

Devonian vertebrates from East Greenland: a review of faunal composition and distribution

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ABSTRACT

The Devonian vertebrate faunas of East Greenland are reviewed and their distribution discussed for the first time in the light of the most recently published stratigraphical framework for the area. The predominantly Middle and Upper Devonian continental sediments have yielded representatives of most major groups of early fossil vertebrates, including heterostracans, placoderms, acanthodians, chondrichthyans, actinopterygians, lungfishes, porolepiforms, “osteolepiforms” and tetrapods, but to date, no single publication has treated them all in their stratigraphical context. We therefore attempt to place them into the most recent, formalised lithostratigraphy, providing improved resolution for their stratigraphical distribution, as a basis for comparing East Greenland with other Devonian faunal successions worldwide. The review highlights the fact that many problems of stratigraphical correlation and dating of the East Greenland Devonian deposits remain to be resolved by further fieldwork. Several

KEY WORDS

Vertebrates,
Devonian,
East Greenland,
stratigraphy,
distribution.

assemblages ranging from Givetian to Famennian in age can be distinguished, that correspond to older superceded subdivisional nomenclature. A possible Frasnian fauna has been recognised for the first time, adding details to an otherwise poorly dated part of the succession. Typical Devonian taxa such as *Holoptychius* Agassiz, 1839 and *Groenlandaspis* Heintz, 1932 have apparently been recorded in an otherwise unique position above the Devonian-Carboniferous boundary in the upper part of the succession. New specimens of rare elements of the fauna including an unknown arthrodire placoderm, a putative chondrichthyan spine and a patch of possibly regurgitated acanthodian spines, are illustrated for the first time.

RÉSUMÉ

Les vertébrés dévoniens de l'est du Groenland: une révision de la composition et de la distribution fauniques.

Les faunes des vertébrés dévoniens de l'est du Groenland sont révisées et leur distribution est pour la première fois discutée sur la base de publications récentes traitant de la stratigraphie de cette région. Les sédiments d'origine continentale, datés du Dévonien moyen et supérieur, ont livré des fossiles attribuables à la plupart des grands groupes de vertébrés dits « inférieurs » : hétéostracés, placodermes, acanthodiens, chondrichtyens, actinoptérygiens, dipneustes, porolépiformes, « ostéolépiformes », et tétrapodes. Jusqu'à présent, aucun travail n'avait traité de ces occurrences dans un contexte stratigraphique. Nous avons donc placé ces occurrences dans le cadre des études lithostratigraphiques les plus récentes afin d'obtenir une meilleure résolution de leur distribution stratigraphique. Ce travail sert également de base pour les comparaisons de successions fauniques entre le Dévonien de l'est du Groenland et les autres localités du monde. Cette révision met également en évidence les nombreux problèmes de corrélation stratigraphique et de datation des dépôts dévoniens de l'est du Groenland, qui nécessitent de nouvelles missions de terrain afin de les résoudre. Plusieurs assemblages faunistiques, s'étendant du Givétien au Famennien, peuvent être distingués. Ces assemblages remplacent les précédentes subdivisions de nomenclature. Une faune frasnienne putative a été reconnue pour la première fois, apportant de nouvelles données à une partie mal datée de la succession. Des taxons typiquement dévoniens tels que *Holoptychius* Agassiz, 1839 et *Groenlandaspis* Heintz, 1932 ont apparemment été reconnus au-dessus de la limite Dévonien-Carbonifère. Des nouveaux spécimens, rares dans la succession, sont ici illustrés pour la première fois : un probable placoderme sélénostéide, une possible épine de chondrichtyen et un ensemble d'épines d'acanthodiens supposé issu d'une régurgitation.

MOTS CLÉS

Vertébrés,
Dévonien,
est du Groenland,
stratigraphie,
distribution.

INTRODUCTION

The Upper Devonian sequences of East Greenland have been famous for vertebrate palaeontology for many decades, especially because they yielded the first specimens of the then earliest known tetrapod,

Ichthyostega Säve-Söderbergh, 1932. Although the stratigraphy of the region has long been studied, no single publication has brought together information about the distribution of all the vertebrate material, because of the practical difficulties of collecting in the area. Moreover, many specimens are talus-derived

and numerous problems remain in resolving the stratigraphical and faunal relations of the taxa. The stratigraphical distribution of the vertebrate taxa was not usually a major focus of interest for many of the earlier vertebrate workers, who tended to concentrate on anatomical descriptions. This review takes in consideration the most recently published lithostratigraphical information, and by including data from previously unpublished field notes from earlier expeditions, locality data available only from specimen labels (e.g., tetrapods, Blom *et al.* 2005) and information from older literature, attempts to assess the current status of understanding of vertebrate biostratigraphy in the area.

After a historical review of the collecting in the area and publications that present data on the vertebrate material, we discuss the distribution of the vertebrate taxa according to the framework of Olsen & Larsen (1993), the most recent survey to deal with the vertebrate-bearing sequences. We show how the historically older stratigraphical divisions and their nomenclature, often based on their vertebrate content, relate to Olsen & Larsen's scheme, attempting to correlate faunas from different areas of the Devonian basin (Fig. 2). Placing Jarvik's (1961) biostratigraphical subdivisions into a modern formal lithostratigraphical context provides a basis for future establishment of biozonations and comparison of East Greenland with other Devonian successions worldwide. We then deal with each of the major vertebrate groups, in turn summarising what is known of each of them, as far as possible where they are found (recorded locality data is often imprecise), their relative abundance, and point out some problems of identification (Table 1). We emphasise that many of the remaining problems can only be resolved by further fieldwork, for example those expressed by Hartz *et al.* (1997, 1998), Marshall *et al.* (1999) and Hartz (2000), regarding boundary definitions, stratigraphical correlation and dating of the East Greenland Devonian deposits.

HISTORY OF COLLECTING

Vertebrate fossils from the Devonian sequences of East Greenland were first discovered on Ymer Ø

TABLE 1. — East Greenland vertebrate fauna.

Heterostraci	<i>Psammolepis groenlandica</i> Tarlo, 1964
Chondrichthyes	<i>Cladodus</i> (tooth)
	Chondrichthyes gen. et sp. indet. 1 (spine)
	Chondrichthyes gen. et sp. indet. 2 (spine)
Placodermi	<i>Homostius kochi</i> Stensiö & Säve-Söderbergh, 1938
	<i>Heterostius groenlandicus</i> Stensiö & Säve-Söderbergh, 1938
	<i>Clarkeosteus</i> cf. <i>C. halmodeus</i> (Clarke, 1893)
	<i>Phyllolepis orvini</i> Heintz, 1930
	<i>Phyllolepis nielseni</i> Stensiö, 1939
	<i>Groenlandaspis mirabilis</i> Heintz, 1932
	Arthrodira gen. et sp. indet. 1
	Arthrodira gen. et sp. indet. 2
	Arthrodira gen. et sp. indet. 3
	<i>Asterolepis saevesoederberghi</i> Stensiö & Säve-Söderbergh, 1938
	<i>Asterolepis</i> cf. <i>A. saevesoederberghi</i> Stensiö & Säve-Söderbergh, 1938
	<i>Bothriolepis groenlandica</i> Heintz, 1930
	<i>Bothriolepis jarviki</i> Stensiö, 1948
	<i>Bothriolepis nielseni</i> Stensiö, 1948
	<i>Remigolepis incisa</i> (Woodward, 1900)
	<i>Remigolepis cristata</i> Stensiö, 1931
	<i>Remigolepis acuta</i> Stensiö, 1931
	<i>Remigolepis kochi</i> Stensiö, 1931
	<i>Remigolepis kullingi</i> Stensiö, 1931
	<i>Remigolepis? tuberculata</i> Stensiö, 1931
	<i>Remigolepis emarginata</i> Säve-Söderbergh, 1932 (<i>nomen nudum</i>)
Acanthodii	Acanthodii gen. et sp. indet. 1 (spine) (<i>Onchus</i> sp.)
	Acanthodii gen. et sp. indet. 2 (scales)
	Acanthodidae gen. et sp. indet. (spines + scales)
Actinopterygii	<i>Cuneognathus gardineri</i> Friedman & Blom, 2006
Porolepiformes	<i>Glyptolepis groenlandica</i> Jarvik, 1972
	<i>Holoptychius</i> spp.
	Porolepiformes gen. et sp. indet.
Dipnoi	<i>Dipterus</i> sp.?
	<i>Nilsenia nordica</i> Lehman, 1959
	<i>Soederberghia groenlandica</i> Lehman, 1959
	? <i>Soederberghia</i> sp.
	<i>Jarvikia arctica</i> Lehman, 1959
	<i>Oervigia nordica</i> Lehman, 1959
	Dipnoi gen. et sp. indet.
Osteolepiformes	<i>Gyroptychius groenlandicus</i> Jarvik, 1950
	<i>Gyroptychius dolichotatus</i> Jarvik, 1985
	<i>Thursius? minor</i> Jarvik, 1985
	<i>Spodichthys buetleri</i> Jarvik, 1985
	<i>Eusthenodon waengsjoei</i> Jarvik, 1952
	Tristichopteridae sp.
	<i>Panderichthys</i> sp.?
Tetrapoda	<i>Acanthostega gunnari</i> Jarvik, 1952
	<i>Ichthyostega stensioei</i> Säve-Söderbergh, 1932
	<i>Ichthyostega watsoni</i> Säve-Söderbergh, 1932
	<i>Ichthyostega eigilli</i> Säve-Söderbergh, 1932
	Tetrapoda n. gen. et sp.

