

First occurrence of a fish otolith from the Eocene Fur Formation, Denmark

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Bony fishes are among the best represented macrofossils from the earliest Eocene Fur Formation of Denmark. However, until now, otoliths from this formation have never been reported. Here we describe the first otolith from the Fur Formation, which was found isolated in a carbonate concretion. The specimen exhibits the typical features of an argentinoid otolith. To date, only a single argentiniform species, based on skeletal remains, has been documented from the Fur Formation – *Surlykus longigracilis* Schrøder & Carnevale, 2023 – which also represents the most abundant teleost species. Therefore, we refer the isolated otolith to *Surlykus longigracilis*. The discovery of this otolith offers the opportunity to review the many argentiniform otolith-based taxa known from the Paleocene of Denmark. One species is now also placed within the genus *Surlykus* - *S. procerus* (Schwarzhans, 2003) and another argentiniform otolith-based taxon from the Paleocene of Denmark is described – *Pseudonansenia hauniensis* n. gen., n. sp.

Keywords: north-western Limfjord area, Ypresian, carbonate concretion, Argentiniformes, *Surlykus longigracilis*.

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<http://zoobank.org/urn:lsid:zoobank.org:pub:859388AA-E6B7-4FAB-ABF6-5E16252AE99C>

Otoliths have neither been documented nor described from the Ypresian (earliest Eocene) Fur Formation in northern Denmark. This is striking as the formation is world-renowned for its exquisitely preserved fossils, particularly the articulated skeletal remains of the ichthyofauna, especially also considering the different modes of fossil preservation related to the lithologies (e.g. Kühne 1941; Bonde 1982; Pedersen *et al.* 2012, Schrøder *et al.* 2023b). With its wealth of exquisitely preserved and abundant fossil teleosts, the Fur Formation ichthyofauna is considered as one of the earliest and best preserved immediately succeeding the K/Pg-boundary (e.g. Bonde 1979, 1982, 2008; Pedersen *et al.* 2012; Schrøder *et al.* 2022, 2023a, b; Schrøder &

Carnevale 2023). Thousands of well-preserved specimens are housed in museum collections across Denmark, e.g. Fur Museum (Museum Salling), Fossil and Mo-clay Museum (Museum Mors), and the Natural History Museum of Denmark (Copenhagen University). In addition, the collection assembled by Walter Kühne (Kühne 1941) was purchased in the 1930th by the British Museum, and is hence kept at the Natural History Museum (London).

While no otoliths have so far been reported from the early Eocene Fur Formation, there is abundant knowledge of otoliths from the middle Paleocene (Selandian) of Denmark (Koken 1885; Schwarzhans 2003). The Selandian sediments of Denmark, chiefly around

Copenhagen, are rich in otoliths and have shown a high degree of diversity. We review those findings in the light of this isolated finding of a single argentiniform otolith from the Fur Formation. The otolith from the Fur Formation is preserved as a mold with the otolith body having fallen out during recovery and the remainder having been removed during preparation.

The aim of the present paper is, therefore, to document and describe the first and thus far only known otolith from the earliest Eocene Fur Formation, and to review the middle Paleocene argentiniform otolith records from Denmark.

