Pedersen and Buchardt, 1996; Pedersen et al., 2004). Where concretions sometimes formed wholly or partially around dead organisms, the bones and shells were fossilized as calcite-phosphate (containing also a significant input of strontium), and are sometimes three-dimensionally preserved (e.g., Pedersen and Surlyk, 1983; Pedersen and Buchardt, 1996; Pedersen et al., 2004; Schröder et al., in press). Prior to the formal designation of the Fur Formation, the marine diatomite strata were known under the old Danish name 'Moler' (English: Moclays). 'Moejord', 'Moeleer', 'Moler' or 'Mo-ler' are old terms that simply suggest that the clayey sediment is fine-grained with a lighter colour (see Abildgaard, 1776; Pedersen and Surlyk, 1983; Pedersen et al., 2012). There are no official spelling rules concerning the English translation of the word 'Moler', and several forms are used in the literature, e.g. Mo clay, Mo-clay, Moclays. Museum Mors uses the spelling mo-clay and the same spelling is therefore applied throughout in this paper.

MATERIAL AND METHODS

The present study is based on seven nearly complete, well-preserved specimens, collected from carbonate concretions, NHMD-869392 (Fig. 2), MM-264, MM-340, MM-341, MM-10738, FUM-N-10321, FUM-N-15290 (Fig. 3). Five specimens (Figs. 2, 3A, B, C, D) were collected from the Ejerslev mo-clay pit at a stratigraphic level between ash series +25 to +30, Silstrup Member, Fur Formation, Denmark (Fig. 1, Table 1). The specimen FUM-N-10321 (Fig. 3E) was also collected from the Ejerslev mo-clay pit, but the stratigraphic horizon is unknown. The locality and stratigraphic level of FUM-N-15290 (Fig. 3F) are unknown. The specimens are housed within the collections of Natural History Museum of Denmark (Copenhagen, Denmark), Fossil and Mo-clay Museum (Mors, Denmark) and Fur Museum (Fur, Denmark).

The holotype (designated herein, NHMD-869392) and paratypic specimens from Museum Mors were collected, and acid prepared with Synocryl®, by Henrik Madsen (Museum Mors). Paratypes from Fur Museum are not acid prepared; however, a protecting layer of Paraloid B72 covers FUM-N-10321. Specimens were studied using the μ XRF method, demonstrated by Schrøder et al. (in press), using a Bruker M4 Tornado (a bench-top μ XRF instrument), and traditional studies using stereomicroscopy (Leica MS5 and Leica M80). The holotype specimen NHMD-869392 was declared Danekræ fossil trove in December 2020 (trove no. DK-1141, 30.11.2020, Danekræ Fossil Trove achieves, Natural History Museum of Denmark, Copenhagen) (Schrøder, 2020). Danekræ fossil trove are objects of fossil or subfossil nature, rare minerals or meteorites found in Denmark of unique scientific or exhibitional value. Danekræ fossil trove is covered by the fossil trove legislation and thereby belongs to the Danish state (Christensen and Hald, 1990).

Counts and measurements follow Hubbs and Lagler (1958). Measurements were obtained with a digital calliper to the nearest 0.1 mm.

Institutional Abbreviations—**FUM-N**, Fur Museum, Museum Salling, Denmark; **MM**, Fossil and Mo-clay Museum, Museum Mors, Denmark; **NHMD**, Natural History Museum of Denmark, Copenhagen University. [Fossil- og Molermuseet is a division of Museum Mors and Fur Museum is a division of Museum Salling].

Morphometrics—**AFB**, anal-fin base; **AFSL1**, 1st anal-fin spine length; **AFSL2**, 2nd anal-fin spine length; **CPD**, caudal peduncle depth; **CPL**, caudal peduncle length; **DFB**, dorsal-fin base; **DFSL1**, 1st dorsal-fin spine length; **DFSL2**, 2nd dorsal-fin spine length; **HD**, head depth; **HL**, head length; **MBD**, maximum body depth; **MAFR**, length of the longest anal-fin ray (second anal-fin ray in the holotype, and first one in some paratypes); **MAFS**, length of the longest anal-fin spine (the eighth spine in all specimens); **MDFR**, length of the longest dorsal-fin ray (second ray in the holotype NHMD-869392 and paratype FUM-N-10321, and the first ray in the remaining paratypes);

MDFR, length of the longest dorsal-fin spine (the ultimate spine in all specimens); **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; **SMXL**, 2nd supramaxilla length;

Anatomical—**aa**, anguloarticular; **ah**, autogenous haemal spine; **ach**, anterior ceratohyal; **ant**, antorbital; **as**, autosphenotic; **br**, branchiostegal rays; **bs**, basisphenoid; **cc**, compound centrum; **clt**, cleithrum; **co**, coracoid; **dn**, dentary; **ds**, dermosphenotic; **ect**, ectopterygoid; **enpt**, entopterygoid; **ep**, epural; **ex**, extrascapula; **fr**, frontal; **hh**, hypohyal; **hspu**, haemal spine of preural; **hyo**, hyomandibula; **hyp**, hypural; **io**, infraorbitals; **iop**, interopercle; **la**, lachrymal; **le**, lateral ethmoid; **me**, mesethmoid; **mtp**, metapterygoid; **mx**, maxilla; **na**, nasal; **ob**, orbitosphenoid; **op**, opercle; **pas**, parasphenoid; **pcl**, postcleithrum; **per**, pectoral-fin radials; **phy**, parhypural; **pmx**, premaxilla; **pp**, preopercle; **ptm**, posttemporal; **pto**, pterotic; **pts**, pterosphenoid; **qu**, quadrate; **ra**, retroarticular; **sc**, scapula; **scl**, supracleithrum; **smx**, supramaxilla; **soc**, supraoccipital; **sop**, subopercle; **sym**, symplectic; **u**, ural centrum; **uh**, urohyal; **un**, uroneural.

