The Givetian vertebrate fauna from the Fiskekløfta Member (Mimerdalen Subgroup), Svalbard. Part I. Stratigraphic and faunal review. Part II. Acanthodii

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Two body fossils of the Middle Devonian acanthodian *Cheiracanthus intricatus* Valiukevičius have been collected from the Fiskekløfta Member, the upper member of the Tordalen Formation in the Mimerdalen Subgroup of Spitsbergen. One of the specimens is articulated, the first such known of this species. In the Baltic region the species is only known from scales, from the upper part of the Eifelian and the Givetian (Narva to Burtneki regional stages). Previous workers investigating the Mimerdalen strata speculated that Givetian spores found in the Fiskekløfta Member have been reworked from older deposits, and have given the member a Frasnian age. However, the reworking of an articulated acanthodian from older deposits is a near impossibility, so we are confident in dating the Fiskekløfta Member as Middle rather than Late Devonian. Furthermore, other genera identified from this member include the sarcopterygians *Laccognathus* Gross, 1941 and *Miguashaia* Schultze, 1973 and the arthrodire *Plourdosteus* Ørvig, 1951, also supporting an upper Givetian age, and confirming recent dating based on analysis of the spores. Overall, the fish fauna indicates that the Fiskekløfta Member is most likely contemporary to the Gauja Regional Stage in the Baltic region.

Keywords: Acanthodii, Devonian, Givetian, Spitsbergen, Arctic, biostratigraphy

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Introduction

Most research on the Mid Palaeozoic palaeontology of Svalbard over the last half century has concentrated on Early Devonian deposits, particularly in the northern part of the main island of Spitsbergen. This region is considered to have been part of the Old Red Sandstone continent at that time. General overviews of the faunal composition and biostratigraphy of these Devonian deposits were provided by Blicek et al. (1987) and Blicek & Cloutier (2000); the most recent study of microremains was by Zigaite et al. (2013), with a comprehensive

description of thelodont taxa from Lower and Middle Devonian strata. The Middle Devonian strata (present in the Mimerdalen area, near the town of Pyramiden) have been less well-studied palaeontologically since the 1940s (see below), which has led to some debate on the boundary of the Givetian and Frasnian in Spitsbergen. This question was addressed by Berry & Marshall (2015) based on palynological data. However, at the request of those two workers, one of the authors of the present work (MJN) was invited to bring a team to Svalbard and look at the vertebrate fauna of these deposits, to test Berry & Marshall's (2015) conclusions.

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Previously, most of the material collected from the Middle Devonian of Spitsbergen has been disarticulated and from a limited number of taxa. However, many new, articulated, well-preserved specimens of numerous species were collected by MJN's team over three field seasons (July 2016, July 2017 and July 2018). All these taxa (many new to science) will be described in due course; in this paper, we describe new material of the only acanthodian species found (by MJN) so far as articulated specimens in these deposits.

Materials and methods

The specimens were found loose in a scree slope. Thin-sections were made by JdB using epoxy resin and various grain sizes of corundum grinding powder down to 4 microns, with sections photographed using a Sony DSC-H2 camera on a Nikon Eclipse E 400 microscope. Isolated scales, squamation fragments and Exalex impressions of squamation fragments were imaged, uncoated, in a Hitachi Tabletop TM-1000 Environmental Scanning Electron Microscope at the Queensland Museum by CJB. Institutional collection abbreviations: LGMT – Lithuanian Institute of Geology, Vilnius; NMS – National Museums of Scotland; PMO – Paleontological Museum, Oslo.

Part I. Stratigraphic and faunal review

The Mimerdalen Subgroup is universally considered to be Middle to Upper Devonian in age, although there had been some debate on the precise age of individual units (Piepjohn & Dallmann, 2014). The latter authors summarised the geological and stratigraphic research history of Mimerdalen (i.e., Mimer Valley), particularly the Mimerdalen Subgroup, which is the uppermost Old Red Sandstone deposit of Svalbard. Figure 1 is a locality map showing the areas of interest in this paper. As Piepjohn & Dallmann's (2014) report is extensive, we only detail the research history relevant to the faunal composition and stratigraphy of the main fish-bearing unit here.

Of particular interest in this regard was the discovery in 1892 by Nathorst (1884) of a black shale full of ironstone nodules rich in fossil fish. He named this locality Fiskekløfta (also known as Fish Cleft or Fish Ravine) and collected a large suite of specimens, which he took back to the Swedish Museum of Natural History. Lankester (1884) was the first to describe some of the specimens. He identified scales and teeth of sarcopterygians and concluded they were more likely to be rhizodontid than holoptychiid. From this he deduced the stratum was either at the top of the Devonian or the lower part of the Carboniferous.

