A new species of ischnacanthiform acanthodian from the Givetian of Mimerdalen, Svalbard

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A new ischnacanthiform acanthodian *Serradentus armstrongi* nov. gen. et sp. has been collected from the Middle Devonian (Givetian) Fiskekløfta Member, the upper member of the Tordalen Formation in the Mimerdalen Subgroup of Spitsbergen. The specimen comprises both pairs of upper and lower jaw bones, jaw cartilages, tooth or denticle whorls, dentition cones and spiky denticles. The latter two features have previously only been identified in Early Devonian ischnacanthiforms. The geology is consistent with a depositional environment of a brackish backwater lagoon with an anoxic bottom. The fish probably entered the lagoon during storm action and died due to the storm churning up bottom anoxic waters, or from being trapped and killed by hypersalinity. The fish possibly partially decomposed on the surface before the head detached and sank to the lagoon floor. The lack of scavengers due to the anoxic conditions prevented scattering of the individual elements, with denticles preserved along the labial surface of the dentigerous jaw bone, and jaw cartilage under the jaw bone.

Keywords: Lagoon, Devonian, histology, Spitsbergen, Arctic, *Serradentus*

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Introduction

An extensive vertebrate fauna has been collected from Fiskekløfta, in the Fiskekløfta Member of the Tordalen Formation of Spitsbergen (see Newman et al., 2019 for information on the geology and history of research in the area). Access to the site has improved in recent years, with the outcrop now free of snow cover for longer periods in the summer months, allowing collection of many new, impressive fossils including complete, metre-long coelacanths. Jaw bones assigned to *Atopacanthus* sp. from this locality were first mentioned by Ørvig (1957a), but not described until later that year (Ørvig, 1957b). The genus *Atopacanthus* Hussakof and Bryant, 1918 was erected for incomplete jaw bones from Frasnian deposits of Erie County, New York State (Burrow, 2004), and the

type species *Atopacanthus dentatus* Hussakof and Bryant, 1918 was based on these remains. The genus has also been recorded from Germany (Jessen, 1973; Otto, 1999) and Russia (Novitskaya & Obruchev, 1967; Beznosov, 2006). All occurrences are of isolated jaw bones, except for one articulated fish from Germany described by Jessen (1973).

The dentigerous jaw bones from the Fiskekløfta Member which Ørvig (1957b) assigned to *Atopacanthus* sp. include fairly complete specimens about 3–4 cm long, which he categorised as Type A (Ørvig, 1957b, fig. 15C; Fig. 1A) for those with a median tooth row, and Type B (Ørvig, 1957b, fig. 15A; Fig. 1B) for those lacking this row. He observed that they were closely related to the North American *Atopacanthus*, but the specimens he examined seem to have been quite worn (Fig. 1C, D &

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Figure 1. Ischnacanthiform jaws from Fiskeløfta. (A) NRM P.slide S141 Ørvig's 1957 *Atopacanthus* type A jaw. (B) NRM P.slide 144 Ørvig's 1957 *Atopacanthus* type B jaw (now synonymised with *Serradentus armstrongi* nov. gen. et sp.) (C) PMO A.2154 6 & 7. (D) NRM P.5060. (E) NRM P.5061. djb – dentigerous jaw bone, psp – psammosteid plate, ss – sarcopterygian scale. Scale bars = 1 mm in A & B, 10 mm in C & E, 5 mm in D.

E). Here we describe new material from the same strata at Estheriahaugen North, which shows several newly recognised characters that prompt us to assign the Type B form of jaw bones to a new genus and species.

Materials and methods

The material was found loose in ironstone nodules within a shale unit at the localities of Fiskeløfta and Estheriahaugen North (Lat. 78°39'N, Long. 16°09'E), both of which are considered to be the same bed (Newman et al., 2019). Only mechanical preparation was possible. Thin-sections were made by JdB along the edges of the rocksaw cut through the whole slab as well as through elements other than the set of jaws exposed on the slab, with slices prepared using epoxy resin and ground using various grain sizes of carborundum grinding powder down to 4 microns. Sections were photographed using a Sony DSC-H2 camera on a Nikon Eclipse E400 microscope. International collection abbreviations: PMO – Palaeontological collections of the Natural History Museum at the University of Oslo. NRM – Natural History Museum of Sweden, Stockholm.