SYSTEMATIC PALEONTOLOGY

Order POLYMIXIIFORMES Rosen and Patterson, 1969

Family POLYMIXIIDAE Bleeker, 1859

Genus *POLYSPINATUS* gen. nov.

Type species—Holotype, *Polyspinatus fluere* gen. et sp. nov. (NHMD-869392). Nearly complete, well-preserved articulated, acid-prepared specimen on a single plate. SL equals 118.5 mm (Fig. 2, 4, and previously figured on p. 48 of Madsen and Rasmussen, 2021).

Etymology—The name is derived from the Latin words ‘poly’ (many) and ‘spina’ (spine) referring to the remarkably high number of dorsal- (11–12) and anal-fin (eight–nine) spines.

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

Diagnosis—*Polyspinatus* gen. nov., a genus of the Polymixiidae unique in having the following combination of morphological characters: head length less than one third of SL; lachrymal rather large, with a rounded and finely crenulated ventral profile, and five prominent pores of the infraorbital lateral-line canal; subocular shelf present on infraorbitals 2–4; jaws with small conical teeth arranged in multiple rows; three anteriormost branchiostegal rays modified, possibly forming the sinuous bases of fleshy hyoid barbels; three dorsally expanded supraneurals (predorsal formula 0+0/0/2/1+1/ or 0+0/0//2+1/ or 0+0/0//2+1+1/); 44–46 (15–16 + 28–30) vertebrae; ossified epineurals from the third through to the 20th vertebra; epipleurals from vertebrae 12th to 23th; caudal skeleton with six autogenous hypurals, autogenous parhypural, hypurapophysis absent, three epurals, and three autogenous haemal spines on the second to fourth preural vertebrae; caudal fin deeply forked comprising 18 principal caudal-fin rays plus nine to ten epaxial and hypaxial procurrent rays; dorsal fin long-based with 11–12 spines and 27–28 soft rays; anal fin with eight to nine spines and 23–26 soft rays; pectoral fin with 17 rays, the two uppermost articulating with the scapula; seven pelvic-fin rays; scales spinoid, covering the entire body including the bases of the dorsal, anal, and caudal fins.

Remarks—The possession of fleshy hyoid barbels is considered as a remarkable distinctive feature of the extant polymixiiforms. In the extant beardfish genus *Polymixia*, the proximal ends of the hyoid barbels are supported by three modified anterior branchiostegals (Starks, 1904; Ono, 1982). Due to this osteological modification of the hyoid apparatus, this feature can be traced also on fossil material. The close morphological similarity between the modified anterior

branchiostegals of *Polyspinatus* and those of *Polymixia*, makes it reasonable to hypothesize that they supported the proximal ends of fleshy hyoid barbels in origin.

POLYSPINATUS FLUERE sp. nov.

(Figs. 2–4; Table 1; Table 2; Table 3)

Holotype—*Polyspinatus fluere* gen. et sp. nov. (Figs. 2, 4)

Etymology—Named after the μ XRF-element mapping method (micro-X-ray fluorescence), successfully applied for the first time as a useful and valuable tool for the taxonomic descriptions presented herein. *Fluere* ‘to flow’ is the Latin root of fluorescence, referring to the secondary x-rays generated during μ XRF-element mapping, enabling the construction of digital 2D-element images applied in here.

Type locality of holotype—Fur Formation, lowermost Eocene. Collected from Ejerslev mo-clay pit, on the island of Mors, northwestern Limfjord area, Denmark. The holotype originates from a stratigraphic level between ash series +25 to +30, Silstrup Member (Figs. 1–2, 4; Tables 1–3).

Paratypes—MM-264, well-preserved articulated specimen on a single plate, lacking the caudal fin; MM-340, well-preserved articulated specimen, on a single plate, the most posterior part of body and caudal fin and are missing; MM-341, well-preserved articulated specimen on a single plate, but a larger part of the caudal fin is missing, SL equals 85.4 mm; MM-10738, nearly complete, well-preserved articulated specimen on a single plate, however the anteroventral part of head is missing; FUM-N-10321, nearly complete, well-preserved articulated specimen on plate and counterplate (mostly imprints are preserved on the counterplate), SL equals 92.3; FUM-N-15290, nearly complete, well-preserved articulated specimen on a single plate, SL equals 88.8 (Fig. 3; Tables 1–3).