Geological setting

The Ypresian Fur Formation crops out in the north-western Limfjord area of Denmark (Fig. 1A). The exposed formation localities and near surface occurrences cover a large region from the western part of Himmerland to the northern part of Salling, the islands of Mors and Fur, to the area of Thy (Fig. 1B). The majority of exposures are present at Mors and Fur, i.e. old digging pits and costal outcrops. The formation comprises a 60 m thick fossil-rich, marine diatomite interbedded with more than 180 distinctive ash layers. It was deposited below storm wave base in the North Sea Basin, presumably in a local, nutrient-rich area, leading to extensive diatom blooms (see Bonde 1979; Pedersen & Surlyk 1983; Pedersen *et al.* 2012; Schröder & Carnevale 2023). The original ash sequence of the Fur Fm was subdivided into a negative and positive series, assigned official numbers from -39 to -1, and from +1 to +140 (Bøggild 1918). Additional recognised ash layers, not included in the original series, have been assigned letters together with the number of the original ash layer (Gry 1940; Pedersen & Surlyk 1983; Pedersen & Buchardt 1996; Larsen *et al.* 2003). The negative and positive sequences also reflect the two separate formation members: the lower Knudeklint Mb (-33 to -1) which is largely laminated with relatively few ash layers, and the upper Silstrup Mb (+1 to +140), which is dominated by structureless beds with numerous ash layers (Fig. 1C). Together with the overall scarce benthic fauna, laminated beds and tetany evident from the well-preserved fossil fishes, the sequences indicate a fluctuating oxygen level, varying from anoxic to slight dysoxic conditions (Pedersen 1981; Pedersen & Surlyk 1983; Heilmann-Clausen *et al.* 1985; Schröder *et al.* 2022; Schröder & Carnevale 2023). The ash layers originate from the volcanic eruptions related to the opening of the North Atlantic. Radiometric $^{39}\text{Ar}/^{40}\text{Ar}$ -dating of ash layers -17 and +19 resolved the age of the formation to ~55.6

Ma and ~54.4 Ma, respectively (e.g. Chambers *et al.* 2003; Storey *et al.* 2007; Stokke *et al.* 2020). The ash layers below -33 belongs to the lowermost part of the Haslund Mb of the Ølst Formation, i.e. the so-called Stolleklint clay unit (Fig. 1C; Heilmann-Clausen *et al.* 1985; Heilmann-Clausen 1995; Heilmann-Clausen & Schmitz 2000). The Paleocene–Eocene boundary was identified in the lowermost part of the Stolleklint clay established on the onset of the Carbon Isotope Excursion (Schmitz *et al.* 2004; Stokke *et al.* 2020, 2021).

Only the Stolleklint clay unit of the lowermost Ølst Fm is exposed on the islands of Mors and Fur. The Ølst Formation, which is largely replaced by the Fur Fm in the western Limfjord area of northern Denmark, is otherwise present across most of the Danish Eocene (Heilmann-Clausen 1995; Sheldon *et al.* 2012).

Material and methods

The material of the present study contains a single otolith, FUM-N-13271. It was collected as a loose slab from the Østklinten locality (klint = cliff) at the island of Fur (Fig. 1). The stratigraphic level, i.e. which ash layer the carbonate concretion originate from, is unknown. At present, this is the only known otolith retrieved from the Fur Formation. The specimen is preserved mainly as an imprint *ex situ* in a carbonate concretion originating from the Fur Formation. Scarce original matrix of the otolith body was still present, mostly in the ventral part of the impression, when the specimen was loaned from the Fur Museum (Fig. 2). The authors were subsequently granted official permission by Fur Museum to remove the remaining matrix to get a clean imprint, in order to expose as much of the morphological details. The cleaning was performed mechanically with a fine needle (Fig. 3A).

The otolith was initially examined and photographed, using a Zeiss Stemi 508 microscope, applying the Zeiss Zen Core 3.5 software, and later using a Wild M3C for visual inspection and a Wild M400 macroscope for photographing. Individual photographs of several fields of depth intervals were captured by a Canon EOS-1000D mounted on the macroscope and connected to a computer. The individual photographs were then stacked using the HeliconFocus software of Helicon Soft (Kharkiv, Ukraine) to generate a continuously focused image. Comparative figures are drawings refigured from Schwarzhans (2003). We also conducted μXRF -analyses before removal of the remaining otolith matrix using a Bruker M4 Tornado Plus Amics (see Schröder & Carnevale 2023 for machine settings). However, the element-mapping did not yield additional morphological results.