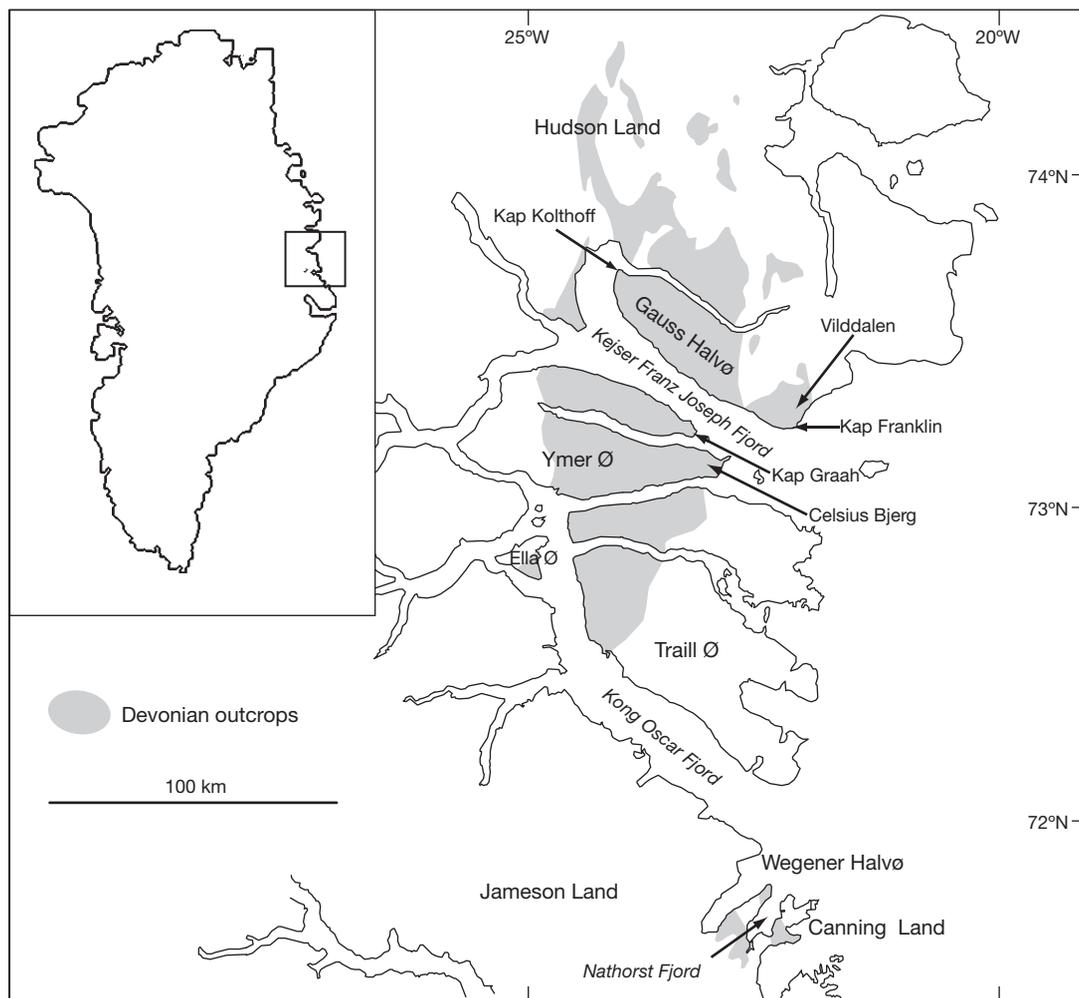


FIG. 1. — Map of East Greenland showing extent of the Devonian outcrops. Based on Olsen & Larsen (1993).

(Fig. 1) in 1899 by the Swedish palaeobotanist Nathorst, and described by Woodward (Woodward 1900; Nathorst 1901). In 1929 activities were intensified by a Danish expedition under the direction of Koch (1930) and a Norwegian expedition led by Orvin (1930). Norwegian field research in East Greenland ended with a second expedition in 1930, yielding only a few vertebrate fossils that were described by Heintz (1930, 1932). However, since the Danes wanted to secure their interests in East Greenland, Koch was easily able to raise funds for several Danish expeditions in the area, which

would continue more or less for the next two and a half decades (Jarvik 1996; Ries 2002, 2003). During the first Danish expedition in 1929, collecting and stratigraphical work in the Devonian sequences were done primarily by Kulling (1930, 1931), who brought back fossil vertebrates that were later described by Stensiö (1931). Following the success of this work and, more importantly, the discovery in 1931 of skulls of the first Devonian tetrapod, *Ichthyostega* (Säve-Söderbergh 1932a; Jarvik 1952, 1985, 1996), fieldwork continued regularly until 1957. This period of thorough col-

lecting provided the raw materials for extensive work on the Devonian vertebrates from East Greenland (see Jarvik 1996 for review). Detailed studies have been made on placoderms (Stensiö 1931, 1934, 1936, 1939, 1948; Stensiö & Säve-Söderbergh 1938), actinopterygians (Friedman & Blom 2006), lungfishes (Lehman 1959), osteolepiforms (Jarvik 1952, 1985), porolepiforms (Jarvik 1972; Ahlberg 1989a) and tetrapods (Säve-Söderbergh 1932a; Jarvik 1950a, 1952, 1985, 1996; Clack 1988a, 1989, 1992, 1994, 1998, 2002a, b, 2003; Coates & Clack 1990, 1991; Coates 1996; Ahlberg & Clack 1998; Clack *et al.* 2003; Ahlberg *et al.* 2005; Blom 2005). The rare remains of heterostracans, chondrichthyans and acanthodians have heretofore only been described briefly or their presence merely reported (Jarvik 1961; Tarlo 1964, 1965; Bendix-Almgreen 1976).

A brief review of the Devonian vertebrates of East Greenland and biostratigraphical subdivisions of these sediments was originally presented by Jarvik (1961), and later updated by Bendix-Almgreen (1976). Both presented very broad pictures of the distribution of taxa, which were based on previous stratigraphical studies by workers such as Bütler (1935, 1940, 1954, 1959, 1961) and Säve-Söderbergh (1932b, 1933, 1934). Their conflation of both bio- and lithostratigraphical units was confusing and the correlation between different areas and their successions were not fully explored. More detailed recent studies have, however, resulted in a change in the stratigraphical framework as a result of modern sedimentological methods and formalised unit terminology (Alexander-Marrack & Friend 1976; Friend *et al.* 1976a, b; Nicholson & Friend 1976; Yeats & Friend 1978; Friend *et al.* 1983; Olsen 1993; Olsen & Larsen 1993). Vertebrates have also been the subject of new studies since Jarvik's (1961) and Bendix-Almgreen's (1976) reviews. Jarvik (1985) produced a detailed review of known osteolepiforms and described three new taxa. The tetrapods in general, and *Acanthostega* Jarvik, 1952 in particular, have also been re-examined in great detail (Clack 2002b). Central to this latter study was fieldwork in 1987 and 1998 that resulted in new material of both tetrapods and fishes (Clack 1988a, b; Bendix-Almgreen *et al.* 1990; Clack & Neininger 2000).