Diagnosis—As for the genus

Description

Measurements and meristic features are shown in Tables 2 and 3. The body is deep, oblong, laterally compressed and tapering posteriorly. The maximum body depth measured at the anal-fin insertion is contained slightly more than two times in SL. The head is antero-posteriorly compressed, its depth is contained more than two times in SL, and its length is contained less than three times in SL. The snout is rather short and compressed, representing about 7% of SL. The orbit is almost rounded and relatively large; its diameter is approximately one third of the head length. The mouth is terminal, and its gape does not reach the level of the rear margin of the orbit. The upper jaw is approximately 10% of SL and the mandible is approximately 12% of SL. The caudal peduncle is compact and deep, with its length representing approximately 8% of SL, and its depth about 14% of SL. The caudal fin is deeply forked. The predorsal distance is about 31% of SL. The dorsal-fin base is greatly elongate, representing 64% of SL. The outer profile of the dorsal fin is gently curved with spines gradually increasing in size, followed by rays gradually decreasing in size posteriorly. The first (shortest), second, and eleventh or twelfth (longest) dorsal-fin spines represent approximately 2%, 4% and 16% of SL, respectively (MM-10738 and FUM-15290 only possess eleven dorsal-fin spines, with the eleventh being the longest one in those). The outer profile of the anal fin is straight in the spinous portions and feebly concave in the soft portion. The shortest (the first anal-fin spine in all specimens) and longest anal-fin spines (the eighth anal-fin spine in all specimens) constitute 2% and 16% of SL, respectively. The anal fin is long-based; its length represents about 37% of SL. The preanal distance is approximately 49% of SL. The pectoral fin inserts in the lower half of the body, and the prepectoral distance represents 34% of SL. The prepelvic distance is almost 35% of SL.

Neurocranium—The neurocranium is deep and bears a very high and thick median supraoccipital crest, which extends forward up to the anterior margin of the orbit. The otic and most of the occipital regions of the neurocranium are not exposed in the available material, hidden by the bones of the suspensorium and opercular apparatus. The bones of the skull roof are almost unornamented. The frontals are moderately large and articulate anteriorly with mesethmoid and lateral ethmoids. Each frontal articulates posteriorly with the parietal, supraoccipital, sphenotic and pterotic. The morphology of the outer surface of this bone is rather complex and characterized by well-developed tubular supraorbital lateral-line canal, which shows at least three main lateral pores. The supraorbital lamina is moderately developed and shows a finely crenulated outer margin. There is a median frontal ridge emerging abruptly from the supratemporal fossa, which is continuous with the supraoccipital crest. The anastomosis between the supraorbital and infraorbital lateral-line canals occurs on the frontal, with the supraorbital one passing posteriorly on the pterotic, and the infraorbital one passing through the sphenotic. The outline of the parietal is difficult to define. Due to the anterior extension of the supraoccipital crest, the two contralateral parietals do not contact each other along the midline. The supraoccipital crest is almost triangular in outline showing a gently convex dorsal margin, which provides the dorsal profile of the head. A thickened lateral ridge that almost reaches the dorsal corner of the supraoccipital crest is also present. The mesethmoid is poorly exposed in the investigated material and shows a rounded anterior margin. The lateral ethmoid is columnar and forms the anterior margin of the orbit. The orbitosphenoid emerges mediodorsally in the interorbital region and shows an irregular outline. The pterosphenoid is not exposed in the examined specimens. The basisphenoid is thin and rodlike and does not contact the parasphenoid. The parasphenoid is long and prominent, and extends throughout most of the basicranial length. The autosphenotic is barely recognizable, being partially covered by the

dermosphenotic and the anterior articular head of the hyomandibula. The pterotic is large, nearly quadrangular in outline, bearing a thick lateral ridge.

Circumorbital bones—The nasal is partial recognizable in the holotype (Fig. 2, 4) and the paratype MM-340 (Fig. 3B). The antorbital is a small tubular and delicate bone, which was connected to the anterior portion of the lachrymal in origin. Six infraorbital bones surround the lower and posterior margins of the orbit. The lachrymal is rather large, with a rounded and finely crenulated ventral profile; at least five prominent pores of the infraorbital lateral-line canal can be easily recognized. The third, fourth and fifth infraorbitals bear a laminar flange characterized by a crenulated profile that emerges ventrally to the infraorbital lateral-line canal. A reduced subocular shelf appears to be present only on the second, third and fourth infraorbitals. The dermosphenotic is irregular; its outer portion is posteroventrally reflected due to its connection to the bones of the infraorbital series.

Jaws—The premaxilla has a moderately elongate ascending process, whose length represents less than one fourth of that of the alveolar process. The ascending and articular processes are only marginally separated from each other by a short furrow. The alveolar process is laterally curved and dorsoventrally flattened and terminates posteriorly in front of the posteroventral spine of the maxilla. There are numerous closely spaced tooth sockets arranged in multiple rows; the teeth are minute and conical, with slightly recurved tips. The maxilla is elongate and broadly expanded posteriorly; the posterior margin of the maxilla is distinctly rounded and terminates ventrally into a thick spine, which forms the posterior end of the mouth gape. There are two supramaxillae. The first supramaxilla is greatly reduced, whereas the second is subrectangular in outline, large and extending along the posterior half of the underlying maxilla.

The mandible is almost triangular in outline, and the dentary is deeply forked posteriorly to accommodate the pointed anterior process of the anguloarticular. The ventral margin of the dentary

is almost straight for most of its length becoming slightly concave posterior to the symphysis. The alveolar process is medially curved and bears numerous closely spaced tooth sockets arranged in multiple rows, like in the premaxilla. The dentary teeth are identical to those of the premaxilla. The anguloarticular is massive and bears a thick posterodorsally directed retroarticular process. The posterior edge of the anguloarticular is thickened and terminates dorsally into a small coronoid process. The retroarticular can be observed in the posterior-ventral corner of the mandible. The mandibular lateral-line canal is mostly enclosed, pierced by three or four openings.