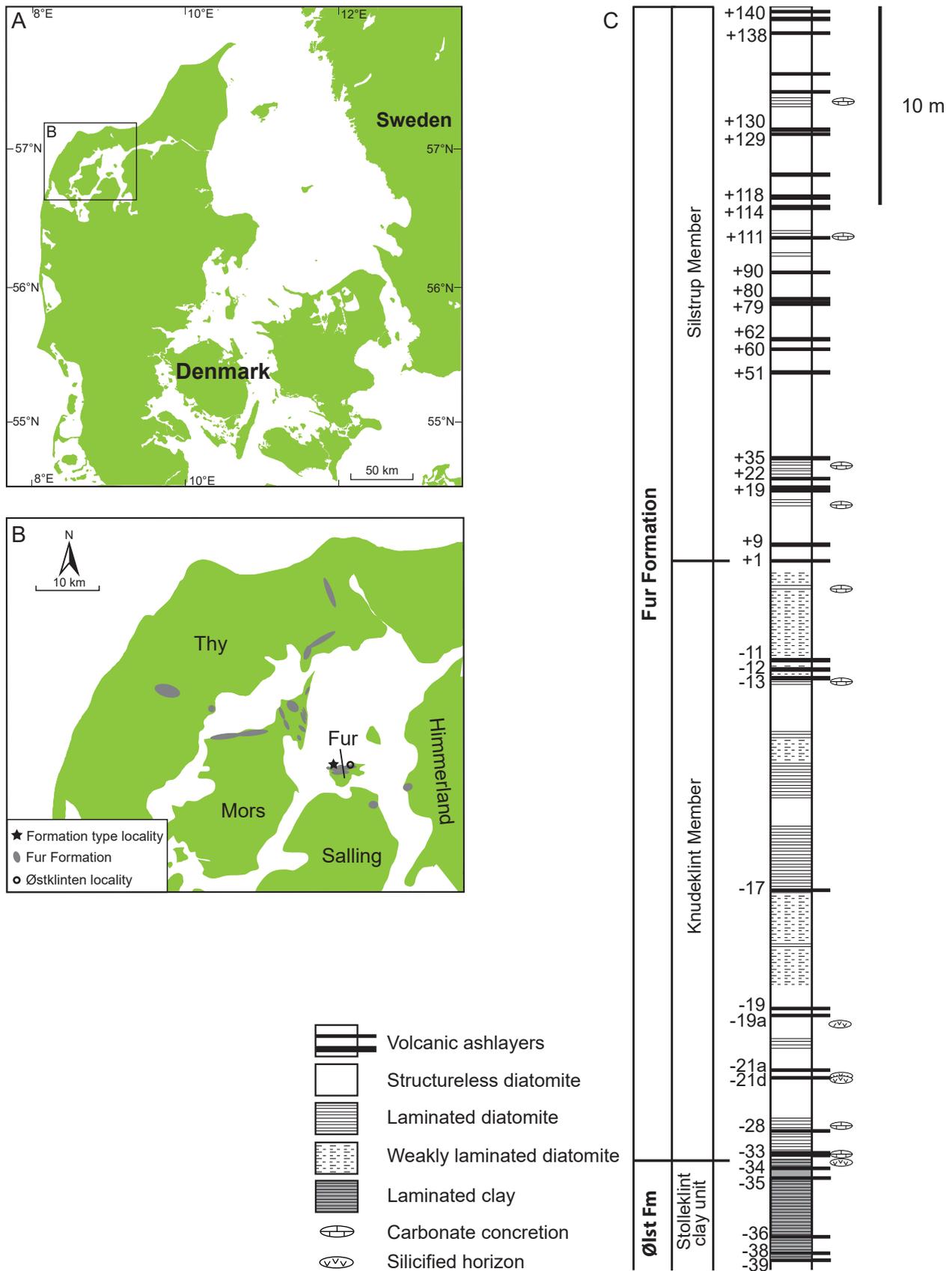


Fig. 1. **A:** map of Denmark with the western Limfjord area marked out. **B:** Fur Formation outcrop localities and near surface occurrences. The Fur Formation type locality is indicated by a black star, and the Østklinten locality by a circle. **C:** sedimentological log of the Fur Formation and lowermost part of the Ølst Formation, the Stolleklint clay, which is exposed at Mors and Fur. Levels with carbonate concreted horizons are indicated. Modified from Schröder and Carnevale (2023).