GEOLOGICAL SETTING AND STRATIGRAPHICAL FRAMEWORK

In East Greenland, Devonian sedimentary rocks containing fossil vertebrates crop out 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 small outliers further south in Canning Land and on Wegener Halvø (Fig. 1). The whole succession is more than 8 km thick and was deposited in a Mid to Late Devonian continental basin, which accumulated sediments representing a number of different depositional facies and environments (Olsen 1993; Olsen & Larsen 1993). The age of the upper basin deposits have been argued to be Carboniferous (*c.* 335 Ma) rather than Devonian as previously suggested, based on ⁴⁰Ar/³⁹Ar plagioclase ages from basalts and palaeomagnetic data (Hartz *et al.* 1997, 1998). Stemmerik & Bendix-Almgreen (1998) argued against this age on the basis of lithostratigraphical correlation between the basalts and sediments dated by spores. Marshall *et al.* (1999) have subsequently used new detailed palynology data to show that the deposits are Devonian in age. This conclusion appears to have satisfied Hartz (2000).

In the most recent lithostratigraphic framework for the continental Devonian sediments of East Greenland, Olsen & Larsen (1993) proposed a scheme with four groups: Vilddal Group, Kap Kolthoff Group, Kap Graah Group and Celsius Bjerg Group. Their study was based on a review of previous work (Bütler 1935, 1940, 1954, 1959, 1961; Alexander-Marrack & Friend 1976; Friend *et al.* 1976a, b; Nicholson & Friend 1976; Yeats & Friend 1978; Friend 1978; Friend *et al.* 1983) plus new observations in the field. It included an analysis that revealed a coherent picture of sedimentary basin evolution, with four major stages corresponding to the above-mentioned groups and eleven individual depositional complexes (Olsen 1993). Their lithostratigraphical subdivision has since been challenged by researchers who find their boundary definitions awkward (Hartz *et al.* 1997; Hartz 2000), and who favour the approach proposed by Bütler (1959). These more recent studies emphasise the lithological heterogeneity and diachronous nature of the deposits,

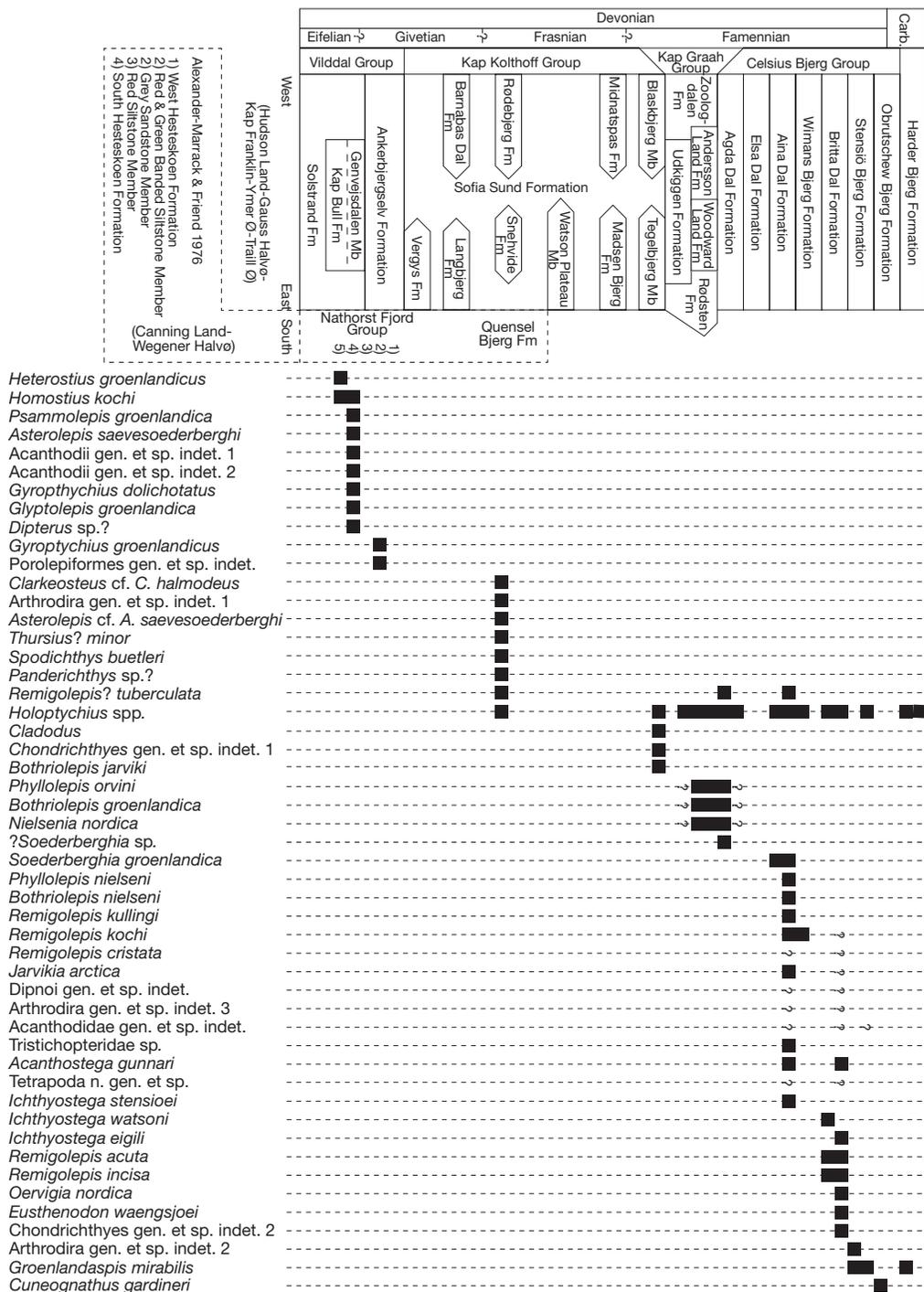


FIG. 2. — Distribution of vertebrates in East Greenland.

which has great implications for the relationship between the Vilddal and Kap Kolthoff groups and potentially also for the distribution of vertebrates. However, the validity of their arguments cannot be tested without further extensive fieldwork and mapping. The distribution of vertebrates presented here is therefore put in the framework given by Olsen & Larsen (1993), but continuing problems with stratigraphy, correlation and age are elaborated and discussed further below.

The Vilddal Group is the oldest of the four groups and considered to be deposited by meandering and braided rivers, ephemeral streams and associated floodplains (Olsen & Larsen 1993). Jarvik (1950b) suggested a late Mid Devonian (Givetian) age for these rocks, on the basis of fossil fishes from eastern Gauss Halvø. Spores and megaspores found more recently on Ella Ø support this age (Allen 1972; Friend *et al.* 1983; Marshall & Hemsley 2003). The Solstrand and Kap Bull formations comprise the lower part of this group, while Ankerbjergselv Formation makes up the upper part (Fig. 2). To the south of the main Devonian field lie Canning Land and Wegener Halvø. Alexander-Marrack & Friend (1976) erected the Nathorst Fjord Group for the successions there, but it was not incorporated into the Vilddal Group by Olsen & Larsen (1993), because the detailed relations between these two lithostratigraphic units were considered uncertain. Alexander-Marrack & Friend (1976), however, suggested that the Vilddal Group does correlate with the Nathorst Fjord Group on the basis of fossil fish as well as depositional history. They subdivided the Nathorst Fjord Group into the South Hesteskøen Formation, the Red Siltstone, Grey Sandstone and Red and Green Banded Siltstone members of the Vimmelskafet Formation, and the West Hesteskøen Formation (Fig. 2). Alexander-Marrack & Friend (1976) correlated their formal lithostratigraphical units with the series originally established by Säve-Söderbergh (1937) on the basis of fossil content. They showed that: the "*Heterostius* Series" of Säve-Söderbergh corresponds to the South Hesteskøen Formation; the "*Asterolepis säve-söderberghi* Series" (this old incorrect spelling of *Asterolepis saeve-soederberghi* Stensiö & Säve-Söderbergh, 1938 is only used when referring to the originally named