Suspensorium—The suspensorium is slightly inclined forward. The hyomandibula is large and massive, and characterized by two dorsal articular heads. The main shaft of the hyomandibula tapers ventrally. The opercular process of the hyomandibular is short. The symplectic is rod-like and only partially recognizable. The quadrate is triangular in outline; its posterior-ventral border is particularly thickened, terminating ventrally into a massive condyle. The metapterygoid is large and laminar, almost quadrangular in outline. The endopterygoid is only partially recognizable, in large part covered by the bones of the infraorbital series; it is not possible to determine whether endopterygoid teeth were present or not in origin. The ectopterygoid is curved, with the horizontal and vertical limbs forming an angle of about 120 degrees. As for the endopterygoid, it is not possible to determine if ectopterygoid teeth were present in origin. The palatine is covered by the lachrymal for the most of its length. A thick and short maxillary process of the palatine can be recognized in the holotype (Fig. 2) and the paratype MM-341 (Fig. 3C).

Opercular series—The preopercle is robust. The elongate and tapering vertical limb is twice as long as the horizontal one. The anterior border of this bone is reflected, forming an emerging flange covering the preopercular lateral-line canal. The posterior and ventral margins of the preopercle are finely crenulated. Eight pores of the preopercular lateral-line canal, four on each limb, are recognizable in the holotype (Fig. 2) and the paratype MM-10738 (Fig. 3D).

The opercle is laminar, and its original outline is difficult to determine due to the usually inadequate preservation of its posterior margins. There is no evidence of ornamentations on the lateral surface of this bone. The interopercle is subtriangular in outline, with a rounded ventral margin. The subopercle has an almost triangular outline, being characterized by a rounded ventral profile and a slightly thickened anterior margin, extending dorsally into a pointed tip.

Hyoid apparatus and branchial skeleton—The hyoid bar is thick and robust. The hypohyals are small and irregular in outline, and only visible in the paratype MM-341 (Fig. 3C). A large and elongate beryciform foramen pierces the anterior ceratohyal. The posterior ceratohyal is triangular. There are seven branchiostegal rays, of which only the posterior one articulates with the posterior ceratohyal. The first three branchiostegal rays are short, resembling those of the extant beardfish *Polymixia* (see Ono, 1982). The first and second branchiostegal rays are sinuous and parallel to each other, while the third is wide and plate-like. Due to their close morphological similarity to those of *Polymixia*, it is reasonable to hypothesize that these modified branchiostegals supported the proximal end of fleshy hyoid barbels in origin. The branchiostegal rays four to seven are saber-like and increase in size posteriorly.

Numerous gill rakers can be observed in some specimens, especially in the paratype MM-341 (Fig. 3C).

Vertebral column and intermuscular bones—The vertebral column comprises 44–46 vertebrae, including the compound centrum and the autogenous second ural centrum; the abdominal region consist of 15 to 16 vertebrae, representing almost one third of the entire vertebral column. The vertebral centra are compact, subretangular, slightly higher than long. Their lateral surface is ornamented with deep fossae and pits separated by strong ridges and struts. The abdominal vertebrae exhibit short dorsal and ventral prezygapophyses, while the caudal vertebrae show a full complement of dorsal and ventral pre- and postzygapophyses. Parapophyses of gradually increasing

size occur from the sixth abdominal vertebra backward. The length of the parapophysis of the posteriormost abdominal vertebra is approximately the half of that of the first haemal spine. The neural spines are distally pointed and obliquely oriented in the abdominal region, becoming slightly curved for most of the caudal region. The haemal spines are almost specular to their corresponding neural spines. Both the neural and haemal spines originate from the anterior half of their vertebral centrum.

Ribs occur from the third to the last abdominal vertebra. The ribs extend ventrally up to the midpoint of the abdominal cavity, and articulate with the lateral side of the centra three to 11, and with the outer margin of the parapophyses posteriorly in the series. The epineurals are evident from the third through to the 20th vertebra. However, their occurrence on the two first vertebrae cannot be excluded. The epineurals articulate with the neural arches up to the 12th abdominal vertebra, inserting at the basal portion of the neural spines posteriorly. Ossified epipleurals articulate with the ribs of the vertebrae 12th to 16th, and with the haemal spines of the vertebrae 17th to 23th. There is no evidence of ossified epicentrals in the available specimens.

Caudal skeleton and fin—The structure of the caudal skeleton is difficult to define. However, it is possible to recognize a compound centrum (ostensibly formed by fused first preural and first ural centra) and what appears to be a separate second ural centrum. A fully developed spine on the second preural centrum is present. There are six autogenous and almost triangular hypurals, of which the first two articulate with the compound centrum. The epaxial hypurals articulate with the second ural centrum, except for the sixth one, which is only marginally recognizable in the paratype MM-341 (Fig. 3C). The autogenous parhypural is subrectangular and seems to lack the hypurapophysis. The haemal spines of the second, third and the fourth preural vertebrae are autogenous (Fig. 5). Three rod-like epurals are moderately preserved in the paratype MM-341 (Fig. 3C). The first uroneural is autogenous, articulating with the lateral side of the compound centrum,

and bears a small dorsal bony lamina characterized by an irregular dorsal margin. The second uroneural is elongate and rod-like. There are 18 principal caudal-fin rays, of which the inner 16 are distally branched (I,8+8,I). There is a moderate degree of hypurostegy, namely an anterior elongation of the bases of the outer principal caudal-fin rays that partially covers part of the hypurals, both epaxially and hypaxially. There are nine or ten dorsal and ventral procurrent rays.

