New Late Jurassic teleost remains from the Agardhfjellet Formation, Spitsbergen, Svalbard

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The Agardhfjellet Formation (Middle Jurassic to lowermost Cretaceous) of Svalbard (Norwegian Arctic) is well known for its abundant and unique marine reptile fauna, of ichthyosaurs and plesiosaurs. In an attempt to reconstruct the palaeoecology and palaeoenvironment of the Agardhfjellet Formation, a study of the invertebrate fauna, geochemistry and stratigraphy was conducted. During this study numerous small vertebrate fossils were encountered. Only a few reports of Jurassic teleost from the Arctic were known previously, from the Agardhfjellet Formation on Svenskøya, Kong Karls Land, described as *Leptolepis nathorsti*, and at Lardyfjellet, East Spitsbergen. We describe more teleost material from the Kimmeridgian and Volgian of the Agardhfjellet Formation in central Spitsbergen and assign a new age, Kimmeridgian, to the original material. This new material also provides more information on the palaeoecology of the Jurassic of Svalbard, showing that fish were probably common in the pelagic fauna of central Spitsbergen together with the better known cephalopods, and could have been important elements of the diet of the marine reptiles.

Keywords: Teleost, Leptolepidae, Jurassic, Arctic, Spitsbergen

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Introduction

The fossil record of small vertebrates from the Middle Jurassic–Upper Cretaceous of the Arctic is scarce. Woodward (1899) was the first to describe isolated cranial and postcranial elements from an early teleost from the Arctic, which he named as *Leptolepis nathorsti*. The remains were found in Jurassic “bituminous limestone” and “black shale” on Svenskøya and Kong Karls Land, Svalbard. This refers to the Agardhfjellet Formation (Smith et al., 1976), of mostly Bathonian to Volgian (Tithonian) age. In this study, we describe new teleost remains from the Agardhfjellet Formation in Central Spitsbergen. The goal of this study has been to compare and identify the remains and to extend/ improve the age of teleost finds in Central Spitsbergen. The Agardhfjellet Formation is a shallow-marine deposit consisting mainly of organic-rich black to grey shales and siltstones (Dypvik, 1984; Mørk et

al., 1999; Dypvik et al., 2002; Koevoets et al., 2016) with subordinate carbonates and sandstones. The uppermost member, the Slottsmøya Member, is well known for its numerous plesiosaur and ichthyosaur remains (Druckenmiller et al., 2012; Hurum et al., 2012; Knutsen et al., 2012b; Roberts et al., 2014; Delsett et al., 2015).

Our study is largely based on drillcore samples collected in the framework of the CO₂ Svalbard project (Sand et al., 2014) (Fig. 1). The primary aim of the project is to document high-resolution biostratigraphy, facies development and sequence stratigraphy in order to evaluate the feasibility of the Agardhfjellet Formation as a suitable seal for CO₂ storage in the vicinity of Longyearbyen (Braathen et al., 2012). Six wells were drilled within a 50 m radius in Adventdalen 5 km southeast of Longyearbyen, and two wells were drilled 2 km northwest of Longyearbyen (Braathen et al., 2012). Four of the wells have completely

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Figure 1. The localities at which isolated elements were discovered in this study in Central Spitsbergen (left) and the location of elements discovered by Nathorst in 1899 on Svenskøya (right).

cored the Agardhfjellet Formation. The drillcore provides a continuous record from the Middle Jurassic (Bathonian) to the lowermost Cretaceous (Ryazanian) and has proven to contain well preserved external moulds of invertebrate fauna (Koevoets et al., 2016).

The genus *Leptolepis* is somewhat ill-defined as some characteristic features are common among other teleost genera, and many species previously belonging to *Leptolepis* have been reassigned (e.g., Arratia, 1997, 1999, 2001, 2003, 2013, 2015; Arratia & Thies, 2001; Arratia & Hikuroa, 2010). We will compare the presented material to the material of the teleost fish reported from eastern Svalbard (Woodward, 1899), referred to as *Leptolepis nathorsti*. The definition and characterisation of Leptolepididae follows Arratia (2017), and for *Leptolepis* Konwert & Stumpf (2017) are followed without amendments.