Depositional Environment

The fauna, flora, geology and stratigraphy of the Fiskeløfta Member have been discussed in many papers (Newman et al., 2019 and references therein) but relatively little has been mentioned on the depositional environment. Of interest to this article is the exposure of unit 6 of Vogt (1941) of the Fiskeløfta Member (Fig. 2) on the northern side of Estheriahaugen (see Newman et al., 2019, fig. 1 locality map). Unit 6 at Estheriahaugen North (Fig. 3) consists of a 30 metre-thick, poorly stratified, brownish-black mudstone. Within this mudstone are two sandstone units c. one metre thick (Fig. 2) and a band of much thinner sandstone units (labelled A in Figs. 3 & 4). The thicker sandstone units are sheet-like and continuous across the outcrop with no sorting or cross-bedding. The base of the lower thick sandstone unit in the outcrop (labelled B in Figs. 3 & 4) is covered in *Cruziana* trackways (Fig. 5). The thinner sandstone units range from just a few centimetres to 10 cm thick and are very variable and discontinuous across the entire outcrop. Below the lower thick sandstone unit is an abundance of rounded ironstone nodules containing fossil fish remains, commonly articulated, with some fully articulated (Fig. 2). They are particularly common around two metres below this sandstone unit at the same level as the thinner, discontinuous sandstone. Vertebrates preserved within these nodules include large sarcopterygians, psammosteids and coccosteids (all pers. obs.); the coccosteids appear to be absent in

Figure 2. Stratigraphical column of the Fiskekløfta Member at Estheriahaugen North partly based on Piepjohn & Dallmann (2014, fig. 5).

Figure 3. Estheriahaugen North. View of the outcrop. (A) is the most productive level of the mudstones with articulated fish in nodules between thin sandstone units and (B) the sandstone unit with *Cruziana* trackways at the base. John Armstrong (for whom the new species is named) is first from left.

higher strata. Above the lower thick sandstone unit are thinner ironstone nodules rich in acanthodians and actinopterygians. These remains are generally well-preserved and articulated. Fish remains become rarer in the higher strata but are still found within nodules at the top of unit 6 (Fig. 2). In fact, just above and below the upper thick sandstone unit (Fig. 2) there is a relative abundance of nodules with articulated antiarchs and psammosteids as well as very large disarticulated sarcopterygians. However, these are still scarcer than in the underlying units.

The black mudstone contains acritarchs, but no other definitive marine fauna (Berry & Marshall, 2015). A gastropod (Fig. 6) has been collected from the same strata at Estheriahaugen South but in its crushed state it is not identifiable to genus (R.T. Becker, pers. comm., 2018). This indicates a backwater marine environment, most likely a lagoon. The black mudstone would represent a warm wet high stand and the thicker sandstone units a cool arid regression, with the sands being reworked at the lagoonal edge (J. Marshall pers. comm., 2019). Alternatively, the thick sandstones could be short-

Figure 4. Detail of the stratigraphy at Estheriahagen North, labeled as in Fig. 3.

duration events where beach sands (barrier islands) have been broken through during storms and simply represent storm washovers (N. Davis pers. comm., 2019). The thinner sandstone units seem more likely to represent storm deposits as they are unsorted, uneven in thickness even as individual units and discontinuous across the outcrop. These units lack terrestrial detritus such as plant material which could indicate an alternative scenario such as a flash flood deposit. There are numerous coprolites within the black shale indicating that fish were present at some times in the water column above, but the coprolites are much less common than the fish remains. This disparity may indicate that the majority of the fish were washed into or entered the lagoon during storms, rather than living there long-term. The mudstones lack bioturbation and other evidence of scavenging, indicating an anoxic environment at the sediment-water interface, which is normally associated with a stratified water column. During violent storms the water would be churned up, causing mixing of the anoxic bottom water which could have caused mass mortality of the fish. However, the thin sandstone units (which would not normally be associated with anoxic depositional conditions) also lack bioturbation or any evidence of faunal activity, suggesting that a process other than anoxia could have caused at least some of the mortality. The lack of any other true marine fauna (other than the microscopic acritarchs mentioned above) indicates that there was a significant barrier (barrier islands?) from the open sea. If the normal environment in the lagoon was hypersaline, fish trapped there following storm surges could have died from hypersalinity rather than anoxia once the barrier reformed and 'normal' brackish to hypersaline conditions of the subtropical lagoon ensued.