subdivision) to the Red Siltstone Member and the "*Gyroptychius groenlandicus* Series" to the Red and Green Banded Siltstone Member. It is, however, uncertain whether the "*Gyroptychius groenlandicus* Series" also included sediments equating to the Grey Sandstone Member and the West Hesteskøen Formation. Spores in the lower part of the Red Siltstone Member unequivocally indicate an Eifelian age (Marshall & Astin 1996). Although the Vilddal Group at Kap Franklin is difficult to date palynologically because of thermal maturation, some spores from the Red and Green Banded Siltstone Member do indicate a Givetian age for the top of the group (Marshall & Astin 1996). The overlying Kap Kolthoff Group, with its predominantly sandy braidplain deposits, is composed mainly of undifferentiated Sofia Sund Formation, except for the locally and sedimentologically distinct Barnabas, Rødebjerg, and Midnatspas formations in the West and Vergys, Langbjerg, Snehvide and Madsen Bjerg formations in the East (Olsen & Larsen 1993). Fossil vertebrates are found in the upper and lower parts of the Sofia Sund Formation and in the Rødebjerg Formation (Olsen & Larsen 1993). The Kap Kolthoff Group spans from the undoubtedly Givetian Vilddal Group (Allen 1972; Friend *et al.* 1983; Marshall & Astin 1996; Marshall & Hemsley 2003) to the Kap Graah Group, suggested to be Famennian in age (Olsen & Larsen 1993) but there is nothing within the sequence to indicate the position of the upper or lower boundaries of the Frasnian. The possible diachronous nature of the lower deposits further complicates age assignment in general and the lithological relation to the Vilddal Group in particular, as discussed further below. The boundaries between the Givetian, Frasnian and Famennian strata thus remain unclear throughout the basin.

The Upper Devonian (Famennian) Kap Graah Group, which succeeds the Kap Kolthoff Group, according to Olsen & Larsen (1993) was deposited both by fluvial systems and aeolian sand seas. The Udkiggen Formation dominates the lower part of the group, although in places it is partly replaced by the Zoologdalen and the Rødsten formations. The upper part of the Kap Graah Group consists of the Zoologdalen and Rødsten formations, as

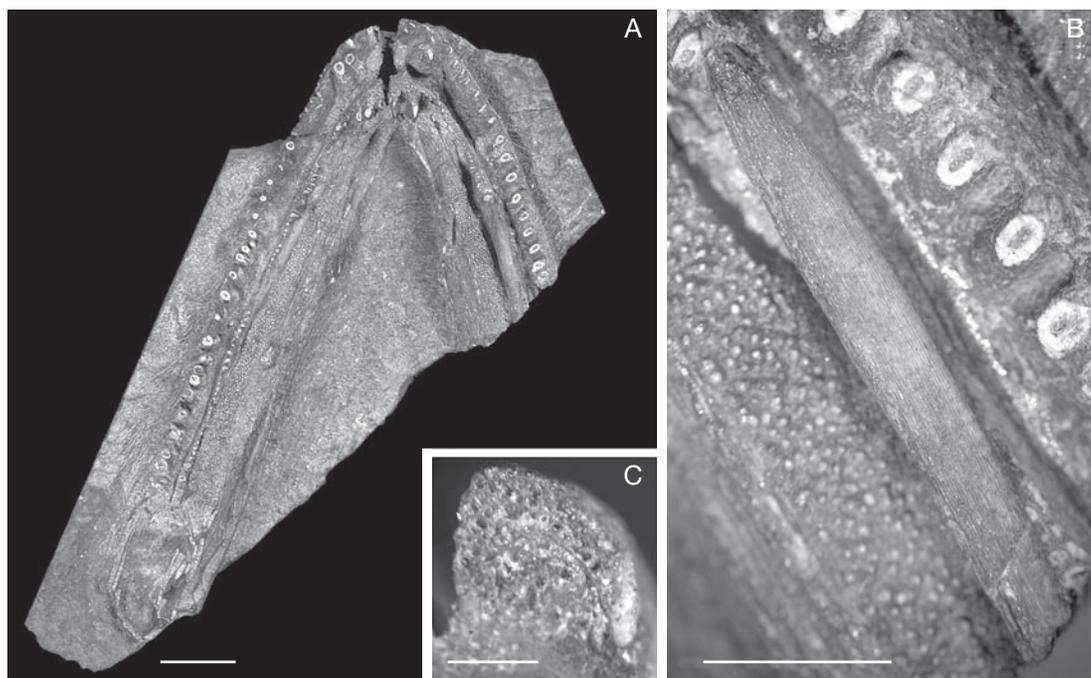


FIG. 3. — Chondrichthyes indet., spine lodged in the right lower jaw of the tetrapod *Acanthostega* (MGUH f.n. 1300): **A**, overview of lower jaws and spine; **B**, close up of spine; **C**, spine in cross section. Scale bars: A, 1 cm; B, 0.5 cm; C, 0.1 cm.

well as the Woodward Bjerg and Andersson Land formations. Only the Zoologdalen and Rødsten formations are rich in fossil vertebrates, such as *Bothriolepis groenlandica* Heintz, 1930 and *Phyllolepis orvini* Heintz, 1930. Jarvik (1961) suggested that both these taxa indicate a Famennian age, but only *Phyllolepis* is age diagnostic for the Famennian in Laurussia (Young 2005).

The Celsius Bjerg Group and the succeeding Harder Bjerg Formation represent the remaining part of the succession (Fig. 2), and are interpreted as being primarily of fluvial origin (Olsen & Larsen 1993). The Celsius Bjerg Group is subdivided into the Agda Dal, Elsa Dal, Aina Dal, Wimans Bjerg, Britta Dal, Stensiö Bjerg and Obrutschew Bjerg formations as described by Olsen & Larsen (1993). These correspond respectively to the “*Phyllolepis* Series” (Agda and Elsa Dal formations) and the “*Remigolepis* Series” (Aina, Wimans and Britta Dal formations) of Säve-Söderbergh (1934), with the latter three corresponding to his “Lower Dark Red”,

“Middle Dark Grey” and “Upper Reddish” divisions. The Celsius Bjerg Group is rich in fossil vertebrates including the tetrapods, with the exception of the Elsa Dal and Wimans Bjerg formations. Spore analysis suggests that the Devonian-Carboniferous boundary lies in the middle of the Obrutschew Bjerg Formation (Marshall *et al.* 1999), which is unconformably overlain by the Harder Bjerg Formation in sections on Celsius Bjerg, Stensiö Bjerg and Obrutschew Bjerg (Olsen & Larsen 1993). The boundaries within the Celsius Bjerg Group remain unclear on Celsius Bjerg itself (see below).

TAXONOMIC OVERVIEW

HETEROSTRACI

Heterostracans are known only from a single dermal bone fragment originally recognised as the drepanaspid *Psammolepis* Agassiz, 1844 by Ørvig (1961) and later described as *Psammolepis groenlandica*

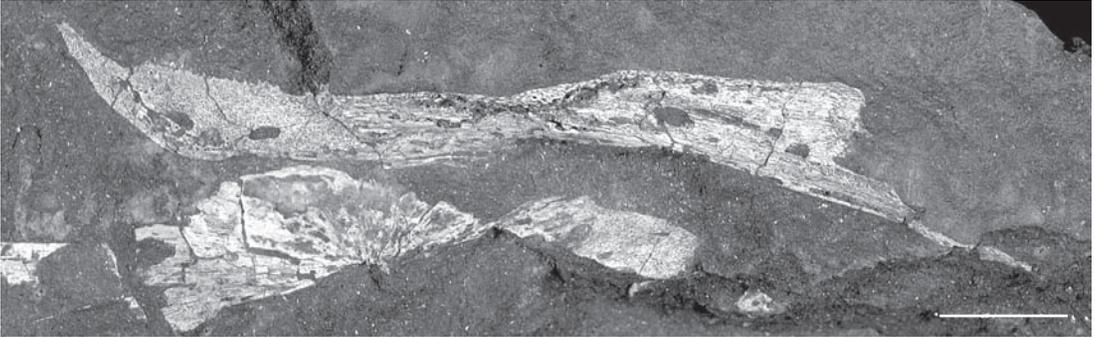


FIG. 4. — Infragnathal? of *Arthrodira* gen. et sp. indet. 3 (MGUH f.n. 1612). Scale bar: 1 cm.

