

Vertebrate micro-remains from the Upper Devonian of East Greenland with comments on the Frasnian–Famennian boundary

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Blom, H., Carlsson, A. & Marshall, J.E.A. 2006–11–09. Vertebrate micro-remains from the Upper Devonian of East Greenland with comments on the Frasnian–Famennian boundary. *Bulletin of the Geological Society of Denmark*. Vol. 53, pp. 39–46. © 2006 by Geological Society of Denmark. ISSN 0011–0297. (www.2dgf.dk/publikationer/bulletin). <https://doi.org/10.37570/bgsd-2006-53-03>

Vertebrate micro-remains of jawless vertebrates (psammosteid heterostracans) and gnathostomes (acanthodians and sarcopterygians) occur in a residue collected from the Late Devonian Kap Graah Group sandstones of East Greenland. Fragmentary and isolated elements of psammosteids are assigned to *Psammosteus* sp. The acanthodians are represented by scales of acanthodiform type and poorly preserved fin spines. Tooth and scale fragments of sarcopterygians may suggest a porolepiform affinity. This assemblage and the associated macro-vertebrate fauna indicate a Frasnian age for an otherwise assumed Famennian part of the East Greenland succession, and do rather effectively bracket the Frasnian–Famennian boundary.

Keywords: Upper Devonian, East Greenland, Kap Graah Group, jawless vertebrates, psammosteids, acanthodians, sarcopterygians.

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Middle and Upper Devonian rocks of East Greenland contain a diverse record of fossil vertebrates, and many detailed studies have been made on the rich material of placoderms (Stensiö 1931, 1948; Stensiö & Säve-Söderbergh 1938), lungfishes (Lehman 1959), osteolepiforms (Jarvik 1952, 1985), porolepiforms (Jarvik 1972) and tetrapods (Ahlberg *et al.* 2005; Blom 2005; Blom *et al.* 2005). Very rare elements of heterostracans, chondrichthyans, acanthodians and actinopterygians have previously only been described briefly or merely reported (Bendix-Almgreen, 1976; Jarvik, 1961; Tarlo, 1964, 1965).

Stensiö and Säve-Söderbergh (1938, plate 9, fig. 4) described an acanthodian spine from the Givetian Red Siltstone Member ('*Asterolepis saevesoederberghi* Series') of the Nathorst Fjord Group of Canning Land as '*Onchus* sp.' (Fig. 1). The specimen is quite badly preserved and it is difficult to assign it to any known acanthodian taxa. Jarvik (1961) further reported undetermined acanthodian scales from the same sediments, but these specimens have not yet been located in any collections. Jarvik (1961) also reported the

occurrence of the acanthodian scales described in the present paper, but did not illustrate them or assign them to any known taxa. A patch of disarticulated spines from the talus of the Famennian Britta Dal Formation on Stensiö Bjerg has recently been found in association with what seems to be a tetrapod element (Blom, personal observation). The spines appear to be from an acanthodid similar to the Frasnian *Homalacanthus* (Russell 1951) from the Escuminac Formation of Miguasha, Quebec, Canada (Gagnier 1996).

Heterostracans are in Greenland, prior to this paper, known only from a single dermal bone fragment originally recognized as the drepanaspid *Psammolepis* Agassiz, 1844 by Ørvig (1961) and later described as *Psammolepis groenlandica* by Tarlo (1964, 1965). The specimen was collected at Sydryggen on Canning Land, in sediments originally referred to as the Givetian '*Asterolepis saevesoederberghi* Series', which on Canning Land has been formalized as the Red Siltstone Member (Fig. 1) of the Nathorst Fjord Group (Alexander-Marrack & Friend 1976).