Figure 5. *Cruziana* sp. trackways at the base of the lowest thick sandstone unit at Estheriahagen North. (A) View of tracks in situ. (B) PMO 234.599 closeup of a single trackway. Scale bars = 10 cm in A, 10 mm in B.

Figure 6. Gastropod from Estheriahaugen South. PMO 234.600. Scale bar = 10 mm.

As noted earlier, the degree of preservation of carcasses varies greatly in the deposit. On dying, the fish would have sunk to the bottom of the lagoon and been preserved intact, or decayed while floating on the surface, with disarticulated bones (many isolated jaws are found, presumably falling off carcasses floating on the surface) dropping onto the lagoon floor (see Trewin, 1986, fig. 26). This scenario fits in with the style of preservation, as the nodules often have a perfectly preserved fish embedded within a detritus of bits of other fish of different species. The mudstones themselves also preserve a detritus of bits of fish, such as scales and teeth. The fish preserved within the thin sandstones (A in Figs. 3 & 4) are rarer, but often very large and complete.

SYSTEMATIC PALAEONTOLOGY

Order Ischnacanthiformes Berg, 1940

Genus *Serradentus* nov. gen.

Type species: *Serradentus armstrongi*

Derivation of name: After serra, Latin for saw, and dente, Latin for tooth.

Included Taxa: *Atopacanthus* sp. NRM P 7718 from An der Loh quarry, Bergisch Gladbach, Germany.

Diagnosis: Ischnacanthiform acanthodian having jaw bones up to 60 mm long, with lateral row of c. 16 postero-medially curved teeth lacking side cusps; teeth increase in size from posterior to anterior of jaw bone; teeth with weakly striated/ridged lingual face, smooth labial

face, and anterior and posterior carinae; carinae have serrations near the tooth base; posterior part of lower jaw bones flaring out laterally at about 70–80° to long axis jaw bone, and posterior part of upper jaw bones flaring out laterally at about 30° to long axis; thin, horizontal bone lamellae forming inner tissue of bone base; multiple small tooth whorls with five strongly striated, curved tooth cusps; dentition cones, with single row of denticles, in the mouth or branchial region; spiky denticles on labial face of dentigerous jaw bones; scales with wide thin crown ornamented with low sinuous subparallel longitudinal ridges, narrow neck, and flat thin base.

Serradentus armstrongi sp. nov.

?1918 in part Fragmente von Coccosteiden-Kiefern; Stensiö, p. 65.

1957a *Atopacanthus* sp. in part; Ørvig, p. 393.

1957b *Atopacanthus* sp. in part; Ørvig, p. 285–287, 329, 337–344, figs. 14–15, pl. 2.

1979 *A. sp.* in part; Denison, p. 39.

1995 *Atopacanthus* in part; Burrow, p. 338.

1986 *Atopacanthus* sp. in part; Reed, p. 415.

1999 *Atopacanthus* type B (Spitsbergen); Otto, p. 117, table 1.

2004 *Atopacanthus* sp. Type B; Burrow, p. 263.

2004 *Atopacanthus* sp. in part; Long, Burrow & Ritchie, p. 152.

2012 *Atopacanthus* in part; Voichyshyn & Szaniawski, p. 883.

2019 *Atopacanthus* sp.; Newman, Burrow & den Blaauwen, p. 4–5, 7.

Remarks: Ørvig (1957b) interpreted all mention of coccosteid jaws by Stensiö (1918) and later authors as mistaken identifications of *Atopacanthus*. However, jaws of an undescribed species of arthrodire are present in the

same deposits as the ischnacanthiform remains and so this interpretation is not supported.

Holotype: PMO 234.601

Derivation of name: Named after John Armstrong of Edinburgh (see Fig. 3), one of the team that excavated Estheriahaugen North to yield the new fauna.

Diagnosis: *Serradentus* lacking a median tooth row on the dentigerous jaw bones.

Material: Oslo A21548; Uppsala P 474, P 491c; Stockholm NRM P 5060.

Type locality and horizon: Estheriahaugen North (Lat. 78°40'N, Long. 16°13'E) 3 km NE of the abandoned Russian mining town of Pyramiden, Spitsbergen, Svalbard, in the Fiskeløfta Member of the Mimerdalen Subgroup (late Givetian).