Tarlo, 1964 by Tarlo (1964, 1965). The specimen was collected at Sydryggen (Southern Ridge by Säve-Söderbergh [1937]) on Canning Land, in sediments originally referred to as the Givetian “*Asterolepis säve-söderberghi* Series”, which on Canning Land has been formalised as the Red Siltstone Member of the Nathorst Fjord Group (Alexander-Marrack & Friend 1976).

CHONDRICHTHYES

A “cladodont”-like tooth and an indeterminate fin spine were the first chondrichthyan remains to be recorded from the Devonian of East Greenland (Stensiö 1948). The specimens were reported from the “*Phyllolepis* Series”, in a part of the succession that correlates with the uppermost part of the Kap Kolthoff Group (i.e. the top of the Sofia Sund Formation). Apart from this rare occurrence, only one other spine has been reported, found lodged in the lower jaw of an *Acanthostega* specimen bearing Geological Museum, University of Copenhagen, field number, MGUH f.n. 1300 (Fig. 3). It comes from the Britta Dal Formation on Stensiö Bjerg. It was originally identified as a ctenacanth shark (Clack 1994; Ahlberg & Clack 1998), but later Clack & Neininger (2000) suggested it was possibly misidentified. The spine fragment is almost 2 cm long with rounded leading edge and almost flat posterior face, giving it a half oval cross section (Fig. 3C). A U-shaped furrow along its posterior surface forms an open core. The spine tapers towards a blunt point distally, and also narrows proximally. A

polished cross section surface indicates a trabecular core and traces of weak or early ossification in the open central canal (Fig. 3C).

PLACODERMI

The placoderms are by far the most common and diverse of all Devonian vertebrates in East Greenland. The earliest known placoderms from this succession are the arthrodires *Homostius kochi* Stensiö & Säve-Söderbergh, 1938 and *Heterostius groenlandicus* Stensiö & Säve-Söderbergh, 1938 from the Givetian South Hestekoen Formation (“*Heterostius* Series”) of the Nathorst Fjord Group in Canning Land. *Homostius kochi* also occurs in the overlying Red Siltstone Member (“*Asterolepis säve-söderberghi* Series”) in Canning Land. At Kap Franklin in the Kap Kolthoff Group several specimens of a cocco-steomorph arthrodire have been found, which according to Ørving (1960: footnote p. 309) resembles *Coccosteus halmodeus* Clarke, 1893 (= *Clarkeosteus halmodeus* after Obruchev [1964]). However, Miles (1966) indicated that these two forms might not be conspecific.

The phyllolepid placoderms are represented by two Famennian species, the large *Phyllolepis orvini* Heintz, 1930, from the Zoologdalen, Rødsten and Agda Dal formations and the smaller *Phyllolepis nielsenii* Stensiö, 1939, from the Aina Dal Formation.

Groenlandaspis mirabilis Heintz, 1932 is an arthrodire known from the upper part of the succession. The form from East Greenland is

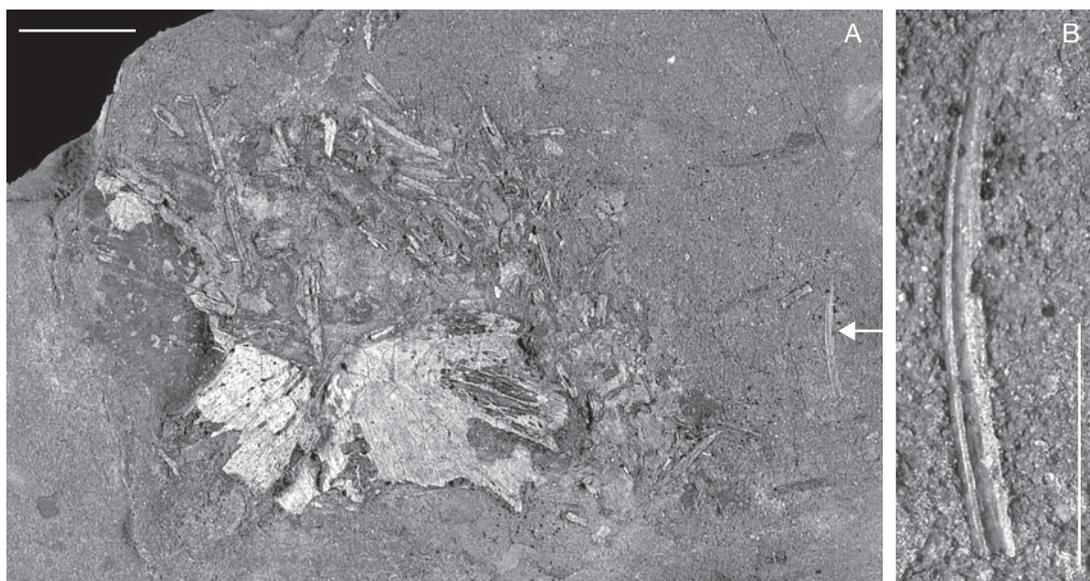


FIG. 5. — Patch of vertebrate remains containing acanthodian fin spines and scales, and possible interclavicle of a tetrapod (MGUH f.n. 155): **A**, overview; **B**, Acanthodidae indet., close up of spine. Scale bars: A, 1 cm; B, 0.5 cm.

still poorly known (Stensiö 1934), but specimens assigned to the genus have been found in both the Famennian Stensiö Bjerg Formation and the overlying Harder Bjerg Formation (Olsen 1993; Olsen & Larsen 1993). The present authors have not been able to confirm the identity, exact locality or current whereabouts of the fossils reported from the Harder Bjerg Fm, nor whether they were even collected. However, the measured section through the “*Grönlandaspis* Group” described by Nicholson & Friend (1976: table 11), places the occurrence of *Groenlandaspis* and *Holoptychius* above the black shales containing actinopterygian material and which marks the Devonian-Carboniferous boundary. Thus this would be the only record of these taxa in the Carboniferous, and further study is required to confirm either the identity of the material or their stratigraphical level.

A few undetermined arthrodires have also been reported from the Stensiö Bjerg Formation and the lower parts of the Kap Kolthoff Group (Jarvik 1961; Bendix-Almgreen 1976). One of these is specimen MGUH f.n. 1612 collected from the talus “behind

the Western Coulisse” on Celsius Bjerg, Ymer Ø and is either from the Aina Dal Formation or the Britta Dal Formation. This dermal plate may be a broken infragnathal (Fig. 4).

Antiarchs are very common in the Devonian of East Greenland and are represented by three genera: *Asterolepis* Eichwald, 1840, *Bothriolepis* Eichwald, 1840 and *Remigolepis* Stensiö, 1931. *Asterolepis saevesoederberghi* Stensiö & Säve-Söderbergh, 1938 was described from Canning Land and Wegener Halvø. In the type area material comes from the Red Siltstone Member of the Nathorst Fjord Group. *Asterolepis* specimens have also been reported from the Givetian lake deposits on Ella Ø (Marshall & Stephenson 1997). Specimens that appear to be conspecific with *Asterolepis saevesoederberghi* have been reported from different parts of the succession that is now recognised as the Kap Kolthoff Group (Jarvik 1961; Alexander-Marrack & Friend 1976; Bendix-Almgreen 1976).

The globally distributed genus *Bothriolepis* Eichwald, 1840 is common in the rocks of East Greenland. *Bothriolepis groenlandica* Heintz, 1930 was the first to be described and is known to occur

together with *Phyllolepis orvini* Heintz, 1930 in the Agda Dal Formation and within the Kap Graah Group. Another species, *Bothriolepis jarviki* Stensiö, 1948, occurs below *Bothriolepis groenlandica* in the upper part of the Kap Kolthoff Group. A third species, *Bothriolepis nielseni* Stensiö, 1948, is known from the Aina Dal Formation.