Median fins and supports—There are three widely spaced and almost straight supraneurals. The predorsal formula is $0+0/0/2/1/$ or $0+0/0//2+1/$ or $0+0/0//2+1+1/$ (Table 3; see also Patterson, 1993). The supraneurals are expanded dorsally and apparently bifurcated distally in all investigated specimens; however, it is not possible to rule out that such a morphology is related to the original cartilaginous nature of their distal tips. There are 11 to 12 stout and pointed dorsal-fin spines often characterized by a lateral shallow longitudinal furrow, followed by 27–28 rays. Overall, the dorsal-fin spines and soft rays are supported by 37–38 pterygiophores (see Table S1 for meristic counts and Table S2 for dorsal-fin formulae). The dorsal-fin proximal pterygiophores are long, nearly straight, and deeply inserting in the interneural spaces, especially in the anterior portion of the fin. The first dorsal-fin pterygiophore inserts in the second interneural space and bears two supernumerary dorsal-fin spines. The pterygiophores decrease in size posteriorly in the series.

The anal fin comprises eight to nine stout and pointed spines often characterized by a lateral shallow longitudinal furrow, plus 24–26 rays. There are 29–31 anal-fin pterygiophores (see Table S1 for anal-fin formulae). The first anal-fin pterygiophore inserts in the first haemal space together with the second one, being much larger than the successive ones; its lower portion is considerably expanded anteriorly, forming a nearly triangular anterior blade-like process that results in a gently concave anterior border of the whole pterygiophore. There are three supernumerary spines on the first anal-fin pterygiophore.

Paired fins and girdles—The prominent posttemporal bone is bifurcated anteriorly. The extrascapula is partially recognizable in the holotype (Fig. 2, 4A–B). The supracleithrum is elongate and blade-like, with a thickened anterior margin. The cleithrum has a relatively short dorsal limb and a well-developed ventral limb. An almost triangular bony lamina occurs where the two limbs converge, just above the pectoral-fin insertion. The anterior margin of the cleithrum is partially reflected. There are two postcleithra, the dorsal one blade-like and the ventral one slender and distally pointed. The scapula is quadrangular, pierced by a large central, rounded foramen. The coracoid is thick and bears a short, blunt, posterior process. There are four hourglass-shaped pectoral-fin radials, of which only the ventral one articulates with the coracoid. The pectoral fin contains 17 moderately elongate rays. The two uppermost rays articulate directly with the lateral margin of the scapula, while the other pectoral-fin rays articulate with the pectoral-fin radials.

The pelvic-fin origin is located slightly posterior to that of the pectoral fin in the first half of the abdominal cavity. The pelvic fin consists of seven moderately elongate rays. The morphology of the basipterygia is difficult to determine. There are short lateral and posterior pelvic processes.

Squamation—Spinoid scales, characterized by triangular, delicate marginal and submarginal spines cover the whole body and most of the head, including the nape, supraoccipital crest, opercle, cheek and throat. The scales extend posteriorly onto the caudal-fin rays and along the dorsal- and anal-fin bases. At least 11 epaxial and 17 hypaxial, vertical scale rows can be recognized. The lateral-line scales are difficult to recognize.

DISCUSSION

Comparative discussion

The morphoanatomical analysis of the fossil material documented herein revealed a number of characters that support the attribution of this new taxon within the Acanthomorpha, including unsegmented, bilaterally fused dorsal and anal-fin spines [‘true spines’ in the sense of Johnson and Patterson, 1993], seven soft rays in the pelvic fin, and presence of the so-called haemaxanal complex, i.e. the first anal-fin pterygiophore is the most prominent in the series, inserting in the first interhaemal space (see Blot, 1969; Radovčić, 1975; Otero and Gayet, 1996). Within the acanthomorphs, the new taxon can be assigned to the Polymixiiformes, based on the possession of a high supraoccipital crest, skull roof without large tubular canals, fully developed neural spine on the second preural centrum, 18 principal caudal-fin rays (of which 16 are unbranched), and no spines in the pelvic fin (see Patterson, 1964, 1968; Murray and Cumbaa, 2013; Murray and Wilson, 2014; Murray, 2016). The order Polymixiiformes comprises several Cretaceous and Paleogene families, including the Boreiohydriidae, Dalmatichthyidae, Digoriidae, Dinopterygidae, Polymixiidae, and Pycnosteroididae. The Boreiohydriidae, Dalmatichthyidae, Dinopterygidae and Digoriidae are all monotypic (see Patterson, 1964, 1968; Radovčić, 1975; Bannikov and Daniltshenko, 1985; Patterson and Rosen, 1989; Murray and Cumbaa, 2013; Murray and Wilson, 2014; Murray, 2016), while the Pycnosteroididae comprises two species arranged in two genera (Patterson, 1964; Murray and Wilson, 2014).

Polyspinatus differs from the Boreiohydriidae in several aspects. The Turonian genus *Boreiohydrias* from Lac de Bois, Canada, shows a fusiform body shape with maximum body depth reaching about 35% of SL, presence of an edentate maxilla, eight non-modified branchiostegal rays, seven spines and 23 soft rays in the dorsal fin, four spines and 20 rays in the anal fin, and 14 rays in the pectoral fin (Murray and Cumbaa, 2013).