Woodward (1889) erected the sarcopterygian species *Onychodus arcticus* Woodward, 1889, based on a single presymphysial bone, and later (Woodward, 1891)

Figure 1. Locality map, central Spitsbergen, Svalbard. Locality 1 – Fiskekløfta, locality 2 – Estheriahaugen north.

described more material from Fiskekløfta. In this work he also figured the *O. arcticus* specimen described earlier, identified the heterostracan *Psammosteus arenatus* Agassiz, 1845 (now known to be a junior synonym of *Psammolepis paradoxa* (Agassiz, 1844), see below), and more importantly the arthrodire *Asteroplax scabra* (mentioning that the isolated plate for which the species was erected was asterolepid in nature). Woodward (1891) also confirmed Lankester's (1884) opinion that rhizodont scales were present but said the teeth were more holoptychiid in nature. He concluded from the fish remains that the Fiskekløfta shale was Upper Devonian in age.

In 1916 and 1917, Erik Stensiö visited Mimerdalen and in two important papers described the geology and palaeontology (Stensiö, 1918a, b). Stensiö published detailed work and described many sections of the whole valley (Stensiö, 1918a). He collected numerous specimens from Fiskekløfta and correctly identified *Asteroplax scabra* as an *Asterolepis*, thus *Asterolepis scabra* (Woodward, 1891). He also identified arthrodire jaws and a probable coelacanth *Dictyonosteus arcticus* Stensiö, 1918b, based on a partial skull from Fiskekløfta.

Stensiö (1918a) was the first person to collect fish remains from Estheriahaugen (also known as Estheria Hill), publishing detailed geological sections of both the north and the south sides of the hill (Stensiö, 1918a, figs. 3–4). He concluded that the black shales with nodules at Fiskekløfta and Estheriahaugen (his unit Sk3) were the same deposit. He described very large nodules with remains of a large sarcopterygian and a heterostracan. Stensiö (1918a) also erected a new heterostracan species, *Psammosteus spinosus*, but this is now considered a nomen nudum (see below). He also identified the same species suite at Estheriahaugen as seen at Fiskekløfta, including *Psammosteus arenatus* and *Asterolepis scabra* as well as teeth and scales of sarcopterygians. However, he stated in the text that his units Sk1 to Sk4 were Upper Devonian, so dating the fish-bearing nodular black shale (Sk3, but also Sk4, see below) as Upper Devonian.

Heintz (1935) later described some very large *Holonema* remains from Fiskekløfta. He did not feel comfortable erecting a new species based on the material at his disposal, but considered it closest to *Holonema radiatum* Obruchev, 1932, an Upper Devonian form from Russia. From this he also concluded that the Fiskekløfta deposits were Upper Devonian in age.

Vogt (1941) published a detailed description of the geology and stratigraphy of the higher series of Devonian rocks in Mimerdalen and concluded, based on the fauna and flora (contra the earlier workers), that the deposits were Middle Devonian in age. He also confirmed that the Fiskekløfta sequence was repeated on Estheriahaugen. He split up and correlated individual units partly established by Stensiö (1918a), designating nine units. His unit 6

(equivalent to Stensiö's (1918a) units Sk III, IV and g), which he called Black Shale III or the Fish Ravine Shale, is the unit of interest in this paper. Vogt (1941) noted the presence of *Psammolepis undulata* (Agassiz, 1844) at Estheriahaugen as well as Fiskekløfta, probably based on his personal communication with Heintz. Certainly, a species of *Psammolepis* does occur at both outcrops (MJN pers. obs.)

Nilsson (1941) published a very detailed description of *Asterolepis scabra* and commented on the other fauna and stratigraphy of the Mimerdalen, particularly the supposed Upper Devonian series. Based on the fauna he concluded that this stratum (unit 6 of Vogt (1941)) was in the upper part of the Middle Devonian. Nilsson (1941) considered *Psammosteus spinosus* a nomen nudum and quoted personal communication with Stensiö, who said he did not think it distinguishable from *Psammolepis arenata* (previously in the genus *Psammosteus*). He also quoted Gross (1933) who stated that *P. arenata* was indistinguishable from *Psammolepis paradoxa*, a species from the Gauja Regional Stage (Givetian) of the Baltic region which has priority.

The latest detailed work on the stratigraphy of the Mimerdalen Subgroup was by Piepjohn & Dallmann (2014) and it is to their work we mostly refer here. These authors used the scheme introduced by Pčelina et al. (1986), dividing the Fiskekløfta Formation (as originally erected by Friend, 1961) into five units, with unit 1 equivalent to Vogt's unit 6. This unit marks the base of the Fiskekløfta Member, the upper member of the Tordalen Formation (Piepjohn & Dallmann, 2014) in the Mimerdalen Subgroup. Piepjohn & Dallmann (2014) considered the Fiskekløfta Member to be in the lowest part of the Frasnian (Late Devonian). However, in their description of the Fiskekløfta Member they referred to numerous palynology papers (e.g., Streel et al., 1987 and Streel & Loboziak, 1996) which indicate a late Givetian age. Piepjohn & Dallmann (2014) considered that many of the spore samples were from reworked units and dated the rocks based on the youngest fossils present.

Berry & Marshall (2015) reverted to Vogt's (1941) unit names, and considered unit 6 not only the base of Fiskekløfta Member, but also the base of the late Givetian. Based on palynology, they considered another shale (unit 8b of Vogt (1941)) to mark the top of the Fiskekløfta Member and also the top of the Givetian. This made the overlying Planteryggen Formation effectively the base of the Frasnian.