Morphology:

Dentigerous jaw bones. The holotype (Fig. 7) consists of four dentigerous jaw bones, with each bone being 54 mm long, plus calcified cartilage jaw remnants, tooth whorls, dentition cones, spiky denticles on the labial surface of the jaw bones, and scales with long wide crowns. The jaw elements are interpreted as representing one individual, with the left and right side jaws disarticulated. The dentigerous bones of the left jaw are those preserved on the left of the slab. The upper bone, with its labial face exposed, lies above the lower bone, with its lingual face

exposed; the anterior end of both bones is to the right. The dentigerous bones of the right jaw lie to the right of the left side bones. However, the right upper bone, with its labial face exposed, has rotated by about 120° and lies across the right lower bone, also with its labial face exposed. On each element, one row of evenly spaced monocuspid teeth are borne on a deep axial bone. The teeth increase in size from posterior to anterior, with the posteriormost teeth barely visible, and separated by sockets for the teeth of the opposing jaw (Fig. 8A); the anteriormost teeth are 4 mm high, decreasing in height posteriorly to less than 0.1 mm. The teeth are posteromedially curved and fang-like, particularly the more anterior teeth which show little sign of wear or abrasion. The labial side of the teeth has two low vertical ridges extending down from the apex (Fig. 8B), the lingual side has four to six thin vertical ridges (Fig. 8C), and a carina is developed along each of the anterior and posterior sides (Fig. 8B). The teeth are oval in parbasal section. Each carina is serrated near the tooth base (Fig. 8B). There is a slight overlap between the carinae of adjacent teeth, with the anterior carina of the posteriormost tooth extending slightly labial to the posterior carina of the anterior tooth (Fig. 8B).

Both labial and lingual faces of the basal bone from both the upper and the lower jaws are smooth, without a row of teeth medial to the lateral tooth row. Very small denticles are randomly distributed on the low ridge medial to these main teeth, visible towards the posterior end of the left lower jaw bone (Fig. 8C). This jaw bone appears to have a weak trough between the lateral teeth and the

Figure 7. *Serradentus armstrongi* PMO 234.601 the holotype from Estheriahaugen North. dc – dentition cone, llj – left lower jaw in lingual view, luj – left upper jaw in lingual ? view, rlj – right lower jaw in labial view, ruj – right upper jaw in labial view, tw – tooth whorl. Scale bar = 10 mm.

Figure 8. *Serradentus armstrongi* PMO 234.601 the holotype from Estheriahaugen North. (A) Posterior end of left lower jaw showing detail of sockets for opposing teeth. (B) Right upper jaw in labial view showing details of the teeth. (C) Left lower jaw in lingual view showing details of the teeth and lingual denticles. (D) Right upper jaw in labial view showing detail of the posterior jaw flange, and the right lower jaw in labial view showing details of the concavity for the jaw cartilage. (E) Tooth whorl. (F) Tooth whorl and dentition cones beneath left upper jaw. dc – dentition cone, jd – jaw denticles, otc – opposing tooth socket, pjf – posterior jaw flange, tw – tooth whorl. Scale bars = 1 mm in A, 2 mm in B, C & F, 10 mm in D, 0.5 mm in E.

denticulated ridge. The axial bone extends forward of the anteriormost tooth; slices through the jaws show a concavity for the jaw cartilage (see histology description). The posterior end of the jaw bone flares out laterally behind the end of the tooth row, forming a longitudinally concave surface where the jaw musculature between the upper and lower jaws is confined (Fig. 8D). In the upper jaws the posterior flange is at about 30° to the axis of the basal bone, and in the lower jaws it is at about 70–80°.

The flange on the lower jaw has a maximum height of 14 mm, at its posterior limit, and the bone is about 8 mm high for most of its length. In transverse section, the jaw bones are markedly convex on the labial side, forward of the muscle concavity. Striae on the bone radiate obliquely forward and down from the posterior limit of the tooth row (Fig. 8D). A rugose area on the bone, in front of the muscle concavity near the posterior most tooth, probably represents an attachment for a labial cartilage.