As far as the Dalmatichthyidae is concerned, the genus *Dalmatichthys* from the Cretaceous of Croatia clearly differs from *Polyspinatus* by having a maximum body depth being about 33% of

SL, eight non-modified branchiostegal rays, 26 (13+13) vertebrae, dorsal fin with 13 rays and the third spine being the longest of the series (vs the last dorsal-fin spine being the longest in *Polyspinatus*), anal fin with five spines and ten rays, and 12 rays in the pectoral fin (Radovčić, 1975).

The attribution of *Polyspinatus* to the Paleogene family Digoriidae from northern Caucasus, Russia, can be ruled out as well, given that *Digoria* has seven non-modified branchiostegal rays, dorsal fin with five to seven spines plus 30–33 rays, anal fin with five to eight spines and 27–29 rays, 14 rays in the pectoral fins, and six to seven rays in the pelvic fins (Bannikov and Daniltshenko, 1985)

Polyspinatus cannot be referred to the Dinopterygidae, because the genus *Dinopteryx* only known from the Santonian of Sahel-Alma, Lebanon is characterized by a very deep body, with the maximum body depth being almost equal to SL, seven non-modified branchiostegal rays, dorsal fin with 15 spines (the fourth being the longest) and nine rays, anal fin with seven spines and nine soft rays, and ctenoid scales (see Patterson, 1964).

Polyspinatus clearly diverges from the Cenomanian-Turonian family Pycnosteroididae, which is defined by two supraneurals, eight non-modified branchiostegal rays, 25 vertebrae, dorsal fin with seven to eight spines and 18 soft rays, anal fin with three to four spines plus 13 soft rays, pelvic fin with a single spine plus six rays, and cycloid scales (see Patterson, 1964).

As discussed above, the Polymixiidae is the only polymixiiform family that comprises both fossil and extant species, with seven genera known from the Late Cretaceous (Cenomanian–Santonian), including *Apricenaichthys*, *Berycopsis*, *Berycopsia*, *Homonoichthys*, *Omosoma*, *Omosomopsis*, *Pycnosterinx*, and the single extant genus, *Polymixia* (Patterson, 1964; Radovčić, 1975; Bardack, 1976; Gaudant, 1978; Patterson and Rosen, 1989; Taverne, 2011; Murray, 2016). In his definition of the family Polymixiidae, Patterson (1964) included the following features:

presence of a high and centrally thickened supraoccipital crest; a large pterotic; maxilla expanded posteriorly; presence of two supramaxillae, with or without an overlapping process; opercle partially or completely covered by scales; anterior ceratohyal perforate or imperforate; presence of eight or fewer branchiostegal rays; vertebrae 26–34; about three supraneurals; long-based dorsal and anal fins, with four to 11 and three to four spines, respectively; enlarged first anal-fin pterygiophore; pelvic fin with six to eight rays; and ctenoid scales. Subsequent descriptions of other genera assigned to Polymixiidae resulted in a modified diagnosis. For example, the Santonian polymixiid *Apricenaichthys* exhibits two supraneurals and three dorsal-fin spines (Taverne, 2011), and the highest number of anal-fin spines was expanded to six (Radovčić, 1975). *Omosomopsis*, which is currently grouped with the Polymixiidae, has only three spines in the dorsal fin (see Patterson and Rosen, 1989; Murray and Wilson, 2014). In addition, the scales of the polymixiid genera range from ctenoid, to spinoid, to cycloid (Patterson, 1964; Gaudant, 1978; Taverne, 2011; Grande and Wilson, 2021). As evidenced by Murray (2016), several of the characters listed in family diagnosis provided by Patterson (1964) comprise much of the diversity of the other families assigned to the Polymixiiformes (Radovčić, 1975; Patterson and Rosen, 1989; Murray and Cumbaa, 2013; Murray and Wilson, 2014). Murray (2016) argued that the diagnosis of the Polymixiidae may be too broadly defined, and that relationships among the families and genera assigned to the order are in need of a comprehensive revisions. Taking into account the generalized definition of the Polymixiidae by Patterson (1964), *Polyspinatus* fits well the diagnosis of the family by having a high and centrally thickened supraoccipital crest; a large and irregular pterotic; a posteriorly expanded maxilla; two supramaxillae, the first of which greatly reduced with no overlapping process; anterior ceratohyal perforate; seven branchiostegal rays; 44–46 vertebrae; three widely spaced supraneurals; long-based dorsal and anal fins, with 11–12 and eight–nine spines, respectively; enlarged first anal-fin pterygiophore; and pelvic fin with seven soft rays. Following