To sum up, the currently recognised macrofauna present in Vogt's (1941) unit 6 includes *Psammolepis paradoxa*, *Asterolepis scabra*, *Dictyonosteus arcticus*, *Onychodus arcticus* and undetermined arthrodires, sarcopterygians and actinopterygians. The acanthodian described below is now added to this fish assemblage.

Part II. Acanthodii

History of acanthodian research on Svalbard

Here we refer to Pernègre & Blicek (2016) and Piepjohn & Dallmann (2014) and references therein for the age of the deposits. The acanthodian biostratigraphy is summarised in Table 1.

Early Devonian

Acanthodian remains were first mentioned as being present in Svalbard by Kiaer (1916) and later by Stensiö (1918a) who raised a new species *Onchus mimer* (but with no description before considered as a nomen nudum) from the Pragian to Emsian Wood Bay Formation (the lower formation of the Andrée Land Group) of the Mimerdalen.

Ørvig (1957) noted that *Nostolepis* and “*Gomphodus*” scales were collected in association with thelodont

scales from the Lochkovian Red Bay Group and Wood Bay Formation. He also stated that he had identified in museum collections large tooth whorls similar to *Protodus* (now known not to be *Protodus* s.s., see Turner & Miller, 2008) and toothed jaw bones similar to *Plectrodus* from the Lochkovian Ben Nevis Formation (the upper formation of the Red Bay Group). He also mentioned *Climatius* and “*Onchus*” fin spines from the Lochkovian Frænkelyggen Formation (the formation below the Ben Nevis Formation in the Red Bay Group). Finally, he noted two large spines similar to “*Onchus*” *overathensis* Gross, 1937 of Germany in the upper part of the Pragian Kapp Kjeldsen faunal division.

A decade later, Ørvig (1967) erected a new genus and species *Xylacanthus grandis* Ørvig, 1967 for the toothed jaw bones previously identified, and formally ascribed the large spines to “*Onchus*” *overathensis*. Acanthodian scales were soon after recorded by Ørvig (1969a) from the Lochkovian *primaeva* horizon of the Frænkelyggen Formation, and also from the Emsian Verdalen Member (Stjørdalen faunal division of Blicek et al. 1987 and earlier authors) of the Pragian–Emsian Wood Bay Formation

Table 1. Stratigraphic distribution of acanthodians in the Devonian of Andrée Land and Dickson Land, Spitsbergen, and distribution in the Middle Devonian Baltic of acanthodian species common to both regions based on Valiukevičius (2000, fig. 1); *C. longicostatus* is recorded from the upper Emsian to the middle Givetian in the Baltic.

	Andrée Land				Dickson Land			Baltic (Estonian units)	
Series	Stage	Formation (Fm)/ Group	Formation (Fm)/ Member (Mb)/ Faunal division (Fd)	Acanthodians present	Formation	Member	Acanthodians present	Regional Stage	Acanthodians also found in Spitsbergen
Middle Devonian	Givetian	Wijde Bay Fm			Tordalen	Fiskeløfta	<i>Cheiracanthus intricatus</i> , <i>Atopacanthus</i> sp.	Gauja	<i>Cheiracanthus longicostatus</i> , <i>Cheiracanthus intricatus</i> , <i>Ptychodictyon distinctum</i> , <i>Acanthodes</i> sp.
						Estheria-haugen		Burtneiki Aruküla	
	Eifelian	Grey Hoek Fm	Forkdalen Mb	<i>Ptychodictyon distinctum</i> , <i>Cheiracanthus longicostatus</i> , <i>Ectopacanthus cristiformis</i> , <i>Acanthodes</i> ? sp.				Narva	
			Taylefjellet Mb	<i>Ectopacanthus cristiformis</i> , <i>Watsonacanthus oervigi</i> , <i>Isodendracanthus ramiformis</i>					
Early Devonian	Emsian	Wood Bay Fm	Stjørødalen Fd	<i>Mesacanthus grandis</i> , <i>Xylacanthus minutus</i> , aff “ <i>Onchus</i> ” <i>overathensis</i> , “ <i>Nostolepis</i> ”, “ <i>Gomphonchus</i> ”	Wood Bay			Rezékne	<i>Watsonacanthus</i> cf. <i>oervigi</i>
			Keltiefjellet Fd						
	Pragian		Kap Kjeldsen Fd			Dickson-fjorden			
			Sigurdfjellet Fd			Austfjorden			
	Lochkovian	Red Bay Group		<i>Xylacanthus grandis</i> , “ <i>Climatius</i> ”, “ <i>Onchus</i> ”, “ <i>Nostolepis</i> ”, “ <i>Gomphonchus</i> ”					
			Ben Nevis Fm						
		Fraenkelryggen Fm							

where they are associated with thelodont scales (Ørvig, 1969b).

Much later, a brief mention was made by Goujet (1984) of the discovery of an incomplete, but articulated, acanthodid acanthodiform from the Emsian Lykta faunal division (now known as the Keltiefjellet faunal division in the Wood Bay Formation) at Mount Nidhogg (Goujet, 1984). However, this was not described formally until 1997 (see below).