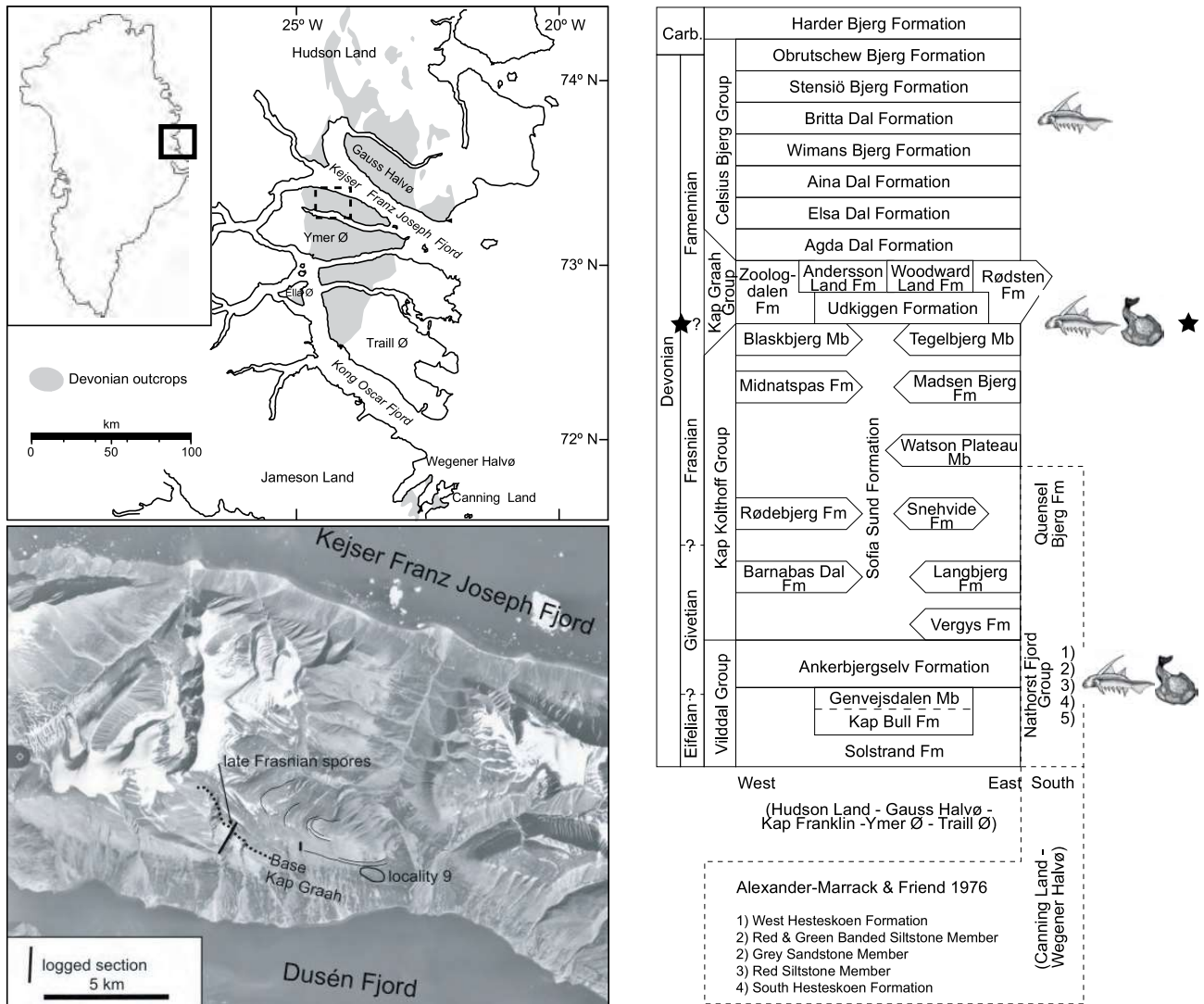


Fig. 1. Map and aerial photograph indicating locality 9 of Stensiö (1948) on Ymer Ø (north side of Düsenfjorden), and a stratigraphic column of the Devonian of East Greenland showing the general occurrence of acanthodians and psammosteids.