this approach, *Polyspinatus* differs from the other known genera of the Polymixiidae by having a peculiar number of vertebrae, and of dorsal- and anal-fin spines and rays. As described above, the hyoid apparatus of *Polyspinatus* is extremely similar to that of *Polymixia* (Zehren, 1979; Ono, 1982), being characterized by three short (one of which is plate-like), modified branchiostegal rays articulating with the anteriormost portion of the anterior ceratohyal, followed by four saber-like elements, the last of which articulates with the posterior ceratohyal. Therefore, despite the different vertebral and median fin counts between *Polyspinatus* and *Polymixia*, the specialized skeletal configuration of the hyoid apparatus clearly reveals the existence of close affinities between the new Eocene taxon from the Fur Formation described herein and the extant members of the family Polymixiidae. According to Stiassny (1986), extant polymixiiforms (= *Polymixia*) exhibit two synapomorphies, including a palato-premaxillary ligament passing between maxillary lateral processes, and chin barbels supported by anterior branchiostegal rays. While the presence of modified branchiostegal rays possibly associated to fleshy barbels is unquestionable in *Polyspinatus*, due to inadequate preservation it is not possible to determine whether the first synapomorphic feature (palato-premaxillary ligament passing between maxillary lateral processes instead of passing between contralateral palatines) was present or not in origin. The occurrence of modified anterior branchiostegal rays, however, has been described or hypothesized also in the Cretaceous polymixiids *Homonotichthys* and *Omosomopsis* (Patterson, 1964; Gaudant, 1978; Patterson and Rosen, 1989).

Even though *Polyspinatus* resembles in many ways *Homonotichthys*, especially for the high triangular supraoccipital crest, suspensorium slightly inclined forward, crenulations of the ventral margin of the lachrymal, supraorbital margins, and posterior and ventral margins of the preopercle, and (putative) modification of branchiostegal rays (Patterson, 1964), it differs from this Cretaceous genus by having the subocular shelf on infraorbitals two to four (vs. subocular shelf on all the

infraorbitals), posterior supramaxilla with no overlapping process (vs. with overlapping process), ceratohyal perforate (vs. imperforate), smooth opercular bones (except the preopercle), posttemporal and supracleithrum (vs. serrated), anal fin with eight to nine spines (vs. four spines), pelvic fin with seven rays (vs. eight rays), and scales spinoid (vs. ctenoid).

Similar to *Homonotichthys*, *Omosomopsis* is characterized by crenulated preopercular margins, and modified anterior branchiostegal rays (Gaudant, 1978; Patterson and Rosen, 1989). However, *Omosomopsis* possesses eight branchiostegal rays, of which only the two anteriormost are reduced in size. Gaudant (1978) suggested that this trait could be interpreted either as an incipient reduction towards six branchiostegal rays as present in percopsiforms, or a modification of the hyoid apparatus to support chin barbels in origin, and concluded that the former hypothesis was the most plausible based on the relative position of the reduced branchiostegals on the anterior ceratohyal (Gaudant, 1978). In addition, *Omosomopsis* clearly differs from *Polyspinatus* by having a less developed supraoccipital crest (extending anteriorly up to the midlength of the orbit), presence of a single supramaxilla, a single supraneural in front of the first neural spine (vs. two in *Polyspinatus*), three to four spines and 15 soft rays in the dorsal fin, anal fin with three spines and 18 soft rays, caudal skeleton with five hypurals plus two epurals and bifid neural spines on the second preural centrum, and 11 pectoral- and six pelvic-fin rays.

Therefore, based on the specialized structure of the hyoid apparatus, *Polyspinatus* most closely resembles the extant species of the genus *Polymixia*. *Polymixia* is defined by the presence of an antorbital, orbitosphenoid, subocular shelf, basisphenoid (without contact to the parasphenoid), two series of ossified intermuscular bones (epineurals and epipleurals), and seven pelvic-fin rays (Starks, 1904; Stiassny, 1986; Patterson and Johnson, 1995; Borden et al., 2013; Grande et al., 2013; Grande and Wilson, 2021). However, these characters constitute plesiomorphies present in a range of basal acanthomorphs including *Polyspinatus*. *Polymixia* is further diagnosed by a blunt

snout, an orbit diameter that constitutes up to 35% of the head length, palato-premaxillary ligament passing between maxillary lateral processes, overlapping process of the posterior supramaxilla absent (like in *Polyspinatus*), villiform teeth, mouth gape extending to or beyond the posterior margin of the orbit, anterior ceratohyal imperforate, distinctive supraneurals [described by Grande and Wilson, 2021, p. 579 as “mountaineering ice picks with the pick’s point facing posteriorly within the dorsal body musculature and the shaft corresponding to the pick’s handle”], 29 vertebrae, caudal skeleton with six hypurals and three epurals, haemal arches of the second and third preural centra autogenous, five dorsal-fin spines, four anal-fin spines, and pelvic fin with seven rays (like *Polyspinatus*), spinoid scales (marginal spinoid in *Polyspinatus*), scales covering the entire body and most of the head, including the nape, supraoccipital crest, opercle, cheek and throat (like in *Polyspinatus*).

Polyspinatus differs from *Polymixia* in having an orbit diameter that constitutes up to 30% of head length; subocular shelf restricted to the second to fourth infraorbitals, mouth gape extending to the rear margin of the orbit, jaw teeth conical with slightly recurved tips, anterior ceratohyal with beryciform foramen, 44–46 vertebrae including the compound and second ural centrum, dorsal fin with 11–12 fin spines and 27–28 rays, anal fin with eight–nine spines and 23–26 rays, and scales extending on the bases of the median fins. Moreover, the presence of three autogenous haemal spines on the second to fourth preural vertebrae (Fig. 5) is a distinctive character separating *Polyspinatus* from all the other known polymixiiforms. This trait is uncommon among acanthomorphs, being reported by Fujita (1990) in the common fangtooth *Anoplogaster cornuta* (Anoplogastridae, Beryciformes).