Remigolepis Stensiö, 1931 is very common in the Aina Dal and Britta Dal formations. Stensiö (1931) demonstrated that the first placoderm described from East Greenland, *Asterolepis incisa* Woodward, 1900, in fact belonged to the new antiarch genus *Remigolepis*. He also described four new species: *Remigolepis cristata* Stensiö, 1931, *R. acuta* Stensiö, 1931, *R. kochi* Stensiö, 1931, *R. kullingi* Stensiö, 1931, all from Kulling's locality 3 (Kulling 1930, 1931) on Celsius Bjerg. Subsequent work on Gauss Halvø suggests that *R. kullingi* is found only in the Aina Dal Formation, whereas *R. acuta* and *R. incisa* are from the Britta Dal Formation (Säve-Söderbergh 1933, 1934; Johansson 1935). It also seems that *R. kochi* may occur in the Aina Dal, Wimans Bjerg and Britta Dal formations, although the taxonomic assignment of the Britta Dal Formation forms is somewhat uncertain. *R. cristata* is only known from Celsius Bjerg.

Stensiö (1931) described *Remigolepis? tuberculata* from what can be interpreted as the "upper *Phyllolepis* Series" (i.e. Agda Dal Formation and/or Kap Graah Group). The same type of ornament was also reported on specimens from the lowermost part of the Kap Kolthoff Group (Jarvik 1985: 38). Säve-Söderbergh (1934) also reported a horizon in the Aina Dal Formation with specimens that may be conspecific. The problematic taxonomic status of *Remigolepis? tuberculata* makes it difficult to assess the significance of its stratigraphical distribution. Species of *Remigolepis* are in need of detailed systematic revision, but resolution may play a part in clarifying correlations between Famennian sequences in the region (Blom 2005).

Säve-Söderbergh (1933, 1934) discussed two *in situ* horizons on Celsius Bjerg, in which he reported a new taxon *Remigolepis emarginata*. This species has never been described and its status remains uncertain (Jarvik 1985).

ACANTHODII

Undetermined acanthodian scales have been reported from the Givetian Red Siltstone Member ("*Asterolepis säve-söderberghi* Series") of the Nathorst Fjord Group of Canning Land (Jarvik 1961; Tarlo 1964, 1965; Bendix-Almgreen 1976). The spine from the same sediments described by Stensiö & Säve-Söderbergh (1938) as *Onchus* sp. is too badly preserved to be assigned with confidence to any acanthodian group, although it resembles those of acanthodids. Scales have also been found in a locality at profile A by Nielsen in 1936 on Ymer Ø (see Stensiö 1948: 601).

A patch of disarticulated spines on specimen MGUH f.n. 155 has been found in association with what seems to be a tetrapod bone, possibly an interclavicle, suggesting that a larger predator, presumably a sarcopterygian such as *Eusthenodon*, might have regurgitated these remains. The spines appear to be from an acanthodid similar to the Frasnian *Homalacanthus* Russell, 1952 from the Escuminac Formation of Miguasha, Quebec, Canada (Gagnier 1996). This specimen originates from the talus of the Britta Dal Formation on Stensiö Bjerg, close to the site where *Acanthostega* was found (Bendix-Almgreen *et al.* 1990) (Fig. 5).

ACTINOPTERYGII

Material of a "palaeoniscid" has been reported (Jarvik 1961; Bendix-Almgreen 1976), and was collected in 1954 by Bütler from what in a letter to Jarvik in that same year he described as "a dark calcareous shale with fish and plant remains at about 1200 m on the western ridge on the south side of Celsius Bjerg [translated from German]". This corresponds well with later descriptions of the Obrutschew Bjerg Formation on Celsius Bjerg (Nicholson & Friend 1976; Olsen & Larsen 1993). This formation straddles the Devonian-Carboniferous boundary (Marshall *et al.* 1999), but spore analysis of specimen matrix suggests that the fossil in question is Devonian in age (Friedman & Blom 2006). The material consists of a few incomplete skulls, trunks and tails, and has been assigned to the new genus *Cuneognathus* (Friedman & Blom 2006).

POROLEPIFORMES

Porolepiform diversity is mainly restricted to two described holoptychiid genera, *Glyptolepis* Agassiz, 1844 and *Holoptychius* Agassiz, 1839. Scales of *Holoptychius* are known throughout the whole upper part of the sequence, with an earliest possible occurrence in Canning Land from strata correlated by Alexander-Marrack & Friend (1976) to the “Randbøl Formation”. According to Olsen & Larsen (1993) this corresponds to the Rødebjerg Formation in parts of the Sofia Sund Formation. *Holoptychius* is extremely common in the fossiliferous sediments of the Celsius Bjerg Group. Despite the abundance of this genus in East Greenland, very little research has focused on it. Material includes scales, detached cranial bones, jaws, bone fragments and parts of endocrania. Although two species, *Holoptychius nobilissimus* Agassiz, 1839 and *Holoptychius giganteus* Agassiz, 1839, have been recorded based on scale type, it is difficult to recognise taxa based on scales only, since different scale types often co-occur (Kulling 1931) and scale morphology clearly varies depending on position on the body in *Holoptychius* (Cloutier & Schultze 1996). Until the *Holoptychius* specimens of East Greenland have been revised, they should all be considered as *Holoptychius* sp.

The taxonomic validity of *Glyptolepis groenlandica* Jarvik, 1972 is not in doubt, as it can readily be distinguished from other described species of *Glyptolepis* on minor but consistent features of the dermal bone pattern (Ahlberg 1989b). The species was erected by Jarvik (1972), and has only been found at Hestekoen on Canning Land, in sediments originally referred to as the “*Asterolepis säve-söderberghi* Series”, i.e. the Red Siltstone Member of the Nathorst Fjord Group (Alexander-Marrack & Friend 1976). A large undescribed holoptychiid snout from Hestekoen, MGUH VP 1527a, bears dense dermal ornament that distinguishes it from the almost unornamented *Glyptolepis groenlandica* (PEA pers. obs.). Similar large, densely ornamented, holoptychiids are known from the Middle Devonian of Scotland and the Baltic States, but these have not yet been described (PPEA pers. obs.).

Material of Porolepiformes indet. has also been reported from the Red and Green Banded Siltstone

Member (“*Gyroptychius groenlandicus* Series”) on Canning Land (Jarvik 1950a), and the Vilddal Group in the Kap Franklin area on Gauss Halvø (Jarvik 1950b).

The putative onychodont tooth whorl figured by Stensiö (1936) is in fact from a porolepiform (PEA pers. obs.).

DIPNOI

Lungfishes are very rare in the lower part of the succession and only a small piece of a skull roof belonging to a *Dipterus*-like form (Jarvik 1961) has been recorded from the Middle Devonian “*Asterolepis säve-söderberghi* Series” (i.e. Red Siltstone Member of the Nathorst Fjord Group) in Canning Land.

Upper Devonian lungfishes are more common and have been described by Lehman (1955, 1959). *Nielsenia nordica* Lehman, 1959 is based on one poorly preserved skull roof that Jarvik (1961) assigned to the upper part of the “*Phyllolepis* Series”. This corresponds to the Agda Dal Formation or the Kap Graah Group. Friend *et al.* (1976a) reported *Nielsenia* from the sediments later formalised as the Zoologdalen and Rødsten formations. However, this poorly preserved material has no morphological overlap with the holotype of this genus, and are best regarded as indeterminate (MF pers. obs.).

Most of the other taxa described by Lehman (1955, 1959) originate from the Aina Dal and Britta Dal formations. The best known species, the long-snouted *Soederberghia groenlandica* Lehman, 1959, is represented by numerous specimens. A recent study of new material (MGUH f.n. 101, 1620, 1645) reveals novel morphological information that may clarify the phylogenetic position of this genus (Friedman 2003, 2005). *Soederberghia groenlandica* is known mainly from the Aina Dal Formation on Stensiö Bjerg and Nathorst Bjerg on Gauss Halvø, but also from Celsius Bjerg on Ymer Ø. The specimen recorded by Lehman (1959) and Jarvik (1961) as ?*Soederberghia* sp. from the Agda Dal Formation at Sederholm Bjerg on Gauss Halvø, shares no uniquely derived characters with that genus, and its affinities are unclear (MF pers. obs.).