The material described herein originates from a residue housed in the vertebrate collections of the Geological Museum, Copenhagen (collection abbreviation, MGUH VP). The residue, which was already processed for micro-remains, contains a wide variety of vertebrate remains of acanthodians, heterostracans and sarcopterygians. This assemblage also focuses discussion on the Frasnian–Famennian boundary, which has been poorly known in the East Greenland succession.

Locality and geological setting

Very little information is available for the residue. However, the containers are labeled 'East Greenland,

Ymer Ø, Düsenfjorden, north side, locality A' (translated from Swedish). There is no doubt that this is the same acanthodian-yielding sample mentioned by Jarvik (1961, p. 199) since he refers his sample to "the lower part of the *Phyllolepis* series on Ymer Island (profile A of Nielsen 1936; see Stensiö 1948, p. 601)". Stensiö (1948, p. 601) in turn describes a locality 9 as "N. side of Dusén Fjord W. of Mt. Blask and W. of Zoologists' Valley, Profile A, measured by Nielsen 1936". It is, however, uncertain where in the profile the sample comes from, but Stensiö (1948, p. 601) describes two *Bothriolepis jarviki*-yielding horizons; "Horizon 435 m, in a greenish-grey conglomeratic sandstone, and in a whitish-grey sandstone" and "Horizon 977 m, in a greyish rather soft sandstone".

Despite the lack of locality detail, one can by inference from published maps (Stensiö 1948; Olsen &

Larsen 1993) and air photos (Fig. 1) be quite confident that the material comes from the base of the Kap Graah Group, which is one of four groups corresponding to four major stages of basin evolution and eleven individual depositional complexes, all representing different depositional facies and environments (Olsen 1993; Olsen & Larsen 1993). The whole succession of Middle and Late Devonian sediments, which is more than eight kilometers thick, was deposited in a continental basin. Sediments are exposed in a nearly 100 km wide N–S belt, extending about 200 km from Hudson Land in the north to Traill Ø in the south, as well as the outliers further south in Canning Land and on Wegener Halvø (Fig. 1).

On Gunnar Andersson Land, the Kap Graah Group is represented by five formations, the Zoologdalen, Andersson Land, Woodward Bjerg, Rødsten and Udkiggen formations, corresponding well with parts of the now superseded 'Phyllolepis Series' (Olsen & Larsen 1993). Jarvik (1961) referred the acanthodian material to the lower part of the 'Phyllolepis Series', although contradicted this by indicating an allocation to the upper part in the illustration. The lower occurrence is more likely to be correct since this level coincides with two *Bothriolepis jarviki*-yielding horizons as listed by Stensiö (1948), that are below the occurrence of *Phyllolepis orvini* Heintz, 1930. The sample most probably comes from the Andersson Land Formation, which surrounds the thin intercalation of the Zoologdalen Formation (Olsen & Larsen 1993, fig. 61).

This part of the succession has previously been considered Famennian in age from correlation using vertebrates (Jarvik 1961; Olsen & Larsen 1993), but the age of the lower vertebrate assemblage, that includes *Bothriolepis jarviki* Stensiö, 1948 as the only macro-vertebrate, could be either Frasnian or Famennian. It should, however, be noted that the placoderm *Phyllolepis* Agassiz, 1844 is restricted to the Famennian in Laurussia (Young 2005) and that spores from the top of the Elsa Dal Formation, (i.e. the top part of the 'upper *Phyllolepis* Series') indicate a mid Famennian (2b) age for the sediments above the Kap Graah Group (Marshall *et al.* 1999). Recent spore data from the Andersson Land area (Fig. 1) have indicated that late Frasnian spores occur in the lower parts of the Kap Graah Group.

Description of material

The material available consisted residues of variable sizes, together reaching a volume of approximately 200 ml. The size of the original sample is unknown

and very little can be said about how and when the sample was processed.

The sample is rich in vertebrate remains, but only few of the often very small and fragmentary pieces can be recognized and placed in established fossil groups. As most of the fragments are small (few reach a size larger than 2 mm) it seems that the material is well sorted and therefore was transported before deposition. Among the recognizable remains are acanthodian scales and spines, psammosteid elements and sarcopterygian fragments.