Tooth whorls, denticles and scales. Tooth whorls (Fig. 8E), dentition cones (Fig. 8F) and scales (Fig. 9) are also associated with the jaw bones. The tooth whorls have five curved pointed cusps which are strongly striated. There are two dentition cones exposed between the posterior end of the left lower bone and the upper bone of the holotype. They have a single row of denticles running from the base to the apex. These elements were probably originally in either the mouth or the branchial region based on comparison with the position in which they have been preserved in articulated ischnacanthiforms (e.g., Valiukevicius, 1992, 2003).

Separate small monocuspid teeth are also found scattered across the holotype nodule. They are not closely associated with the jaws like the dentition cones and tooth whorls, and are commonly found in most nodules containing various species at the Estheriahaugen site (MJN pers. obs.). Given their wider distribution, there is no certainty that they derive from the new species.

Large remnants of the jaw cartilages which are presumed to have borne the dentigerous jaw bones are also preserved in association within the matrix, with scattered calcified cartilage globules visible on the exposed surface of the slab.

Very few scales are preserved; they have low, sinuous, subparallel longitudinal ridges running the entire length of the scale crown, which is sub-rhombic in outline (Fig. 9), and wider and longer than the scale base. Maximum scale width is c. 1.0 mm, maximum length c. 0.7 mm. The neck is very narrow, and the base is thin and flat.

Histology:

Dentigerous jaw bones. Ørvig (1957b, figs. 14 & 15) described and figured the structure of his Type A and

Type B jaw bones from Estheriahaugen. Both types show the same histology in the structures common to both, i.e., the axial bone and lateral teeth, as detailed by Ørvig. Two of our thin sections (PMO 234.601/03, PMO 234.601/06) of PMO 234.601 (Fig. 10A) show the structure of the adentate detached anterior end of the dentigerous jaw bone (Fig. 10B), which appears rather disorganised, with convoluted lamellae and many longitudinal vascular canals surrounded by osteons. The concavity for the jaw cartilage is quite deep. PMO 234.601/09 (Fig. 10C) shows a more posterior part, which still shows the convoluted lamellations but here overlain by flatter lamellations so that the external surfaces appear much smoother. The concavity for the jaw cartilage is still quite deep at this level, possibly just anterior to the teeth. Bone cell lacunae and processes are present within the layers (Fig. 10D, E). PMO 234.601/10 (Fig. 10F) shows the structure of the jaw bone more posteriorly, where the lateral teeth are very small and worn; most of the tooth has broken and the section only shows the tooth base, which has a wide pulp cavity (Fig. 10F, G). Bone cell lacunae are visible, mainly in the lingual ridge. The cartilage concavity has been infilled by a layered spongiosa; a boundary is visible between the layers forming the axial bone and the infilling.

Layered remnants of the jaw cartilage, presumably of the left lower jaw, are visible in PMO 234.601/01, 02, 07, 08 & 10 (Fig. 10H, I). The form of the cartilage resembles that recently identified in *Cheiracanthus* spp. from the Middle Devonian of Scotland (den Blaauwen et al., 2019). The cartilage mostly comprises contiguous subpolygonal blocks (Fig. 10J, K) with lines of Liesegang visible. In thicker cartilage layers, globular calcified cartilage with rings of Liesegang is present below the blocky cartilage (Fig. 10L).

Tooth whorls, denticles and scales. Small tooth whorls (Fig. 11A–F) are scattered through the matrix around the jaw bones and cartilages, sometimes clustered together (Fig. 11A). Most appear to have a median row of five cusps, each formed of orthodentine with a single central pulp cavity. As far as we can tell, the main cusps lacked secondary cusps. The bases of each cusp are separate and overlap those of the older cusps (Fig. 11F). The whorls are always associated with jaw cartilage, sometimes being preserved on the cartilage (Fig. 11C).

Arched spiky denticles formed of thin lamellae line the labial surface of the jaw bones (Figs. 10F & 11G), and flat-based scales with an arched crown formed of the same type of thin lamellae (Fig. 11H, I & J) are also scattered amongst the jaw cartilage remnants. The sections show that the scales have a high narrow neck and flat thin base, as well as the long thin crown observed in the scales exposed on the surface (Fig. 9).

Comparison: In having monocuspid lateral teeth and lacking medial teeth, the new species resembles

Figure 9. *Serradentus armstrongi* PMO 234.602 from Estheriahaugen North. Scale crown in dorsal view. Scale bar = 0.5 mm.