Material

Material used in this study is surface material collected from outcrops of the Agardhfjellet Formation at Janusfjellet and Criocerasaksla (Koevoets et al., 2016) and samples from drillcore DH2 (Adventdalen) which is part of the CO₂ Svalbard project (Sand et al., 2014) (Fig. 1). Other material collected from the drillcore significant to this study is a stratigraphic abundance of all fauna, including ammonites, onychites, belemnites, bivalves and in a few cases marine reptile remains. From the outcrop material, eight specimens of teleost remains were collected, and from the drillcore 50 specimens were recognised and logged while 14 samples were removed from the core. The frailty and delicacy of the remains in both the outcrop and the core specimens prohibited preparation in fear of damaging the samples.

The remains consist of disarticulated, scattered and flattened bones. The most common occurrences are isolated dentaries. The stratigraphic distribution spans the complete formation and is associated with onychites (Fig. 2). Although the material does not seem to be associated with a specific lithology, it is somewhat more abundant in black shales of the Lardyfjellet and Slottsmøya members.

Figure 2. Distribution of fish elements throughout the Agardhfjellet Formation in the DH2 core, central Spitsbergen, Svalbard. Distributions of onychites and marine reptiles are also shown (marine reptiles data from (Delsett et al., 2015)).

Results

Systematic palaeontology

Actinopterygii Cope, 1887
Teleostei Müller 1845
Order indet.

Leptolepididae Pictet, 1854
Leptolepis Agassiz, 1833

The characteristics of the genus *Leptolepis*

To recognise the genus *Leptolepis* the following characteristics are to be taken into consideration according to Konwert & Stumpf (2017): one suborbital is present, the accessory suborbital (as described by Nybelin (1974)) is absent (Arratia & Thies, 2001), the maxilla has a prominent longitudinal ridge on the lateral side, cranial roof elements do not bear ornamentation, the only location fringing fulcra are present is the dorsal lobe of the caudal fin, sclerotics are large and form a ring-like structure, and the postcleithrum is large and elongated. Arratia & Thies (2001) added the boomerang shape of the preopercle.

The characteristics of *L. nathorsti*

Nybelin (1974) proposed a preliminary diagnosis: Trapezoidal Opercle. Supraorbital sensory canal in the frontal bone, posteriorly with a postero-laterally directed tubule. The preopercular sensory canal has only six to eight tubules and the limbs of the preopercle are angled at 90 degrees and the cephalic sensory canal is near the arched anterior margin (Nybelin, 1974; Arratia, 1997). Nybelin (1974) later in his description remarks on the presence of a characteristic preopercular process on the hyomandibula, and the probable absence of the small notch in the anterior surface of the dentary to separate it from other species. We will use this character as a feature to assign some of our material loosely to *L. aff. nathorsti* with the taxonomic caveats in mind.

Material description

Cranial Bones: The *frontal bone* (Fig. 3) is not completely preserved. The posterior widened end with the sensory canals is preserved, but it seems to be missing most of the narrow anterior end. The supraorbital sensory canal has a slight bend at which issue two postero-medially directed tubules and further backwards a postero-laterally directed tubule. A parietal branch is not present.