Psammosteids

Psammosteid remains are quite rare in this sample and are also very fragmented. They are only preserved as isolated tubercles or as very small patches of tubercles on a small basal portion of spongy bone. The tubercles themselves are quite well preserved, but are often covered by quartz grains that have not become detached during preparation. This can sometimes make it difficult to assess the full morphology of the individual tubercles. The elements and fragments show variable morphology and vary in size, from less than 1 mm to almost 2 mm in diameter.

One type of element has several tightly packed tubercles attached to a broken base (Fig. 2A). These tubercles are usually irregularly elongated with notched or irregular margins. They are also characterized by a smooth and flat or slightly convex upper surface. Although more complex, these elements are broken and do not seem to represent a complete psammosteid 'tesserae' or scale.

Another type represented in the sample is the simple rounded element with a rounded crown-like tubercle on a well-developed base of equal size (Fig. 2B). The rather high tubercle is round and convex. It has ridges and deep notches on the margins and lateral sides, and is separated from the base by a distinct neck. In contrast to the other types of elements from this sample, these thelodont-like elements appear to represent an isolated unit.

Some elements resembles the more complex type with several crowns, but have only one tubercle preserved on the broken base (Fig. 2C, D), which suggests wider spacing between the tubercles when distributed on a larger base/plate. These tubercles are a little higher and more pointed than those tightly packed on the multiple elements. This third type has tubercles which are oak-leaf shaped or more rounded with deep marginal notches and ridges.

The fragmentary nature of these psammosteid elements makes it very difficult to assess their taxo-