Another long-snouted form, *Jarvikia arctica* Lehman, 1959, was originally known from only four

specimens, but material collected in 1998 from the south side of Celsius Bjerg at 380 m includes a well preserved skull (MGUH f.n. 304), palate and broken lower jaw (MF pers. obs.). Jarvik (1961) indicated that this species comes from the Britta Dal Formation, but lithological characters suggest that the specimens in fact may originate from the Aina Dal Formation (HB and MF pers. obs.). It is not obvious why Jarvik assigned the material to the upper part of the “*Remigolepis* Series” (i.e. the Britta Dal Formation), since all known specimens are either from Celsius Bjerg, where the stratigraphy is unclear, or lack detailed locality data. It is, therefore, possible that *Jarvikia* occurs in both formations.

The fourth taxon described by Lehman (1959) is the tooth-plated *Oervigia nordica* Lehman, 1959, which is found in the Britta Dal Formation or perhaps even higher in the sequence. The holotype is a poorly-preserved specimen collected on N Celsius Bjerg. A specimen from the northern slope of Celsius Bjerg may represent a new tooth-plated form (MF pers. obs., MGUH VP 3114).

“OSTEOLEPIFORMES”

Osteolepidids and tristichopterids make up the paraphyletic group Osteolepiformes (Ahlberg & Johanson 1998), and are known virtually through the whole Devonian succession in East Greenland. They have been treated in an extensive monographic work by Jarvik (1985).

The osteolepidid *Gyroptychius groenlandicus* Jarvik, 1950 is known from the “*Gyroptychius groenlandicus* Series” (i.e. the Red and Green Banded Siltstone Member of the Nathorst Fjord Group), of Canning Land, Kollen and Wegeners Halvø. Two specimens found together with *Asterolepis saevesoederberghi* on the south slope of Hesteskoen on Canning Land represent a second species, *Gyroptychius dolichotatus* Jarvik, 1985 from the Red Siltstone Member of the Nathorst Fjord Group. This shows that the two *Gyroptychius* species from East Greenland have separate distributions. Several *Gyroptychius* specimens have been found at various levels in the Vilddal Group of the Kap Franklin area (Jarvik 1985). Although most of these are practically indistinguishable from *Gyroptychius groenlandica*, the second species may

be present, effectively showing a similar distribution to that on Canning Land (Jarvik 1985).

Specimens of a new species of what might be the osteolepidid *Thursius* Traquair, 1888, have been collected in Randbøldalen on Gauss Halvø (Jarvik 1985). The species named *Thursius? minor* Jarvik, 1985 originates from sediments belonging to portions of the Kap Kolthoff Group previously named “Randbøl Formation” (Friend *et al.* 1983) and may be correlated with the Rødebjerg Formation.

The tristichopterid *Spodichthys buetleri* Jarvik, 1985 is known from Högbom Bjerg in Hudson Land (Jarvik 1985). Its exact locality is unknown, but according to Bütler (1959), the fossiliferous deposits that yielded this specimen belong to the lowermost parts of the Kap Kolthoff Group, corresponding to the lowermost parts of the Sofia Sund Formation in that area (Olsen & Larsen 1993).

Eusthenodon waengsjoei Jarvik, 1952 is another tristichopterid from East Greenland, and is mainly known from the Britta Dal Formation on Gauss Halvø. However, several specimens that may be conspecific have also been collected from the Aina Dal Formation. In contrast to *Spodichthys*, which is a small fish and appears to be a rather primitive member of the Tristichopteridae, *Eusthenodon* is very large (reaching at least 2 m) and is also one of the most derived members of the group (Ahlberg & Johanson 1997). *Eusthenodon* is also reported from talus on Celsius Bjerg on Ymer Ø where the lack of clear boundaries between Aina Dal, Wimans Bjerg and Britta Dal formations make the stratigraphical framework uncertain. Material of what may be a new tristichopterid has recently been recognised in the Aina Dal Formation on Stensiö Bjerg (e.g., MGUH f.n. 1331). It consists primarily of fragmentary cranial bones and highly distinctive scales (HB and MF pers. obs.). Olsen & Larsen (1993) have reported scales from the lower part of the Rødebjerg Formation, which were identified by Bendix-Almgreen as *Panderichthys*. The present authors cannot confirm the status of this record since they have been unable to locate the material.

TETRAPODA

Tetrapods are only known from the Upper Devonian (Famennian) Aina Dal and Britta Dal formations,

with localities restricted to outcrops on Gauss Halvø and Ymer Ø. Most specimens of *Acanthostega gunnari* Jarvik, 1952 are from an *in situ* locality of the Britta Dal Formation on Stensiö Bjerg, Gauss Halvø (Clack 1988a, b; Bendix-Almgreen *et al.* 1990; Blom *et al.* 2005). Several specimens were collected from Britta Dal Formation talus on Stensiö Bjerg and the adjacent Wiman Bjerg, while additional material is known from the talus of the Aina Dal Formation in the same area. Specimens have been recorded from Celsius Bjerg, but their stratigraphical origin is uncertain. Despite a sample gap represented by a sequence of rocks about 700 m thick between the *Acanthostega* localities of the Aina Dal and Britta Dal formations, no significant morphological difference between specimens has been recognised (Clack 2002a).

The second genus from East Greenland, *Ichthyostega*, does show morphological variation between the assemblages from Aina Dal and Britta Dal formations (Blom 2005). Säve-Söderbergh (1932a) described two genera (*Ichthyostega* and *Ichthyostegopsis*) and five species in his original work. Of these, only the genus *Ichthyostega* and the three species, *Ichthyostega stensioei* Säve-Söderbergh, 1932, *I. eigili* Säve-Söderbergh, 1932 and *I. watsoni* Säve-Söderbergh, 1932, appear to be valid (Blom 2005). *I. stensioei* occurs within the Aina Dal Formation, while the other two originate from the Britta Dal Formation. It is, however, suggested that *I. watsoni* is stratigraphically older than *I. eigili* (Blom 2005). Material is known from a large collection originating from both Celsius Bjerg on Ymer Ø and numerous localities on Gauss Halvø (Blom *et al.* 2005).

A third tetrapod genus has recently been recognised from specimens collected on the south side of Celsius Bjerg (Clack *et al.* in press). It is, however, not possible to assign these specimens to a precise stratigraphical level (see below).

PROBLEMS WITH STRATIGRAPHICAL FRAMEWORK, CORRELATION AND AGE

VILDDAL AND NATHORST FJORD GROUPS

As noted above, the three subdivisions, “*Heterostius*”, “*Gyroptychius groenlandicus*”, and “*Asterolepis säve-*

söderberghi” series established by Säve-Söderbergh (1937) for strata in the Canning Land area correspond with later formalised lithostratigraphical units of the Nathorst Fjord Group (Alexander-Marrack & Friend 1976). Comparison with rocks of similar age from the Kap Franklin area can be drawn, though based only on their constituent vertebrate taxa. Jarvik’s (1961) comparison used the subdivisions established by Büttler (1954) for the Kap Franklin area, but concluded that correlation with Canning Land was uncertain. Based on new data on lithostratigraphy and faunal composition, it is now possible to discuss further the correlation between the Nathorst Fjord Group on Canning Land and Wegener Halvø, and the succession in the Kap Franklin area.

Büttler’s (1954) “Vilddal Series”, erected for the lower part of the succession on Kap Franklin, was re-named the Vilddal Group by Alexander-Marrack & Friend (1976), who further claimed that it correlates more or less fully with the Nathorst Fjord Group. The Nathorst Fjord Group has a rather rich fossil fish fauna, while the Vilddal Group only has fossils known from the Ankerbjergselv Formation (Alexander-Marrack & Friend 1976; Olsen & Larsen 1993).