Figure 10. *Serradentus armstrongi* PMO 234.601 601 the holotype from Estheriahaugen North. Jaw bone and cartilage histology. (A) Sketch of specimen showing position of thin-sections PMO 234.601/01-12. (B) PMO 234.601/09, detached anterior end probably of left upper jaw bone. (C, D & E) PMO 234.601/09, near anterior end of left upper jaw bone, whole section and closeups of bone lamellae and bone cell lacunae and processes (F–G) PMO 234.601/10, towards posterior end of left lower jaw bone, occlusal surface to top, labial surface to right, latter coated with spiky scales/denticles. (G) Closeup of osteons below tooth. (H–L) Sections through jaw cartilage presumed to be of lower left jaw: (H & I) PMO 234.601/07. (J & K) PMO 234.601/08. (L) PMO 234.601/10, cartilage just below jaw bone. bcl – bone cell lacunae, ccb – calcified cartilage blocks, cjc – concavity for jaw cartilage, eod – extraoral denticles, gcc – globular calcified cartilage. Scale bars = 20 mm in A, 0.5 mm in B, E, G & H, 0.1 mm in C, D, F & I–K.

Cacheacanthus utahensis Burrow, 2007 from the Emsian of Utah, U.S.A. However, *Serradentus armstrongi* nov. gen. et sp. differs from *Cacheacanthus* in having a robustly developed basal bone filled with bone lamellae, and serrations on the tooth carinae. The articulated

fish (Fig. 12) from the Frasnian of Bergisch Gladbach, assigned to *Atopacanthus* sp. by Jessen (1973), also shows similarities with the Spitsbergen taxon, in the form of the lateral teeth, serrations on these teeth, the basal bone morphology and histology. However, the one notable

Figure 11. *Serradentus armstrongi* PMO 234.601 the holotype from Estheriahaugen North. Tooth whorl, denticle and scale histology. (A) PMO 234.601/08, oblique sections through tooth whorls (B & C) PMO 234.601/02, oblique section through tooth whorls on calcified cartilage blocks, these two figure parts are contiguous on the section. (D) PMO 234.601/02, longitudinal section of tooth whorl on cartilage. (E) PMO 234.601/12, longitudinal section through tooth whorl and scale. (F) PMO 234.601/12, oblique vertical section through tooth whorl. (G) PMO 234.601/10, vertical longitudinal sections through denticles on labial surface of left lower dentigerous jaw bone. (H) PMO 234.601/11, transverse section through scale crown. (I) PMO 234.601/11, longitudinal section through scale. (J) PMO 234.601/11, longitudinal sections through scales. b – cusp bases, c – cusp, cc – calcified cartilage, ccb – calcified cartilage blocks, djb – dentigerous jaw bone, gcc – globular calcified cartilage, s – scale, tw – tooth whorl. Scale bars = 0.1 mm.

Figure 12. *Serradentus* sp. from An der Loh quarry, Bergisch Gladbach, Germany. NRM P.7718. Scale bar = 10 mm.

difference is that the Bergisch Gladbach fish and the Type A jaw bones from Spitsbergen differ in having teeth and denticles on the lingual side of the jaw bone. Jessen (1973, plate 26) identified a disarticulated jaw bone with a strongly deflected posterior flange, near the jaws on the Bergisch Gladbach fish, as being from the lower jaw. If this is correct, then the dentigerous bones of *Serradentus armstrongi* nov. gen. et sp. showing a similar angle of deflection are interpreted as from the lower jaws, and the ones showing a low angle of deflection are from the upper jaws, as we have labelled them in the Description. The jaw bones of *Atopacanthus? ambrockensis* Otto, 1999 from the Middle Devonian (middle Eifelian) of Sauerland, Germany do not have serrations of the teeth. They bear a similarity to the type A jaw bones described by Ørvig (1957b) in having a medial tooth row, but differ in other features including having teeth which are more compressed labio-lingually, and having three not two carinae. Otto (1999) considered the holotype bone was from the lower jaw, and we agree with his conclusion as the posterior flange bends at a wide angle to the long axis of the bone. In the shape of the teeth, *A.? ambrockensis* seems more similar to younger species including *Persacanthus simpsonensis* Reed, 1986 from the ?Frasnian Red Hill fish fauna of Nevada, U.S.A. and *Grenfellacanthus zerinae* Long, Burrow & Ritchie, 2004 from the Fammenian Hunter Formation of New South Wales, Australia.