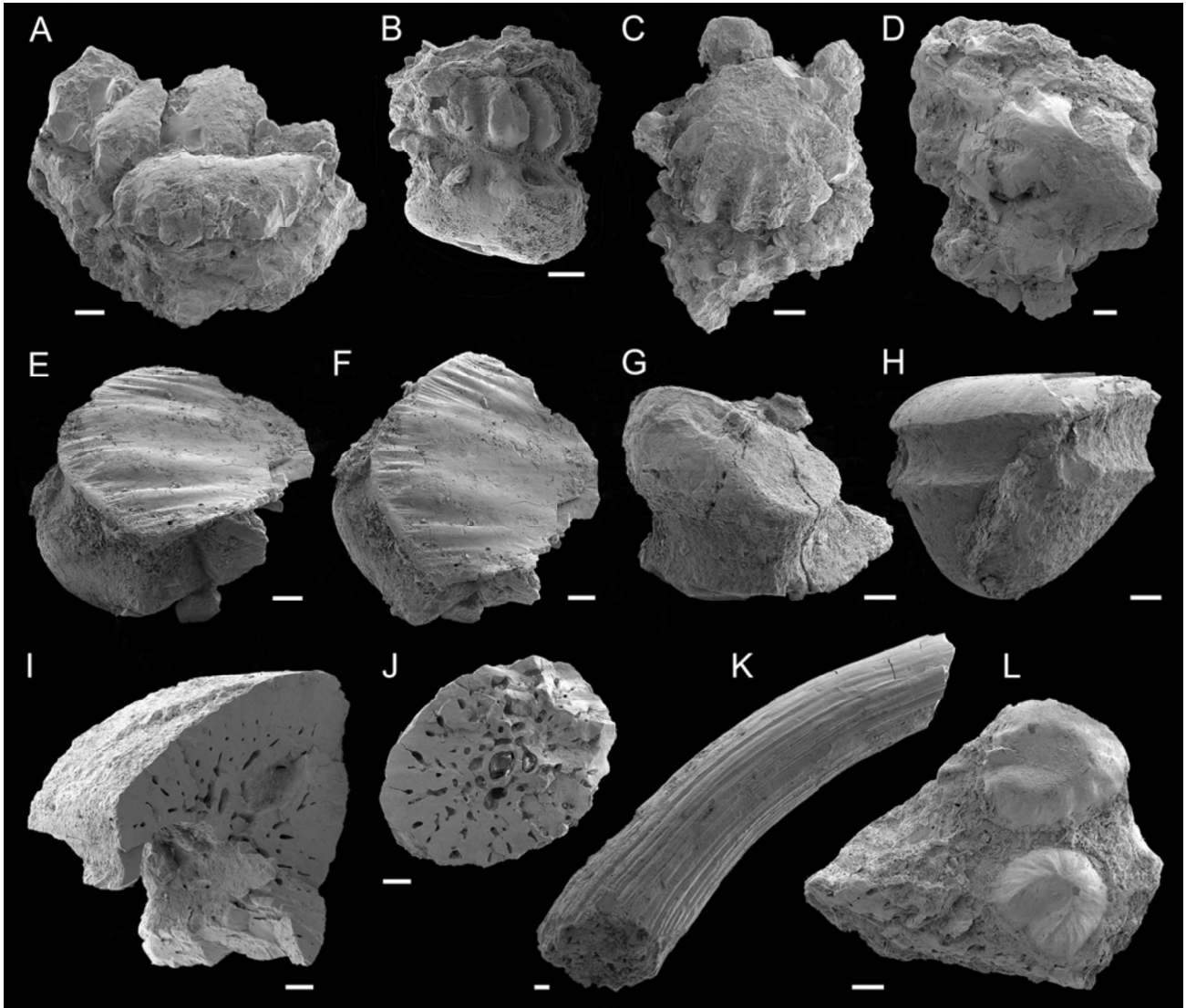


Fig. 2. Micro-remains from the north side of Dösenfjorden, Ymer Ø, East Greenland. A-D, *Psammosteus* sp. A, MGUH VP 28358, oblique external view. B, MGUH VP 28359, lateral view. C, MGUH VP 28360, oblique external view. D, MGUH VP 28361, external view. E-H, Cheiracanthid scales. E, MGUH VP 28362, oblique crown view. F, MGUH VP 28362, crown view. G, MGUH VP 28363, oblique basal view. H, MGUH VP 28364, lateral view. I, Acanthodian spine fragment in oblique distal view, MGUH VP 28365. J-K, *Sarcopterygii* indet. J, MGUH VP 28366, tooth fragment in cross section, distal view. K, MGUH VP 28367, tooth fragment in lateral view. L, MGUH VP 28368, scale fragment in external view. Scale bars equals 0.1 mm.

nomic affinity. This is further emphasized by previous observations that the morphology of the tubercles varies depending on where on the psammosteid fish body they originated (Tarlo 1965; Mark-Kurik 1999). The morphologies described herein show some similarity to most other elements of psammosteids of Late Devonian age (Tarlo, 1965). However, *Psammosteus* Agassiz, 1844 differs from all other psammosteids by the presence of micromeric thelodont-like elements that, in addition, have stages during their exoskeletal growth and development where tubercles are more loosely attached to the bony plates

(Mark-Kurik 1999). This observation suggests that the small broken fragments and isolated elements in our sample belong to *Psammosteus* or a form that is closely related to this genus.

Acanthodians

The acanthodian scales are better preserved than most other elements in the sample. However, their preservation is still somewhat limited, and many scales are broken along the growth layers and there-

by often losing the morphology of the external surface. The scales vary in size from 0.5 mm to 1.5 mm. All the scales fall within one type of morphology with an almost regular diamond-shaped crown and slightly more rounded anteriorly. The crown is flat with two or more, wide, smooth and low ridges extending from the anterior margin to two thirds of the crown posteriorly where they taper. These medial ridges are widest and longest medially and smaller towards the lateral margins. Between these main ridges are much smaller and sharper ridges of various sizes (Fig. 2E, F). These smaller ones only reach a short distance posteriorly from the anterior margin. The neck is rather high and distinct without any major down-turned portion of the crown. The base is high and strongly convex with the highest portion pointing slightly anteriorly.