Institutional abbreviation. FUM-N, Fur Museum (Museum Salling).

Systematic palaeontology

Order Argentiniformes Bertelsen, 1958

Genus *Surlykus* Schröder & Carnevale, 2023

Type species. *Surlykus longigracilis* Schröder & Carnevale, 2023.

Otolith-based diagnosis. Argentiniform otoliths showing the following combination of characters: elongate otoliths with a moderately deep ventral rim, shallower dorsal rim, and a ratio otolith length : otolith height of 1.6 to 1.8. Rostrum strong, pointed or rounded. Postdorsal rim depressed, without prominent angle. Sulcus long, slightly suprmedian, cauda length : ostium length 1.8 to 3.0. Cauda narrow, slightly bending convex along the entire length, slightly narrowed towards the tip. Ostium narrow, with flat, slightly downward bent ventral margin.

Comparison. The slight convex bending of the cauda and its narrowed tip are distinctive features that allow a clear separation from all other otoliths of argentiniform genera, with the exception of the coeval, fossil otolith-based *Protargentinolithus*. Otoliths of *Surlykus* differ from those of *Protargentinolithus* in having the ventral margin of the ostium slightly bent downward (vs. horizontal), and in being more elongate (otolith length : otolith height = 1.6–1.8 vs. 1.3–1.45).

Species. The otolith described below is attributed to *Surlykus longigracilis* based on the observation that the articulated skeletons of this species are the most common, and also the only known argentiniform species of the Fur Formation from which the otolith imprint was obtained. Furthermore, we assign *Protargentinolithus procerus* Schwarzhans, 2003 from the middle Paleocene (Selandian) of Denmark to the genus *Surlykus*.

***Surlykus longigracilis* Schröder & Carnevale, 2023**
Figs 2, 3A

2023 (updated version published 2024)

Surlykus longigracilis, Schröder & Carnevale: figs 2–8.

Holotype. MM-13564_5, nearly complete, well-preserved articulated specimen on a single slab of carbonate concretion, bordered by five designated paratypes.

Paratypes. Five paratypes are associated with the holotype in the single slab of carbonate concretion, MM-13564, which also contains a single referred specimen (MM-13564_7; see figures 2 and 3 in Schröder & Carnevale 2023): MM-13564_1 is the largest nearly complete, well-preserved articulated paratype on the slab, 83.7 mm SL; paratype MM-13564_2 is well-preserved and almost complete, 64.4 mm SL; MM-13564_3 is a well-preserved, nearly complete paratype, however, most of the squamation and neural spines in the precaudal region are not preserved, 54.9 mm SL; MM-13564_4 is well-preserved and nearly complete, 66.0 mm SL; MM-13564_6, a well-preserved, nearly complete paratype, however, most of the squamation in the abdominal region is not preserved, 54.3 mm SL; FUM-N-10506, well-preserved head skeleton, showing exquisitely preserved details of the lateral-line canal, plus the pectoral girdle and anteriormost part of the vertebral column.

Type locality. Fur Formation, lowermost Eocene. The slab containing the holotype, five paratypes and a referred specimen originates from Ejerslev mo-clay pit, on the island of Mors, north-western Limfjord area, Denmark, from a stratigraphic level between ash layer +25 to +30, Silstrup Member.

Description of otolith FUM-N-13271. Otolith size 5.9 mm in length. Ratio otolith length : otolith height = 1.8. Ventral rim moderately deep, regularly curved and finely crenulated. Rostrum long, pointed, occupying 25% of otolith length. Dorsal rim irregularly rounded and irregularly undulating, with small, rounded postdorsal angle and long, depressed postdorsal region. Posterior tip tapering, moderately pointed.

Inner face relatively flat, with long, slightly suprmedian and slightly deepened sulcus. Ratio cauda length : ostium length 1.8. Ostium narrow, with flat, slightly downward bent ventral margin, and broad opening to predorsal rim. No excisura or antirostrum discernable. Cauda narrow, slightly bending convex along entire length, slightly narrowed towards tip, terminating very close to posterior tip of otolith. Dorsal depression wide but with indistinct margins. Ventral field with very weak indication of ventral furrow at some distance from ventral rim of otolith and many fine radial furrows starting from the crenulation of the ventral rim. Outer face not known.