Blieck et al. (1987) reiterated Ørvig's (1957) account of the presence of acanthodian scales of "*Nostolepis*" and "*Gomphonchus*" type and "*Onchus*" fin spines from most of the fossiliferous Lower Devonian strata. As yet these assemblages have not been systematically described, and these historic records have less value (other than as a direction for further study) as these nominal genera basically equate to: scales with ornamented crowns, scales with smooth crowns, and any type of fin spine, respectively.

Ilyes (1995) identified several taxa (*Cheiracanthus*, *Ptychodictyon*, *Acanthodes*?) based on thin-sections of a bonebed from the Kapp Kjeldsen faunal division. He figured these sections, but gave no information on the morphology of the scales.

Gagnier & Goujet (1997) formally described the Mount Nidhogg acanthodid specimen mentioned above as *Mesacanthus grandis* Gagnier & Goujet, 1997. They also erected *Xylacanthus minutus* Gagnier & Goujet, 1997 based on an isolated dentigerous jaw bone found at Mount Wagner, also from the Keltiefjellet faunal division.

Finally, Wisshak et al. (2004) reported trace fossils from the Emsian Dicksonfjorden Member (upper member of the Wood Bay Formation) of northern Andrée Land. They attributed these to an acanthodian, possibly a *Diplacanthus*.

Middle Devonian

Ørvig (1957) first described acanthodian remains from the Middle Devonian of Spitsbergen, namely isolated jaw bones of the ischnacanthiform *Atopacanthus* sp. from the Givetian Fiskekløfta Member.

Later, Ørvig (1969c) figured some acanthodian and associated thelodont scales from the Eifelian Grey Hoek Formation of Eastern Andrée Land. They were, however, in poor condition and he considered them indeterminable. Schultze (1968) also described some actinopterygian scales from the same formation, but they were of the palaeoniscoid type rather than cheirolepid type so not easily confused with acanthodians.

Valiukevičius (1979) was the first to systematically describe the scales from the Tavlefjellet Member

(wrongly transcribed as the Elsvikfjellet Member) and the overlying Forkdalen Member, both part of the Eifelian Grey Hoek Formation of Dickson Land north of Mimerdalen. He erected new genera and species (*Watsonacanthus*, *Isodendracanthus*, *Ectopacanthus*) for scales from the base of the Tavlefjellet Member, noting that the assemblage was clearly distinguished from that in the overlying Forkdalen Member. The taxa he described from the Forkdalen Member included genera also found in the upper Narva Regional Stage of the Baltic region, *Ptychodictyon*, *Cheiracanthus*, *Ectopacanthus*, and *Acanthodes*?. Valiukevičius (1979) assigned the *Cheiracanthus* scales from this stratum to *C. longicostatus*, but did not figure them.

Blieck et al. (1987) also noted the presence of acanthodian scales and spines in the Eifelian Grey Hoek Formation but did not elaborate further.

Systematic palaeontology

Order Acanthodiformes Berg, 1940

Family Cheiracanthidae Berg, 1940

Genus *Cheiracanthus* Agassiz, 1835

Type species: *Cheiracanthus murchisoni* Agassiz, 1835

Cheiracanthus intricatus Valiukevičius, 1985

1985 *Cheiracanthus intricatus* sp. nov.; Valiukevičius p. 93, 98, figs. 20 & 21.1–2, pl. 4, figs. 4–5.

1988a *Cheiracanthus intricatus*; Valiukevičius p. 603, fig. 1.

1994 *Cheiracanthus intricatus*; Valiukevičius fig. 7.

1995 *Cheiracanthus intricatus*; Valiukevičius, Talimaa & Krucke figs. 1, 3 & 5.

1998 *Cheiracanthus intricatus*; Valiukevičius pp. 21 & 23, figs. 11 & 19.

2000 *Cheiracanthus intricatus*; Valiukevičius figs. 1 & 4.

2002 *Cheiracanthus intricatus*; Valiukevičius fig. 2.

?2014 *Cheiracanthus* sp.; Plax & Krucke pl. 4 fig. 2.

2017 *Cheiracanthus intricatus*; Plax p. 28

2018 *Cheiracanthus intricatus*; Pinakhina, p. 47

Type specimen and type locality: LGMT 45–1167, scale, Kalingrad District, Dvoriki-2 boring, depth 1009.2 metres.

Svalbard material: Two specimens preserved in nodules from locality Estheriahaugen north: (housed at the Paleontological Museum, Oslo (PMO)). PMO 234.072a/b (Fig. 2) in part and counterpart, an articulated individual missing the end of the caudal fin and the lower part of

Figure 2. Articulated body fossils of *Cheiracanthus intricatus* from *Estheriahaugen north*. (A & B) PMO 234.072a. (A) Photograph of the part. (B) Line drawing of the part. (C & D) PMO 234.072b. (C) Photograph of the counterpart. (D) Line drawing of the counterpart. a.fs – anal fin spine, br – branchiostegal rays, c.f – caudal fin, d.fs – dorsal fin spine, p.fs – pelvic fin spine, s – scapulocoracoid. Scale bars = 10 mm.