The dentition cones are interesting as they represent by far the youngest record of such elements. Otherwise, they have only been described from Lower Devonian poracanthodid (Valiukevičius, 1992; Burrow, 1995) and acritolepid (Valiukevičius, 2003) ischnacanthiforms; they are not known to occur in ischnacanthid ischnacanthiforms (e.g., *Ischnacanthus gracilis*: Burrow et al., 2018). However, the same type of element, from the same locality as *Atopacanthus? ambrockensis* was described as an acanthodian gill raker by Otto (1999, fig.

2J). The spiky denticles which line the outside of the jaw bones are presumed to have been in the skin originally, and can be compared with the extraoral structures identified in Lower Devonian ischnacanthiforms (Blais et al., 2011; Burrow et al., 2018). The small tooth whorls resemble the multicuspid buccal and extraoral elements of *Ischnacanthus gracilis* (Burrow et al., 2018).

Discussion

Burrow (2004) suggested that a diagnostic character for *Atopacanthus* is the posterior flange only diverging at a low angle from the long axis of the jaw bone. The new material from Spitsbergen and the articulated fish described by Jessen (1973) from Germany, show that in *Serradentus* at least, the angle of divergence depends on whether the jaw bone is from the upper or lower jaw.

Determining the presence or absence of serrations on the teeth appears highly dependent on the preservation of the material. The lateral teeth on the holotype of *Atopacanthus dentatus* are poorly preserved, and the original presence or absence of serrations cannot be determined. Although most specimens assigned to *A. dentatus* appear to lack this feature, Burrow (2004, fig. 4B, C) showed that at least one specimen assigned to the taxon has serrations on the posterior carina of some of the lateral teeth. However, the presence or absence of a medial tooth row is unknown for this specimen, so possibly it is from another species. The main difference between *A. dentatus* and *Serradentus* gen. nov. is the former having a median row of robust teeth which is lacking in the latter.

Conclusions

The depositional environment in which the fish fauna at Estheriahaugen North was preserved was a backwater, possibly brackish lagoon. As coprolites are rarer than the actual fish remains, particularly at certain levels mentioned above, it seems reasonable to suggest that the majority of the fish lived outside the lagoon in an open marine environment. A number of the species from Estheriahaugen North, including the acanthodian *Cheiracanthus intricatus* (Valiukevičius, 2002; Newman et al., 2019), are also found in the marine deposits of the Baltic region. The fish possibly entered the lagoon through a break in a barrier during storms, subsequently dying when anoxic bottom waters of the lagoon were churned up by the storm rendering the whole lagoon anoxic, or later when the lagoon returned to 'normal' hypersalinity. On dying, the bodies of these fish either would have sunk to the bottom of the lagoon intact, or partially intact after gas buildup and subsequent partial decomposition, or as disarticulated bones after near-complete decomposition within the water column. Hence, they are commonly preserved as articulated fish within a debris of disarticulated remains of other species of fish. Another form of preservation is ironstone nodules full of disarticulated fish remains of many forms including acanthodians, porolepiforms and psammosteids such as seen in PMO A21548 (Fig. 1C). Both types of preservation are consistent with the normal conditions in the lagoon, with anoxic conditions near the sediment-water interface excluding scavengers and enabling good preservation of the fish remains.

Serradentus armstrongi nov. gen. is an ischnacanthiform that has features (e.g., dentition cones and spiky denticles) previously only identified in Early Devonian taxa. It had jaw cartilages showing a subtessellate structure similar to that in *I. gracilis*, as well as its contemporary *Climatius reticulatus*, and also Middle Devonian *Cheiracanthus* spp. (den Blaauwen et al., 2019). It is most closely related to the other *Serradentus* sp. from the same deposits, with the main difference being the lack of a lingual tooth row in *S. armstrongi*.

The scales of *Serradentus armstrongi* differ markedly from those described in other ischnacanthiforms. Ischnacanthids have smooth crowned scales with a convex base; poracanthodids have scales with a network of pore canals through the crown which is ornamented with ridges, or smooth; and acritolepids have convex-based scales with crowns ornamented with short ridges running back from the anterior edge. We speculate that the scales of *Serradentus* could have derived from the poracanthodid type, with loss of the pore canal system.

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