Upper Jaw: The *maxilla* (Figs. 4, 5B, 6B & 7D) is an elongated convex bone. Teeth or sockets are not visible in any of the specimens. The posteriormost section of the maxilla shows concentric ornamentation. Slightly posterior of the dorsal margin there is an impressed surface, possibly for overlap of supramaxillae. On the lateral side there is a longitudinal ridge visible. The antero-medial end is long and contracted. The maxilla is

Figure 3. *Leptolepis aff. nathorsti*. Partial frontal bone, level 98 m at Janusfjellet, upper Oppdalssåta Member (PMO 228.899b).

abundant throughout the core and in the surface material. Both *supramaxillae* (Figs. 5B & 6E) have been found in the material. The anterior supramaxilla (SMX1) (Fig. 5B) is not completely preserved and the shape is hard to reconstruct. Nybelin (1974) described it to be long and narrow in *Leptolepis*. The posterior supramaxilla (SMX2) (Fig. 6E) is leaf shaped where the antero-dorsal process tapers into a point, with distinct lateral superficial ornamentation.

Figure 4. *Leptolepis asp.* right maxilla, 677.96 m in DH2, Lardy-fjellet Member (PMO 228.870).

Figure 5. *Leptolepis* sp. (A) quadrate. (B) Left maxilla, supramaxilla 1 & 2. From level 98 m at Janusfjellet, upper Oppdalssåta Member (PMO 228.896b)

Lower Jaw: The *dentary* (Figs. 6C & 8) is the most common preserved element, possibly because of the thickness of the rostral end, coronoid process and postero-ventral process. The ventral side is slightly convex. The size of the dentigerous area is not known since teeth or sockets are not visible in the specimens observed. There does not seem to be a small leptolepid notch in accordance with the criteria for “leptolepids” (Nybelin, 1974). The angle of the oral margin is at roughly 45° compared to the anteroposterior axis. The coronoid process is at a 90° angle and has a thin posterior wing with concentric ornamentation suggesting growth lines. This wing or dentigerous area is not preserved in every specimen. The *angular* (Fig. 7J) is poorly preserved. The elongated triangular outline is clearly visible and the small postero-ventral process is distinguishable.

Circumorbital bones: Two *infraorbitals* (Fig. 7C, I) are preserved; the sensory canal tubules are next to absent. The sensory canal is still visible. The shape of the infraorbital 3 (Fig. 7I) is squared and there is some light concentric ornamentation visible. The second infraorbital bone is harder to identify, but seems to be infraorbital 4 (Fig. 7C).

Hyoid & Palatoquadrate arches: The *hyomandible* (Fig. 7G) is preserved only as an impression. The opercular process is wing-like antero-dorsally like the hyomandible figured by Nybelin (1974). There is no sign of a preopercular process, but this could have been broken off after death. The *quadrate* (Fig. 5B) has a triangular shape and the surface of the bone is smooth. Anteriorly, the condyle is well defined but broken and the base of the postero-ventral quadrato-jugal process present. The length of the process can no longer be derived as it seems to have been broken and partially overlapped by another bone fragment. The *anterior ceratohyal* (Fig. 9) has an hourglass-shaped main structure. The main recognisable feature of this bone is the delicate thread-like ossification connecting the dorsal tips of its extremities. The thread is not preserved in the specimen, but can be derived from the clear hook-like structure at one side of the extremities where the dorsal tip has a small depressed surface.

Opercular bones: The *opercle* (Fig. 6A) is badly preserved and possibly damaged, but the trapezoidal shape, dorsally rounded, ventrally sharp-pointed outline is still visible. The concentric ornamentation of the surface is faint. The *subopercle* (Fig. 7E) has a trapezium shape where the posterior end curves convexly upward and there is a small ascending process at the antero-dorsal corner. The concentric ornamentation is clearly visible. The *preopercle* (Figs. 6D, 7B & 9) is sharply bent at its postero-ventral angle and the dorsal limb is nearly the same length as the anterior limb. Both taper in to sharp points. The outer face shows the distinctive simple sensory canal, with six ventrally branching tubules.

Vertebral column: There are numerous *vertebral centra* present (Figs. 6F, G & 7F, H). They are flattened, thin-walled, somewhat hourglass-shaped bones. Several have smooth surfaces and others show ring-like structures, indicative of chordacentra. Unfortunately, due to poor preservation, articulation surfaces of the arches or parapophyses were not observed. Internal moulds of the vertebrae show the diameter for the notochord was unconstricting.