Figure 3. *Cheiracanthus intricatus* from *Estheriahaugen north*. (A) PMO 234.073a, Photograph of the part. (B) PMO 234.073b, Photograph of the counterpart. fs – fin spine. Scale bar = 10 mm.

the anterior of the head; PMO 234.073a/b (Fig. 3) in part and counterpart, comprising scales and at least four fin spines of a disarticulated individual; thin-sections were made of a spine and scales on the counterpart.

Stratigraphic and geographic distribution: Middle Devonian. Main Devonian Field of the Baltic area, Belarus and Russia: upper part of the Narva Regional Stage (late Eifelian) to the Burtneiki Regional Stage

(mid Givetian). Svalbard: Fiskelofta Member of the Mimmerdalen Subgroup (late Givetian).

Revised diagnosis: Moderate sized *Cheiracanthus*, adults c. 180 mm long. Spines up to 26 mm long, slightly tapering, slightly convex leading edge longitudinally, of equal width and height; lateral groove c. midway between leading edge and lower limit of enameloid surface layer; base of insertion short with irregular, interconnecting

ridges, mostly oriented longitudinally. Circa eight branchiostegal plates each ornamented with two subparallel grooves. Body scales mainly large (0.6–1.2 mm), with flat, rhombic-elongated crown, high neck and massive convex base; scale crown ornamented with c. 14 parallel or fan-like low ridges and grooves not reaching the posterior corner; anterior margin of crown has one or more short ridges and grooves between main ridges, with latter often bifurcated or trifurcated near the anterior margin; posterior half of crown in places has a shallow median depression/sulcus; crown comprises up to 16 growth zones composed of orthodentine and overlying enameloid; main ascending dentine canals in neck, and horizontal canals of crown are of typical cheiracanthid type, with a single canal in each growth zone in the neck; radial canals of neck lie just above base; enameloid entirely composes some upper growth lamellae of crown except in the primordial zone.

Description:

General morphology: PMO 234.072a/b is the only reasonably complete articulated specimen, with its total length estimated to have been about 180 mm. Maximum depth of the fish is about 60 mm, giving a depth to length ratio of 1:3. The pectoral fin spines are not preserved in PMO 234.072a/b, but all other fin spines are; i.e., one dorsal fin spine, an anal fin spine and a pair of pelvic fin spines. The dorsal fin spine is the longest at 26 mm (although the tip is missing) with the anal fin spine about 80% of its length. The pelvic fin spines are about 50% of the length of the dorsal fin spine.

PMO 234.073a/b is disarticulated, and we cannot determine the original anatomical position of the four fin spines preserved.

Head and branchial region: The head is only preserved in PMO 234.072a/b, and then only partially. Unfortunately, the anterior end including the jaws of this specimen was not preserved on the slab (Fig. 2). There appears to be a series of long, thin, branchiostegal rays over the branchial region (Fig. 4). These rays are ornamented with two grooves running subparallel to the length of their long edges. These are slightly displaced in the specimen, but we estimate they number around eight. They extend ventrodorsally from just anterior to the base of the scapulocoracoid up to about three-quarters of its height.

Scapulocoracoid: The scapulocoracoid is only known in PMO 234.072a/b (Fig. 4). It is about 15 mm high (although some of the base may be missing) and about 9 mm wide at its base. The dorsal end of the scapulocoracoid consists of a thin, cylindrical scapular shaft quite sharply inclined to the anterior. It broadens to a triangular area that presumably made contact with the pectoral fin spine, although this area is missing from the slab and not preserved. The triangular area is much crushed and broken with little in the way of describable characters.

Figure 4. *Cheiracanthus intricatus* PMO 234.072a from *Estheriahaugen* north. Detail of the shoulder girdle and branchial region. (A) Photograph. (B) Sketch. br – branchiostegal rays, s – scapulocoracoid. Scale bar = 10 mm.

Figure 5. *Cheiracanthus intricatus* PMO 234.072b from *Estheriahaugen* north. Close-up view of dorsal fin spine and fin web. Scale bar = 5 mm.

Spines: Morphology: PMO 234.072a/b is the only specimen with the fin spines in situ, on the part; height and width of spines are approximately equal. The dorsal fin spine (Fig. 5) is long (26 mm) with a deep

Figure 6. *Cheiracanthus intricatus* PMO 234.072a from *Estheriahaugen* north. Close-up view of pelvic fin spine and adjacent squamation. Scale bar = 2 mm.

groove running along the whole length of the exposed side. The tip of the spine is displaced by a fracture, and the distalmost tip is presumed missing, as the end of the spine is squared-off. Thin striae are visible on the posterior edge of the spine, parallelling the open central cavity. The fin web extends to near the tip of the spine. The pelvic fin spine (Fig. 6) is also long (16 mm) with a deep groove running the whole length. The distal tip is quite sharp, and the fin web extends to near the distal end. The anal fin spine (Fig. 7A) is broken and only the proximal 6 mm is preserved. Morphologically, it is like the other two fin spines with a deep groove running the length of the preserved piece. On the counterpart (Fig. 7B) the anal fin web is intact, and indicates that this fin spine was also probably long (estimated c. 20 mm), with the fin web running to near its distal end. The pectoral fin spines are not preserved.