A few very poorly preserved spine fragments have also been found and show very few diagnostic characters, apart from the fact that they seem to be quite smooth along the anterior surface. The spines are always broken into small pieces and expose a large central cavity (Fig. 2I). It also seem like the breakage occur along a longitudinal groove on each side.

The taxonomic affinity of the acanthodian material is of greatest interest as it emphasizes the poor knowledge of Late Devonian acanthodian micro-remains. The better preserved scales show close resemblance to *Devononchus concinnus* (Gross, 1930) scales as have been illustrated by Valiukevicius (1998, plate 8, figs 17-20). The genus *Devononchus* (Gross, 1940), however, was established on fin spines only and the scales that have subsequently been assigned to the various species of this genus may in fact belong to different genera, for example *Homalacanthus* Russell, 1951 (Beznosov 2005). However, the scale type under discussion is morphologically very different from *Homalacanthus concinnus* scales described by Miles (1966, fig. 1 16A), and more similar to cheiracanthids in general (Valiukevicius 1985). The *Devononchus concinnus* affinity for the scales illustrated by Valiukevicius (1998, pl. 8, figs 17-20) may be questioned since Gross's view of which scales belong to the spines that define this taxon, was only noted and the evidence never properly described or illustrated (Gross 1940), and Valiukevicius' (1998) assignment was morphologically inferred from those notes by Gross (1940) (Valiukevicius personal communication 2006).

Superficially the scales in this sample are also similar to the Frasnian scales named *Haplacanthus perseus* Gross, 1942. However, the latter lack the finer ridges in between the larger ones. Scales similar to this taxon, but with these fine ridges have been found in the lower Famennian of the East European Platform and upper Frasnian of North Timan (Beznosov

personal communication 2005). Until the taxonomy of Upper Devonian acanthodian scale and spine taxa has been better resolved, we feel inclined not to assign our material in greater detail other than saying it is an acanthodiform.

The affinity of the very poorly preserved spines is much more difficult to assess. If the scales indeed belong to cheiracanthids, the spines may also be of that type since *Homalacanthus* spines and most other acanthodiforms are in general smooth with a single longitudinal groove on each side (Denison 1979; Gagnier 1996).

Sarcopterygians

Several small fragments can be assigned to sarcopterygian fishes. Numerous fragments of teeth have been recognized and most of them share the characters of being from a long slender tooth, slightly curved and with numerous fine ridges along the surface of the tooth. In cross section the teeth are characterized by large scale folding of dentine and with the core filled with bone or osteodentine (Fig. 2J). However, it is unclear if there is any degree of secondary folding. The combination of having a slender, fine striated tooth with folded dentine and a filled pulp cavity may suggest a parasymphysial tooth affinity of these fragments, most likely from a porolepiform.

Other smaller fragments include small scale fragments characterized by tubercles with a shallow anterior located concavity (Fig. 2L). The lateral and posterior sides have fine ridges radiating from the apex. Also, in the broken fragments, it is possible to recognize the typical vascular middle layer and the more compact basal layer. This type of horseshoe-shaped ornament is present in porolepiforms (Ørvig 1957), dipnoans (Schultze 1992), onychodonts (Ørvig 1957) and coelacanth (Forey *et al.* 2000). In the context of the assumed porolepiform symphysial tooth whorl it seems reasonable to assign these fragments to a porolepiform such as *Glyptolepis* Agassiz, 1844 or *Laccognathus* Gross, 1941 (see Ørvig 1957).

Discussion and conclusions

The faunal composition of the sample, despite being somewhat fragmentary and taxonomically uncertain, clearly indicates that this part of the succession is not Famennian in age as previously suggested (Jarvik 1961). This observation allows further discussion

on the position of the Frasnian–Famennian boundary in East Greenland.