Pectoral girdle: The *cleithrum* (Figs. 7A & 11) has an ‘s’-shaped anterior edge and bends sharply at its postero-ventral edge. The dorsal limb is stout and short. The ventral limb is longer and more slender.

Discussion

The long antero-medial end of the maxilla (PMO 228.895 and PMO 228.870) places our specimens in the “leptolepid” group according to Nybelin (1974). More recent studies have shown that the length of the anterior end of the maxilla is variable within leptolepid species (Arratia, 2017; Konwert & Stumpf, 2017). A long process can also be found in the Late Jurassic genera *Leptolepides*

Figure 6. The specimen PMO 228.893, level 38 m at Criocerasaksla, Upper Lardyfjellet Member. The slab contains several disarticulated elements belonging to *L. aff. nathorsti*. Highlighted are (A) opercle, (B) maxilla, (C) dentary, (D) preopercle, (E) supramaxilla 2 and (F & G) vertebral centra.

Figure 7. APMO 228.895 found at level 98m at Janusfjellet, upper Oppdalssåta Member, contains the following isolated elements assigned to *Leptolepis* sp. (A) cleithrum, (B) partial preopercle, (C) infraorbital 4, (D) partial maxilla, (E) subopercle. The preopercle (B) possibly belongs to *L. aff. nathorsti*.

and *Orthogonikleithrus* and other Late Jurassic teleosts (Arratia, 2017; Konwert & Stumpf, 2017). The genus *Leptolepis* has been the subject of revisions and is probably polyphyletic (Arratia, 1997, 2003). Some characteristics of *Leptolepis* are based on presence, absence or location of cranial/skeletal elements, useless for the disarticulated, isolated remains presented here, or on cranial elements not encountered. However, the remains collected in this study show strong resemblance to other species referred to the genus *Leptolepis* (Delsate & Thuy, 2005). In particular, the boomerang shape of the preopercle, its well defined limbs, and the prominent longitudinal ridge on the lateral side of the maxilla do compare to those found in *Leptolepis* (Arratia & Thies, 2001; Konwert & Stumpf, 2017). Woodward (1899) did not establish a holotype of

the species *L. nathorsti*, but Nybelin (1974) felt that the preopercle could be used as a lectotype. The frontal bone (Fig. 3), preopercle (Fig. 10) and hyomandible (Fig. 7G) all show characteristic features ascribed to *L. nathorsti* by Nybelin (1974). We therefore refer both the preopercle and the hyomandible to *Leptolepis aff. nathorsti* together with the associated bones on the same slab (PMO 228.893) from 38 m in the Criocerassaksla section, upper Lardyfjellet Member (Lower Kimmeridgian) (Fig. 6) (opercle, vertebra, supramaxilla 2, preopercle, dentary, maxilla) (Koevoets et al., 2016), and slabs found at 98 m in the Janusfjellet section, in the upper part of the Oppdalssåta Member (Upper Kimmeridgian), together with the bones shown in Figure 7 (maxilla, subopercle, cleithrum, frontal bone, supramaxilla 1, infraorbital 4,

Figure 8. Right dentary, level 536.45 m in DH2 core, Slotsmøya Member (PMO 228.781) assigned to *Leptolepis* sp.

Figure 9. Isolated partial anterior ceratohyal, level 553.40 m in DH2 core, Slotsmøya Member (PMO 228.802) assigned to *Leptolepis* sp.

Infraorbital 3, vertebra, quadrate and anterior ceratohyal). A tentative reconstruction of the skull (Fig. 12) based on the cranial material of this study was possible following guidelines from Nybelin (1974).

Other teleost elements of similar size and appearance as in the associations mentioned were found almost throughout the formation (Fig. 2), but since they were isolated and not associated with the diagnostic elements for *L. nathorsti*, they cannot be assigned to a species.