PMO 234.073a/b has four spines, all with a morphology similar to the ones preserved on PMO 234.072a/b. As they are disarticulated, the insertion bases can be seen (Fig. 8); they have an insertion length 4–5 mm, and the spines have maximum width and height of 3–4 mm. The leading edge is slightly convex longitudinally, and the

Figure 8. *Cheiracanthus intricatus* PMO 234.073a from *Estheriahaugen* north. (A) Proximal end of disarticulated fin spine. (B) Detail of the base of insertion of A. Scale bars = 10 mm in A, 5 mm in B.

spines taper only slightly proximo-distally; the tips are either broken off or not exposed. A deep groove separates the smooth leading edge ridge from the smooth sides of the spine. The posterior/trailing face on one spine is exposed, showing at least three, thin, longitudinal ridges edging a median groove. The insertion is also exposed on this spine, showing subparallel ridges and grooves of variable length; the insertion-exsertion boundary is angled at 30° to the trailing edge. The pulp cavity is open at least up to where the spine is buried in the matrix.

Histology: (Fig. 9) Transverse thin-sections of one of the spines on PMO 234.073b show its internal structure.

Figure 7. *Cheiracanthus intricatus* from *Estheriahaugen* north. Anal fin spine. (A) Close-up view of preserved proximal end of spine and adjacent squamation, PMO 234.072a. (B) Close-up view of fin web and impression of spine, PMO 234.072b. Scale bars = 5 mm.

Figure 9. *Cheiracanthus intricatus* PMO 234.073b/1–4 from *Estheriahaugen* north. Histology of the fin spine. (A) PMO 234.073b/1. (B) PMO 234.073b/2. (C–E) PMO 234.073b/3. (F & G) PMO 234.073b/4. (H) Section line drawings of PMO 234.073b. b/o – bone/osteodentine boundary, c – canal to surface, dt – dentine tubules, e – enameloid, g – lateral groove, il – inner lamellar layer, lc – longitudinal canal, ost – osteodentine, pc – pulp canal, pr – posterior ridge, rc – radial canal, s – scale. Scale bars = 1 mm in A–C, F & H, 0.4 mm in D & E, 0.1 mm in G.

Figure 10. *Cheiracanthus intricatus* from *Estheriahaugen* north. Morphology of the scales. (A–G): (A & B) PMO 234.072b/3 patch of squamation from in front of the dorsal fin, crowns and posterior sides of scales exposed. (C) PMO 234.072b/4 crown view of two adjacent scales from in front of the dorsal fin. (D–G) PMO 234.072b/5 patch of squamation from in front of the dorsal fin, crowns exposed. (H–L) PMO 234.073a: (H) PMO 234.073a/11 Exaflex cast of scale crown impression. (I) PMO 234.073a/12 Exaflex mould of scale crown. (J) PMO 234.073a/13 scale in crown view. (K) PMO 234.073a/14 scale in laterobasal view. (L) PMO 234.073a/15 scale in posterocrown view. p – posterior neck protuberance. Scale bars = 1 mm in A & D, 0.5 mm in B, C & E–L. Arrows indicate anterior of scale.

Near the proximal end of the spine (Fig. 9A), a wide open pulp cavity is lined by a thin, dense, laminar inner layer pierced by canals (c. four in this section) extending from the inner surface to join longitudinal and other canals running along the boundary between the inner and middle layers. The middle layer extends through most of the width of the spine, and contains radial and longitudinal canals surrounded by denteons, spaced at c. 0.1 mm apart (Fig. 9A–G). Unfortunately, the fine dentine tubules are poorly preserved and only rarely visible in the sections (Fig. 9D, G). A thin outer layer on the spine is formed of a birefringent enameloid, seemingly lacking dentine tubules (Fig. 9D, G), and clearly separated from the underlying dentine layer (Fig. 9G). This superficial layer is not developed inside the longitudinal grooves (Fig. 9G). These grooves are positioned approximately midway between the leading edge of the spine and the lower limit of the enameloid cover. The pulp cavity is enclosed on the distal half (or more?) of the spine, the inner layer thickens proportionately towards the spine tip, and the thick ridges paralleling the posterior groove are clearly defined (Fig. 9C, E & F). The tissue forming these ridges is denser than the middle layer forming the anterior ridge and sides of the spine, and it appears to be continuous with the inner layer lining the pulp cavity. There is no evidence for dentine tubules radiating from the canals (Fig. 9E), indicating that this tissue forming the posterior ridges is bone rather than dentine. A secondary pulp canal is not developed below the leading edge ridge (Fig. 9A–C, F & G).

Scales: Morphology: (Figs. 7, 10 & 11) All scales are more or less as wide as long. The size range of flank scales on the two specimens is 0.6–1.2 mm. Fin web scales are mostly smaller than body scales; they are largest close to the body and the fin spine, and decrease in size distally (Figs. 2A & 7). The crown surface on flank scales is rhombic and relatively flat (Fig. 10A–J), sloping down slightly from the centre to the anterior edges. Crown ornament comprises c. 14 main ridges radiating back from the anterior rim to mid crown or more posteriorly. In places the ridges bifurcate or trifurcate close to the rim, and are usually intercalated with one or two short lower ridges (Fig. 10E–J). A shallow median sulcus is developed in the posterior area of the crown on most scales (Fig. 10B, E, H & I). The neck is about half the total height of the scale, and the base is strongly convex (Fig. 10K). A pair of small rounded protuberances are sometimes developed low on the posterior neck (Fig. 10A, B & L). On the fin webs, the number of ridges on the scale crowns decreases distally, with a scale ornament similar to that of flank scales near the spine base (Fig. 11), and with c. three to five on the smallest, distal scales.