As has been discussed above, one can conclude that the present sample most certainly originates from the lower parts of the Andersson Land Formation of the Kap Graah Group (Olsen & Larsen 1993). Jarvik (1961) referred this part of the succession ('*Phyllolepis* Series, lower part') to the Famennian, based on the vertebrate assemblage including *Bothriolepis jarviki*, indet Selachii, *Cladodus* sp. and *Holoptychius* spp. This faunal composition does not suggest anything more detailed than a Frasnian–Famennian age. Higher in the succession, in the '*Phyllolepis* Series, upper part' *sensu* Jarvik (1961), the assemblage is characterized by *Phyllolepis orvini* Heintz, 1930, *Bothriolepis groenlandica* Stensiö, 1948, *Nilsenia nordica* Lehman, 1959, ?*Soederberghia*, and *Holoptychius* spp. A Famennian age for this upper assemblage is supported by the presence of *Phyllolepis*. Phyllolepidids, which also include other genera similar to *Phyllolepis* are only recorded in Famennian rocks in Laurussia (Young 2005).

The occurrence of psammosteids in our sample from the lower '*Phyllolepis* Series' assemblage of Jarvik (1961) indicates a Frasnian age. A faunal turnover in the Late Devonian, including the replacement of the Frasnian psammosteids by the phyllolepidids in the Famennian has been observed broadly in Laurussia (Esin *et al.* 2000; Young 2005).

This faunal turnover can also be discussed in terms of the distribution of the various species of *Bothriolepis* in East Greenland when compared with the Baltic region. *Bothriolepis leptocheira* Traquair, 1893 from Scotland and the Eastern European Platform most resembles, but is a different taxon from *Bothriolepis jarviki* (Luksevics 2001). Although generally considered as exclusively Famennian in age (Luksevics 2001), new finds of *Bothriolepis leptocheira* in the Amula Formation of the Baltic section suggest this species in fact crosses the Frasnian/Famennian boundary (Luksevics personal communication 2005). Likewise, *Bothriolepis groenlandica* is very similar to the type species, *Bothriolepis ornata* Eichwald, 1840 (Luksevics 2001), and could well be synonymous (Luksevics personal communication 2005). In the East Baltic and NW Russia, *B. ornata* has always been found together with *Phyllolepis* (Esin *et al.* 2000, Luksevics personal communication 2005).

With the new data presented here, we can with confidence suggest that the Frasnian–Famennian boundary can be found between the upper and lower part of the now obsolete '*Phyllolepis* Series'. The question remains as to how this correlate with the recent lithostratigraphic framework of Olsen & Larsen (1993).

Palynological recovery is generally poor to average through the upper part of the Kap Kolthoff Group. These assemblages are clearly Frasnian in age as they contain a significant number of *Archaeoperisaccus* (Naumova) McGregor 1969. They also contain a number of specific mid Frasnian elements including *Membra-baculisporis radiatus* (Naumova Arkhangelskaya 1985). Spore assemblages then become very impoverished in the lower part of the Kap Graah Group and comparisons with palynological assemblages from northern Russia (e.g. Obukhovskaya *et al.* 2000) suggest a position close to or at the Frasnian–Famennian boundary. However, the lack of any palynological recovery through the remainder of the Kap Graah Group until the uppermost Elsa Dal Formation (Fa2b) of the Celsius Bjerg Group precludes the possibility of any more stratigraphical precision.

Therefore it can be suggested that the Frasnian–Famennian boundary occurs in the lower part of the Andersson Land Formation of the Kap Graah Group on Andersson Land (Ymer Ø).

Acknowledgements

We are grateful to Gilles Cuny (Geological Museum, Copenhagen) for access and loan of material. We also thank Gaël Clement (Paris), Pavel Beznosov (Syktyvkar) and Ervins Luksevics (Riga) for valuable information and discussions. Carole Burrow (Brisbane) and Ervins Luksevics are also acknowledged for reviewing the manuscript. This paper is a contribution to IGCP Project 491 (Middle Palaeozoic vertebrate biogeography, palaeogeography and climate).

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