The morphological similarity of the hyoid apparatus of *Polymixia* and *Polyspinatus* is striking, with the first and second branchiostegal rays being sinuous and parallel to each other, while the third is wide and plate-like, followed by four saber-like elements, of which the last articulates with

the posterior ceratohyal. Therefore, the shared possession of a specialized hyoid apparatus seems to be indicative of the close affinities between *Polymixia* and the new Eocene genus *Polyspinatus*, which possibly forms a sister-pair within the family Polymixiidae (Fig. 6).

Paleoecological notes

The paleobiological features of extinct polymixiiforms are scarcely known and the ecology of *Polymixia* remains in large part elusive. Due to the presumed presence of fleshy hyoid barbels in *Polyspinatus*, it is reasonable to hypothesize that these structure had a tactile function in origin, possibly being a demersal fish like *Polymixia*. The sediments of the Fur Formation were deposited below the storm wave base during conditions of alternating anoxia and slight dysoxia in the North Sea Basin. The greater part of bottom-dwelling invertebrate fossils originates from the structureless or weakly laminated sections, reflecting periodic intervals with slightly higher oxygen levels. However, the overall lack of a diverse benthos is typical of the Fur Formation, commonly interpreted as produced by a generally low level of oxygen in the benthic zone. Interestingly, five of the specimens examined herein originate from the finely laminated horizons between +25 to +30 (the stratigraphic position of the other two specimens is unknown), thus possibly conflicting with the possibility of a demersal lifestyle. The morphology of the studied specimens, however, possibly provides relevant information about their paleoecology. The deeply forked caudal fin with moderately developed hypurostegy (see Mihalitsis and Bellwood, 2019), together with comparatively smaller eyes (versus the eye size in relation to the head size in *Polymixia*) might also be indicative of prolonged incursions into the pelagic realm, which was occupied by many other taxa from the Fur Formation fish fauna, including scombriforms, gadiforms and tarpons (Bonde, 1997, 2008; Pedersen et al., 2012). In any case, additional paleoecological information about the

associated ichthyofauna would be desirable in order to more properly define the physiographic and physiochemical features of the depositional environment of the Fur Formation.

As a final note, it is interesting to remark that in the holotypic specimen, a fossil vertebra lodged in the throat, belonging to another bony fish, can be observed (Fig. 2, 4). Since the holotype originate from the finely laminated carbonate concretions between +25 to +30, post-mortem factors (e.g. the vertebrae being transported by currents or scavenging) can be ruled out. Hence, it seems that adult Eocene polymixiids also feasted on teleosts.

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Caption to figures

FIGURE 1. **A**, Map of Denmark showing the western Limfjord region where the Fur Formation crops out; **B**, Outcrop localities and near surface occurrences. The star indicates the type locality of the Fur Formation. The black circle marks the Ejerslev mo-clay pit, where six of the seven type

specimens were collected. Ejerslev mo-clay pit is also the type locality of the holotype specimen. Modified from Schrøder et al. (in press). [planned for page width]

FIGURE 2. *Polyspinatus fluere* gen. et sp. nov., holotype, NHMD-869392. [planned for page width]

FIGURE 3. *Polyspinatus fluere* gen. et sp. nov. **A**, paratype, MM-264; **B**, paratype, MM-340; **C**, paratype, MM-341; **D**, paratype, MM-10738; **E**, paratype, FUM-N-10321; **F**, paratype, FUM-N-15290. Scale bar in A applies to all. [planned for page width]

FIGURE 4. $K\alpha$ element distribution maps of selected specimens. **A**, **B**, strontium and phosphorous maps, respectively, of *Polyspinatus fluere* gen. et sp. nov, holotype, NHMD-869392. Strontium shows exquisite details of the complete fish skeleton, including minute bone structures covered by sediment or fossilized scales, whereas phosphorous expose the outermost apatite-containing structures, such as the scales. Both maps yield much more detailed view of the anatomical structures compared to the actual fossil. Scale bar in A applies also in B; **C**, enlargement of preopercular area shown in B. Combined strontium-phosphorous-calcium map, showing the delicate crenulation of the preopercle and fourth infraorbital, indicated by the two upper white arrows. Especially the crenulation of the infraorbitals are difficult to discern by use of a conventional stereomicroscope, depending on light settings. The bottom white arrow points to the fossil vertebra, from another fish, lodged in the throat of the holotypic specimen; **D**, **E**, mosaic image and strontium map of the exact same area in MM-264, showing the sixth to eleventh vertebrae. Scale bar applies

to both. The epineurals are not clearly recognizable in the actual fossil in D, but highly evident in the strontium map shown in E. [planned for page width]

FIGURE 5. *Polyspinatus fluere* gen. et sp. nov. Reconstruction of the head and girdle, in right lateral view. **A**, the reconstruction of the head is primarily based on the holotype, NHMD-869392 (Fig. 2; Fig. 4), and paratypes MM-341 (Fig. 3C) and FUM-N-10321 (Fig. 3E); **B**, the caudal skeleton reconstruction is primarily based on the holotype, NHMD-869392 (Fig. 2; Fig. 3A–C; Fig. 4) and paratype FUM-N-15290 (Fig. 3F). [planned for 2/3 page width]

FIGURE 6. *Polyspinatus fluere* gen. et sp. nov. Cladogram showing the hypothetical relationships of *Polyspinatus* gen. nov. within the Polymixiidae. [planned for page width]