Histology: (Fig. 12). The body scales have a highly distinctive histological structure, characterised by the upper crown plate in all growth zones, including the primordial zone, formed only of a birefringent enameloid, completely lacking in dentine tubules (Fig. 12A–D). Each

Figure 11. *Cheiracanthus intricatus* from *Estheriahaugen* north PMO 234.072a. Detail of the dorsal fin web scales. Scale bar = 0.5 mm.

sectioned scale has c. 16 narrow crown growth zones (Fig. 12A, B, E & F) in PMO 234.073a/b and c. 9 at the base of the dorsal fin in PMO 234.072a/b (Fig. 12G–H); a single dentine canal rises up through the centre of each zone (Fig. 12A, B, E & F) from a circular canal at the crown-base boundary. Radial (Fig. 12A) and circular canals (Fig. 12B, D) are positioned just above the base. Each crown growth zone has two or more tiers of these circular canals, with older canals almost encircled by each growth zone (Fig. 12B, D & G). The cone-shaped basal apex extends quite high in the crown, almost to the innermost enameloid layer on the primordial zone (Fig. 12A–C & G). The base shows a typical acanthodiform structure with thin bone lamellae paralleling the basal surface; the growth zone margins of the crown continue into the base as dark lamellae (Fig. 12A, B, D & G). Sharpey's fibre bundles are visible arching through the base from its inner surface, with each successive layer at right angles to the underlying layer (Fig. 12A, B & D). Canals of Williamson penetrate the base (Fig. 12C, E). Caudal fin scales are c. 0.2 mm long and 0.1 mm high, tightly packed and overlapping, and have fewer growth zones than the body scales. The flat bases of the scales from each side of the fin web appear fused together, but this is probably the result of taphonomic processes (Fig. 12H).

Discussion

The two new Svalbard specimens are here identified as *Cheiracanthus intricatus* Valiukevičius, 1985. They are the only occurrences of *C. intricatus* known that have associated fin spines and scales, with all other records being of isolated scales. The fin spines resemble those of *Haplacanthus marginalis* Agassiz, 1844, but differ in having an equal height and width in the proximal

Figure 12. *Cheiracanthus intricatus* from *Estheriahaugen* north. Histology of the scales. (A–F) PMO 234.073b/4–9: (A) PMO 234.073b/5 CHS centre of crown. (B) PMO 234.073b/4 VLS through scale midline. (C) PMO 234.073b/6 cross-nicols image of section through three scales. (D) PMO 234.073b/7 VTS through posterior part of scale. (E) PMO 234.073b/8 high CHS. (F) PMO 234.073b/9 low CHS. (G & H) PMO 234.072a/1–2: (G) PMO 234.072a/1, longitudinal section through the caudal fin web overlain by another squamation layer. (H) PMO 234.072a/2, scales near the dorsal fin spine. bl – base lamellae, cgz – crown growth zones, dc – dentine canals, e – enameloid, ez – embryonic zone, Sf – Sharpey's fibres. Scale bars = 1.0 mm in C & H, 0.5 mm in A, B & D–G.

Figure 13. *Cheiracanthus latus* Egerton, 1861 NMS G.2018.28.26.1 a fin spine from Tarrel Bay on the Tarbet Peninsula (British Grid reference NH 902798). (A) Complete spine. (B) Detail of the base of insertion of A. Scale bars = 10 mm in A, 1 mm in B.

half rather than being laterally compressed. Both *Cheiracanthus* (e.g., *Cheiracanthus latus* Egerton, 1861 National Museums of Scotland (NMS) specimen NMS G.2018.28.26.1 (Fig. 13) and *H. marginalis* (Gross, 1940, fig. 1C–E) have distinct bases of insertion with a clear insertion-exsertion boundary between the exerted ornament ridges and the inserted area. According to the description by Gross (1940), *H. marginalis* spines have a well-developed secondary pulp canal under the leading edge ridge (Gross, 1940, fig. 2A–C), which is lacking in *Cheiracanthus* spines (Fig. 14). The type specimens of *H. marginalis* from near St. Petersburg are poorly known, with no information on their histology. The specimens were in the Keyserling collection housed in the Saint-Petersburg Mining Museum. However, they have not been located in the type and figured collection (Darya Pinakhina, pers. comm.) and so must be considered lost at the present. Despite this, the species has been recorded from numerous localities in the Baltic region (e.g., Gross, 1940; Valiukevičius, 1998, figs. 11 & 19). Our investigations of museum specimens assigned to the species indicate that spines from a number of different genera, including *Rhadinacanthus* and probably *Cheiracanthus*, have been incorrectly assigned to *H. marginalis*. The authors have also noted (pers. obs.) that the fin spines of the articulated Scottish *Cheiracanthus* spp. are very uniform, with only minor differences occasionally observable, and then usually only in thin-section.