“Leptolepids” are distributed throughout the entire Agardhfjellet Formation (Fig 2). Considering the time span of the formation, it is highly unlikely that all specimens belong to *L. aff. nathorsti*. The diagnostic preopercula have so far been found only in the upper part of the Lardyfjellet Member at Criocerasaksla and in the upper part of the Oppdalssåta Member at Janusfjellet. This corresponds to Early and Late Kimmeridgian in age, respectively, which is considerably younger than previously reported for *L. nathorsti* (Woodward, 1899; Nybelin, 1974; Ginsburg & Janvier, 1974).

L. nathorsti was described to be of Early Jurassic age by Woodward (1899). His conclusion was based on the resemblance to a teleost group characteristic of the

Figure 10. Detailed high-contrast image of preopercle (PMO 228.893) belonging to *L. aff. nathorsti*.

Figure 11. Left cleithrum belonging to *Leptolepis* sp. Found at level 676.10 m in DH2, Lardyfjellet Member (PMO 228.867).

Toarcian (Upper Lias, Woodward (1899)) to Bathonian of mainland Europe. The material Woodward described was retrieved from Svenskøya and Kong Karls Land. The latter location was further specified by Nathorst (1901) as the southern slopes of Tordenskioldberget. Judging from the location, strata description as Aucella-shales by Nathorst (1901), collector of the material, and the detailed study ascribing an Early Oxfordian to Kimmeridgian age to these sediments by Smith et al. (1976), it must be concluded that the material is more likely Kimmeridgian in age.

Figure 12. Tentative reconstruction of *Leptolepis* aff. *nathorsti* based on associated cranial material from PMO 228.893 (38 m at Janusfjellet, Middle Volgian). FR – Frontal bone, MX – Maxilla, SMX 1 – Supramaxilla 1, SMX 2 – Supramaxilla 2, D – Dentary, ANG – Angular, Q – Quadrate, IFO 3 – Infraorbital 3, IFO 4 – Infraorbital 4, POP – Preopercle, OP – Opercle, SOP – Subopercle & CL – Cleithrum.

Ginsburg & Janvier (1974) mentioned encountering remains of *L. nathorsti* from the Toarcian at Lardyfjellet, East Spitsbergen. From the original report (Woodward, 1899) it is impossible to determine if the assumption of a Toarcian age is correct, since the mentioned characteristic ammonites are not named or pictured. The sediments are described as fine silts overlain by bituminous shales with thin carbonate beds, containing belemnites and ammonites (Woodward, 1899). This description of the strata bears more resemblance to the lower part of the Agardhfjellet Formation, namely the Oppdalen and Lardyfjellet members (Dypvik, 1984; Mørk et al., 1999; Dypvik et al., 2002; Koevoets et al., 2016).

Nybelin (1974) studied *L. nathorsti* more extensively than Woodward (1899) as part of a revision on “leptolepid” fishes. More material was obtained from a French expedition in 1969, which he described along with the existing material collected by Woodward. The French material was found at Deltanaset, Central Spitsbergen. Nybelin (1974) also based the age on the presence of Toarcian ammonites which in this article also are not depicted or described, making it difficult to verify. There is mention of the material described by Nybelin (1974) being associated with lower Lias “*Tricleidus svalbardensis*” (Persson, 1962), a species of plesiosaur recently redescribed as *Colymbosaurus svalbardensis* from the Slottsmøya Member (Volgian) by Knutsen et al. (2012a) and recent work by Roberts et al. (2017), after new specimens and information on the actual locality were discovered.