Comparison. The otolith allocated to *Surlykus longigracilis* differs from the Paleocene *S. procerus* (Schwarzhans, 2003; Fig. 3B) in being more slender (ratio otolith length : otolith height 1.8 vs. 1.6), a pointed and long rostrum, occupying 25% of otolith length (vs. rounded and length occupying 15% of otolith length), and a lower ratio



Fig. 2. High-resolution photograph of FUM-13271 (reversed). The otolith impression as it was found, before the scarce otolith matrix was removed.

cauda length : ostium length (1.8 vs. 3.0). The Paleocene formations of Denmark yielded a number of further argentiniform otolith-based species. *Protargentinolithus erraticus* (Roedel, 1930; Fig. 3C–E) differs from the two known *Surlykus* species in being more compressed and by having a straight ventral margin of the ostium (see above) and, occasionally, a more pronounced postdorsal angle in front of the depressed postdorsal section. *Protargentinolithus* appears to be closely related to *Surlykus*, and we therefore consider *Protargentinolithus incertae sedis* within the Argentiniformes. Furthermore, there are also two otolith-based species in the Danish Paleocene that are associated with genuine argentinids, which are placed within the genus *Argentina* – *A. tricrenulata* (Stinton, 1965; Fig. 3F–I) and *A. longirostris* Schwarzhans, 2003 (Fig. 3J–K). Otoliths of the genus *Argentina* are characterized by a prominent postdorsal angle, while this region is depressed in *Surlykus* and *Protargentinolithus*. Finally, otoliths that were originally recorded as Argentinidae *indet.* in Schwarzhans (2003) are now described as a new argentiniform genus and species – *Pseudonansenia hauniensis* – as follows.

Genus *Pseudonansenia* n. gen.

Type species. *Pseudonansenia hauniensis* n. sp.

Etymology. Based on the similarity with otoliths of the extant genus *Nansenia* Jordan & Evermann, 1898

Diagnosis. A fossil otolith-based genus of the Argentiniformes with the following combination of characters: otolith shape elongate fusiform, with obtuse mediadorsal and medioventral angles resulting in a nearly symmetrical appearance. Rostrum and posterior tip likewise symmetrical, tapering, with rounded tip. Otolith length : otolith height = 2.0. Ostium nar-

row, much shorter than cauda; cauda length : ostium length = 2.2. Cauda almost straight, slightly convex ventrally.

Discussion. *Pseudonansenia* otoliths resemble slender argentinid and microstomatid otoliths, for example those of the extant genus *Nansenia* (see Lombarte *et al.* 2006 for extant otolith) because of its slender shape. The shape of the dorsal rim with the dominant mediadorsal and the depressed postdorsal region as well as the ventrally sagging cauda does not relate to any known extant argentinid or microstomatid clade. Therefore, we consider *Pseudonansenia* as *incertae sedis* within the Argentiniformes.

Species. *Pseudonansenia* is a monospecific genus with *P. hauniensis* known from the middle Paleocene (Selandian) of Denmark.

***Pseudonansenia hauniensis* n. sp.**

Fig. 3L

2003 genus *Argentinidarum* sp., Schwarzhans: figs. 15H–J

Holotype. MGUH 26090, Sundkrogen, København, Lellinge Greensand, Selandian, middle Paleocene. Fig. 3L (refigured from Schwarzhans, 2003).

Paratypes. MGUH 26091–26092, five specimens, same data as holotype.

Etymology. Named after Hafnia, the Latin name for København.