Valiukevičius (1998, fig. 4) nominated a range for *C. intricatus* from the middle Eifelian to the lower

Figure 14. *Cheiracanthus latus* NMS G.2018.28.26.1 histology of a fin spine from Tarrel Bay on the Tarbet Peninsula (British Grid reference NH 902798). (A) NMS G.2018.28.26.9, thin-section through the fin spine about a third the length from the base. (B) NMS G.2018.28.26.5, thin-section through the fin spine about two thirds the length from the base. Scale bars = 1 mm.

Givetian; fin spine taxa Valiukevičius (1998) recorded from this time range include *Haplacanthus marginalis*, *Homacanthus gracilis* and *Archaeacanthus quadrisulcatus*, with their ranges extending from the base of the Narva RS (lower Eifelian) up to the top of the Burtneki RS (Givetian–Frasnian boundary) or higher. A number of *Cheiracanthus* scale taxa, *C. longicostatus* Gross, 1973, *C. brevicostatus* Gross, 1973, *C. talimae* Valiukevičius, 1985, have been described from the same horizons as *Cheiracanthus intricatus* and *H. marginalis*; thus, even if *Cheiracanthus* fin spines can be separated from *Haplacanthus* spines, we are unable to determine to which species they belong.

The scales on the Mimerdalen acanthodian specimens conform in morphology and histology to the original description of *Cheiracanthus intricatus* (Valiukevičius, 1985, fig. 20, pl. 4, figs. 4–5) from the upper Narva to Burtneki Regional stages of the Baltic region (Valiukevičius, 1988a, b, 1998, figs. 11 & 19, showing borehole occurrences in the Kernavė Formation in eastern Lithuania and Kaliningrad, respectively). Plax (2017) also lists *C. intricatus* from the Eifelian Koshyukovidii RS in Belorussia, which Valiukevičius (1998) noted is the stratigraphic equivalent of the Kernavė Formation. Valiukevičius (2002, fig. 2) wrote that his acanthodian association 25, dominated by *Markacanthus costellatus* and *Cheiracanthus intricatus*, is found in marine sediments of the Kernavė Formation in western Lithuania. A scale from the upper Givetian Moroch beds of the Polotsk Regional Stage of Belorussia, assigned by Plax & Kruckek (2014, pl. 4, fig. 2) to

Cheiracanthus sp., resembles the Mimerdalen scales and fits the morphology of *C. intricatus*, but without knowing its histological structure we cannot be certain of its assignment.

Given the similarity in gross morphology of *Cheiracanthus* and *Haplacanthus* fin spines, listings of *Haplacanthus* in biostratigraphic tables must be suspect. Using only the scales and ignoring the possibility that some occurrences listed for *Haplacanthus* could actually be *Cheiracanthus intricatus*, the biostratigraphic range of the latter species in the Baltic is the Narva to Burtneki Regional stages. Acanthodian scales are rarer in the overlying Gauja Regional Stage, with fin spines more prevalent. *C. intricatus* might also be present in the Gauja Regional Stage, but represented by fin spines that are not determinable.

In Svalbard, as stated above, the Fiskeløfta Member is considered to represent the top of the Givetian and so would be equivalent to the Gauja Regional Stage of the Baltic. This is further confirmed by the presence of certain genera in the Fiskeløfta Member that are found in the Gauja Regional Stage; these taxa will be described in further articles by the authors and others. These genera (as determined by one of the authors, MJN) include the sarcopterygians *Laccognathus* Gross, 1941 and *Miguashaia* Schultze, 1973 and the placoderm *Plourdosteus* Ørvig, 1951 with a species similar to *Plourdosteus livonicus* (Eastman, 1896).

Conclusions

Cheiracanthus intricatus is one of the few *Cheiracanthus* species known from articulated remains from outside Scotland. If *Cheiracanthus costellatus* Traquair, 1893 from the Emsian Atholville beds near Campbellton, New Brunswick in eastern Canada, has been wrongly assigned to *Cheiracanthus* (CJB, pers. obs.), then *C. intricatus* is the only such species. The Scottish articulated *Cheiracanthus* spp. are generally reconstructed as quite slender fish (Watson, 1935, 1937) with *C. intricatus* being considerably more robust and broad. The maximum

Figure 15. Reconstruction of *Cheiracanthus intricatus* based on PMO 234.072a/b. Scale bar = 10 mm.

number of growth zones in sectioned scales of PMO 234.072a/b is nine, whereas the sectioned scales from PMO 234.073a/b have c. 16 growth zones. This could indicate that the latter specimen would have been considerably larger than the former before it died, indicating that the species grew to a considerable size and/or age. Figure 15 is our reconstruction of a complete fish. Although the large suite of other genera collected from Estheriahaugen north is yet to be described, we can be fairly certain that the Fiskeløfta Member is equivalent to the Gauja Regional Stage of the Baltic area because of the associated vertebrate genera, and evidence from spore analysis (Berry & Marshall, 2015).

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