Later studies have shown that the only substantial Toarcian deposits in the Svalbard archipelago are found in Kong Karls Land, and these deposits consist mainly of sandstones (Harland et al., 1997; Mørk et al., 1999). This does not resemble the description of the black paper shales in which *L. nathorsti* was found by Nathorst (1901), Ginsburg & Janvier (1974) or Nybelin (1974). The only recent find of Toarcian ammonites in central and eastern Spitsbergen is in the Brentskardhaugen Bed (Bäckström & Nagy, 1985), which is a reworked conglomerate deposit marking the end of a hiatus (Harland et al., 1997; Mørk et al., 1999). Black paper shales are characteristic for the Oppdalen and Lardyfjellet members of the Agardhfjellet Formation (Dypvik, 1984; Mørk et al., 1999; Koevoets et al., 2016).

Comparing the finds in this study, which are Kimmeridgian to Volgian in age, and the recent research on stratigraphy in Kong Karls Land and Spitsbergen, it is more likely that the material described by Woodward (1899) was found in the paper shales of the Kimmeridgian Dunerfjellet Member (Smith et al., 1976; Dypvik, 1984; Mørk et al., 1999; Koevoets et al., 2016). This is in compliance with the characteristic cranial elements found in this study, associated with ammonites like the Lower Kimmeridgian cf., *Amoeboceras pingueforme* (Wierzbowski, 1989; Rogov, 2014; Koevoets et al., 2016) and the Upper Kimmeridgian *Haplocardioceras elegans* and *Zenostephanus* sp. Other teleost jaw elements are distributed throughout the formation and are also found at levels associated with the Bathonian *Kepplerites (Seymourites) svalbardensis* (Kopik & Wierzbowski, 1988; Koevoets et al., 2016), Oxfordian

Cardioceras sp. (Koevoets et al., 2016) and Middle Volgian *Dorsoplanites* sp. (Nagy & Basov, 1998; Rogov, 2010; Koevoets et al., 2016). These bones resemble the dentary and maxilla of *L. aff. nathorsti*, but the features are too similar to the jaw elements of other *Leptolepis* species and other teleosts to assign to *L. aff. nathorsti* beyond any reasonable doubt.

The teleost remains follow the occurrences of onychites closely (Fig. 2), suggesting they preferred similar habitats or preservation environment. Their occurrences extend into the Slottsmøya Member, coinciding with the numerous ichthyosaur and plesiosaur finds in the Jurassic of Central Spitsbergen (Hurum et al., 2012; Delsett et al., 2015). Several ichthyosaurs from the Jurassic around the world have been found with stomach contents. Most contain a mixture of cephalopod hooklets (Hammer et al., 2013) and teleost fish remains (Pollard, 1968; Keller, 1976; Bürgin, 2000), and this is also true for the coprolites where fish remains are more common (Pollard, 1968). A few larger vertebrates like ichthyosaurs, turtles and birds are identified in singular finds (Kear et al., 2003). The stomach contents of Jurassic long-necked plesiosaurs are similar to the ichthyosaurs, with cephalopod hooklets (Martill, 1993) and teleosts (Storrs, 1995). The Late Jurassic ichthyosaurs and long-necked plesiosaurs found in the Slottsmøya Member are mostly found without stomach contents, but it is likely that both groups fed on a mixture of cephalopods and teleosts.

Conclusions

Comparing the finds from the Lardyfjellet Member and the Oppdalssåta Member presented here to the material of *L. nathorsti* presented by Woodward (1899) and Nybelin (1974), with special focus on the preopercle which appears identical, there is little doubt that some of these remains belong to the same species. The stratigraphic location of the characteristic preopercles places *L. nathorsti* in the Kimmeridgian, not the Toarcian as previously assumed. Non-diagnostic elements of teleosts of similar size in the Agardhfjellet Formation suggest the presence of at least one species of “leptolepid” in the Volgian of Spitsbergen.

The presence of cephalopod hooklets in the Agardhfjellet Formation was already confirmed by Hammer et al. (2013), allowing for an educated guess that the larger Arctic marine reptiles fed upon belemnoids. Now, with the confirmed presence of teleosts in the Middle to Upper Jurassic of Spitsbergen, the spectrum of possible prey can be increased with more certainty.

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