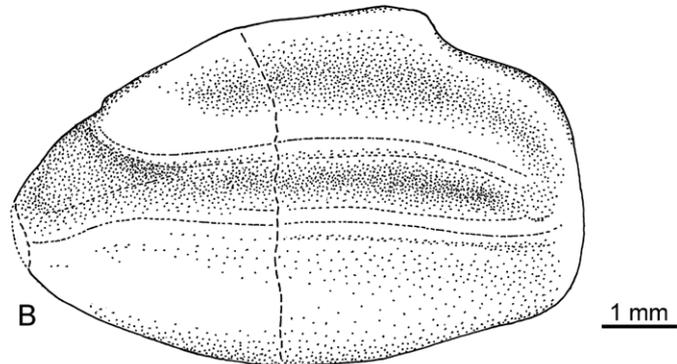
Diagnosis. See diagnosis of *Pseudonansenia* (monotypic genus).

Description. Slender, thin otoliths up to a size of about 2.4 mm in length (holotype). Otolith length : otolith height = 2.0. Dorsal rim low, anteriorly and posteriorly straight, inclined, joined at obtuse mediodorsal angle.

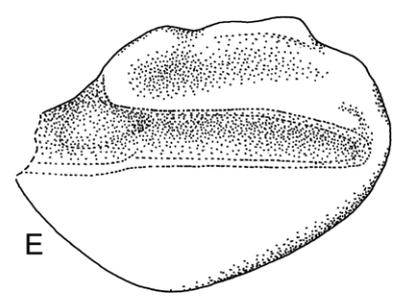
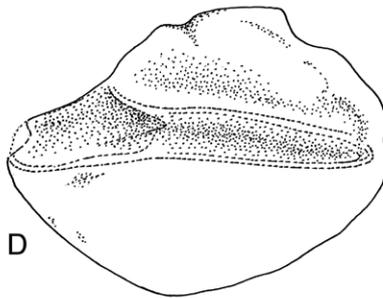
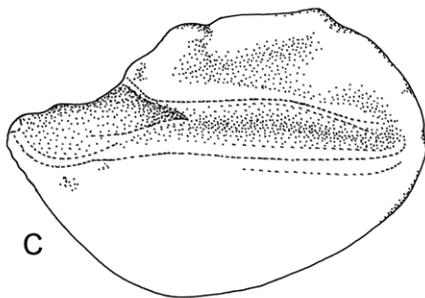
Ventral rim slightly deeper than dorsal rim, otherwise nearly symmetrical to dorsal rim with more broadly rounded medioventral angle and posteriorly faintly and irregularly undulating. Rostrum bluntly rounded,



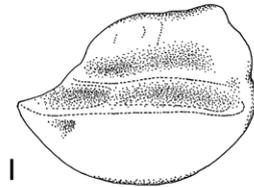
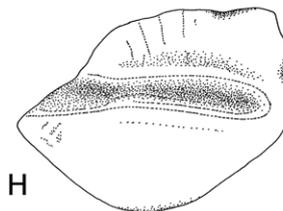
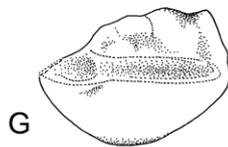
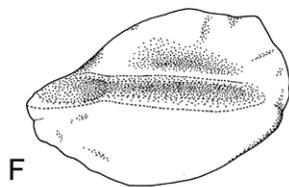
Surlykus longigracilis
Schröder & Carnevale, 2023



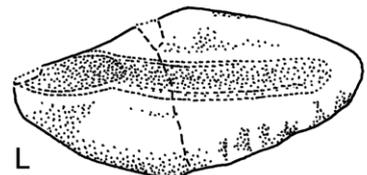
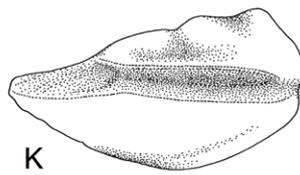
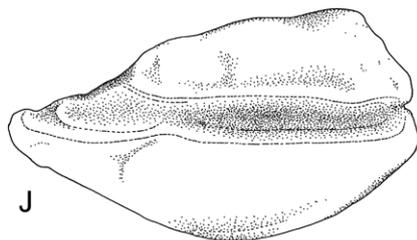
Surlykus procerus (Schwarzahns, 2003)



Protargentinelithus erraticus (Roedel, 1930)



Argentina tricrenulata (Stinton, 1965)



Argentina longirostris Schwarzahns, 2003

Pseudonansenia hauniensis n. gen., n. sp.

Fig. 3. Comparison panel. **A:** *Surlykus longigracilis* Schröder & Carnevale, 2023 (updated 2024), Fur Formation, high-resolution photograph of FUM-13271 (reversed). **B–L:** otolith drawings refigured from Schwarzahns (2003): **B:** *Surlykus procerus* (Schwarzahns, 2003), paratype, Selandian, Vestre Gasværk, København, MGUH 26071. **C–E:** *Protargentinelithus erraticus* (Roedel, 1930), Selandian, Sundkrogen, København, MGUH 26063–26069. **F–I:** *Argentina tricrenulata* (Stinton, 1965), Selandian, Kongedyb, off København, MGUH 26076–26079. **J–K:** *Argentina longirostris* Schwarzahns, 2003, J = paratype, MGUH 26085, K = holotype, MGUH 26084, Selandian, Sundkrogen, København. **L:** *Pseudonansenia hauniensis* n. gen. et n. sp., holotype, MGUH 26090, Selandian, Sundkrogen, København.

occupying 23% of the otolith length. No antirostrum or excisura discernable. Posterior tip of otolith tapering, nearly symmetrical in appearance to rostrum.

Inner face nearly flat, with long, slightly supramedian and moderately deepened narrow sulcus. Ostium narrow, nearly as narrow as cauda, and much shorter; cauda length : ostium length = 2.2. Ostium widely open to anterior-dorsal rim, slightly deepened against cauda. Cauda almost straight, slightly convex towards ventral, reaching very close to posterior tip of otolith. Dorsal depression extremely faint; no ventral furrow discernable but a few radial furrows at postventral rim. Outer face nearly flat and smooth.

Discussion. The holotype is the only complete preserved specimen of the species, although broken into two parts. That was also the reason for leaving the specimen in open nomenclature in 2003. However, the otoliths of *P. hauniensis* are indeed unmistakable and now with the finding of an otolith that we link to the skeleton-based *Surlykus longigracilis*, we consider it pertinent to formally describe *P. hauniensis* and make it available for faunal and phylogenetic evaluations.

The nomenclatural acts of this paper is registered on ZooBank: <http://zoobank.org/urn:lsid:zoobank.org:act:F514C08F-EBE7-40B0-8BCF-BE23CFF30D59> (LSID of the new genus *Pseudonansenia*) and <http://zoobank.org/urn:lsid:zoobank.org:act:22B11054-36E6-415F-80F6-1D8002507F61> (LSID of the new species *Pseudonansenia hauniensis*).

Discussion

Through 2019 to 2023 several thousand fossil fish specimens from the Fur and Ølst formations were thoroughly checked for otoliths *in situ*, or possible otolith voids, by the first author. The most abundant species from the Fur Formation, *Surlykus longigracilis* Schröder and Carnevale, 2023, represents the only known argentiniform identified from the Fur Formation. Thus far, no otoliths have been found *in situ* in any of the studied articulated skeletons. The otolith impression described herein therefore represents the first to be described from the Fur Formation. It shows all the typical characteristics of an argentiniform otolith, which is the roughly pentagonal otolith shape with a deep ventral rim and a long and pointed rostrum, a suprmedian sulcus divided into a long, almost straight and narrow cauda reaching very close to the posterior tip of the otolith and a shorter and narrow ostium with a nearly flat ventral margin. Since only a single argentiniform species (*Surlykus longigracilis*) is known by very abundant, articulated

skeletons from the Fur Formation, it seems reasonable to assume that the otolith impression, FUM-13271, belongs to the same species.

However, five different otolith-based argentiniform taxa are known from the middle Paleocene (Selandian; Schwarzhans 2003) and early Paleocene (Danian; Schwarzhans & Milán 2017) of Denmark. The otolith impression from the Fur Formation does not represent any of these Selandian taxa, although one of the species can be attributed to the same genus, *Surlykus procerus* (Schwarzhans 2003).

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