The record of *Gyroptychius groenlandicus* and porolepiforms from fossiliferous parts of the Vilddal Group (Jarvik 1985) suggests that that part of the group is time equivalent to the Red and Green Banded Siltstone Member on Canning Land, where the type material of *G. groenlandicus* was found (Jarvik 1950, 1985). The Red Siltstone Member of the Nathorst Fjord Group contains a second species, *Gyroptychius dolichotatus* Jarvik, 1985, suggesting that the two *Gyroptychius* species have different stratigraphical distributions. Alexander-Marrack & Friend (1976) also recorded *Gyroptychius* from rocks of the Vilddal Group at Kap Franklin, which now are formalised as part of Ankerbjergselv Formation (Olsen & Larsen 1993). Jarvik (1985) reported specimens that are virtually indistinguishable from *Gyroptychius groenlandicus* from different levels within the 1500 m thick succession of the Vilddal Group, but did not rule out the possibility that different species may be present at various levels in the succession. If both named *Gyroptychius*

species are present and exhibit a similar distribution as on Canning Land, they could potentially help to correlate the Nathorst Fjord Group with the Vilddal Group at Kap Franklin in better detail, but this would require further collection and research. The alpha taxonomy of *Gyroptychius* is currently in need of review. The British species are being studied by R. Wade (University of Cambridge) whose work may also help elucidate diagnosis of species from elsewhere.

Age data from spore analysis on Canning Land show that the lowermost part of a measured section in the Red Siltstone Member of the Nathorst Fjord Group is of Eifelian age (Marshall & Astin 1996), whereas spores from the Red and Green Banded Siltstone Member indicate a Givetian age. Although there is no indication of Eifelian in the lower part of Vilddal Group in the west (i.e. Ella Ø) it is not clear whether the whole group in the Kap Franklin area is Givetian, or whether the lower part may be Eifelian. Marshall & Astin (1996) also showed that some of the problems relating to previous correlations using vertebrates were caused by the environmental control of the distribution of *Asterolepis*. *Gyroptychius*, spores and previously lithostratigraphical considerations now allow fairly confident correlation between the Vilddal and the Nathorst Fjord groups, with the exception of the lower parts of the Nathorst Fjord Group, which might be slightly older.

KAP KOLTHOFF GROUP

Considerably more problematic is how parts of the Vilddal group relate to the Kap Kolthoff Group in a regional context. This results from the possibly diachronous relationship between the Vilddal group in some areas and the Kap Kolthoff Group. In the Kap Franklin area the "Randbøl Series" (Bütler 1954; Jarvik 1961) was subsequently named "Randbøl Formation" (Alexander-Marrack & Friend 1976). The formal name for that part of the succession is now the Kap Kolthoff Group (Olsen & Larsen 1993) and it is clearly separated from the underlying Vilddal Group at Kap Franklin by an unconformity and about 1000 m of unfossiliferous beds.

The relationship between the Vilddal and Kap Kolthoff groups is clear in the Kap Franklin area.

Further east, however, these deposits have been considered heterogenic and diachronous (Hartz 2000), a factor which must be considered when looking at the distribution of vertebrates within the Kap Kolthoff Group. In certain localities this could mean that sediments of the upper part of Vilddal Group are of the same age as, and correlate with, lower parts of Kap Kolthoff Group (Hartz 2000: fig. 2). Despite this, only the genus *Asterolepis* among the vertebrates found in the Kap Kolthoff Group shows a faunal overlap with the Vilddal Group. Nevertheless, specimens of *Asterolepis* have been reported from the Kap Franklin area, in the Kap Kolthoff Group well above the local upper boundary of the Vilddal Group (Alexander-Marrack & Friend 1976). It may suggest that this occurrence of *Asterolepis* may be a different and younger species than is seen in other parts of the basin (Alexander-Marrack & Friend 1976), but since the stratigraphical context of that part of the succession is problematic no further conclusions can be drawn.

Although it contains several taxa, including *Asterolepis*, *Holoptychius*, *Spodichthys buetleri*, *Clarkosteus halmodeus?* and *Thursius? minor*, the fauna of the Kap Kolthoff Group reveals nothing definite about the age of these strata, because each of these fossil fishes is problematic. As discussed further below they are either of uncertain taxonomical status, poorly studied, endemic to East Greenland, or a combination of these. However, it is certain that the Kap Kolthoff Group spans from the Givetian at the top of the Vilddal Group to the Frasnian, and probably passes into the Famennian where it meets the Kap Graah Group. It is therefore almost certain that the Frasnian is represented in the group, but to pinpoint the boundaries and extract better knowledge of fossil distribution requires a great deal further fieldwork and both stratigraphical and taxonomic research.

CELSIUS BJERG GROUP

Locally there are major problems with the stratigraphical context of the tetrapod-yielding parts of the Celsius Bjerg Group, exemplified by the *Remigolepis*-yielding strata of Celsius Bjerg on Ymer Ø. Faunal compositions suggest that the Aina Dal, Wimans Bjerg and Britta Dal formations make

up the succession, just as they do in the type area on Gauss Halvø (Olsen & Larsen 1993). In early work these sediments on Celsius Bjerg were simply described as belonging to the “*Remigolepis* Series” and were not subdivided as they were on Gauss Halvø (Säve-Söderbergh 1932b, 1933). Nicholson & Friend (1976) used the term “*Remigolepis* Group” for the same part of the succession and pointed out that the Wimans Bjerg Formation was not developed on Ymer Ø. Although they presented data from sections on both sides of Celsius Bjerg, only relative thickness and sample groups were given for the boundaries. Olsen & Larsen (1993), however, recognised and reported the occurrence of the Wimans Bjerg Formation on Celsius Bjerg. They also used a reference section on SE Celsius Bjerg to try to define the Wimans Bjerg Formation, but that part is very poorly exposed in this area and therefore the boundaries could not be satisfactorily clarified. In addition little (or no) work has attempted to correlate strata between the north and south sides of Celsius Bjerg, and the relationships between these beds remain problematical. A study of the distribution of various *Remigolepis* species may be particularly helpful in this case. Summarizing all the information on Celsius Bjerg, the detailed stratigraphy on both sides of Celsius Bjerg is still very uncertain. The relationship between these strata and the distribution of various facies in different parts of the basin are of particular interest for future fieldwork in the area.

FAUNAL ASSEMBLAGES

Despite the problems of stratigraphical framework discussed above it is possible to recognise a number of assemblages throughout the East Greenland Devonian succession (Fig. 2), and these relate closely to the series reviewed and listed by Jarvik (1961) and Bendix-Almgreen (1976). The earliest faunal assemblage corresponds to the three subdivisions that were established by Säve-Söderbergh (1937) for the lowermost vertebrate bearing sediments in the Canning Land and Wegener Halvø area. Some vertebrates assignable to this assemblage, such as *Gyroptychius* and *Asterolepis*, mainly recognized in

the Nathorst Fjord Group, have also been found in the Kap Franklin area. The basal South Hestekoen Formation (“*Heterostius* Series”) (Alexander-Marrack & Friend 1976) is characterised by *Heterostius groenlandicus*, but also contains *Homostius kochi*. The overlying Red Siltstone Member (“*Asterolepis säve-söderberghi* Series”), contains a more diverse fauna that includes *Psammolepis groenlandica*, *Asterolepis saevesoederberghi*, *Gyroptychius dolichotatus*, *Glyptolepis groenlandica* and undetermined acanthodian scales and fin spines, as well as the only apparent remaining species from the South Hestekoen Formation, *Homostius kochi*. The youngest vertebrate occurrence, in the Red and Green Banded Siltstone Member (“*Gyroptychius groenlandicus* Series”) is characterised by *Gyroptychius groenlandicus* and also includes porolepiforms. Palynological evidence suggesting that this assemblage straddles the Eifelian-Givetian boundary (Marshall & Astin 1996) is not in conflict the vertebrate faunal composition, but the latter does not help to refine the dating. *Homostius*, *Heterostius*, *Psammolepis*, *Asterolepis* and *Glyptolepis*, for example, are known from both the Eifelian and the Givetian on the East European Platform (Mark-Kurik 2000). *Psammolepis* and *Asterolepis* species also occur in the Frasnian in that region (Esin *et al.* 2000) and in Scotland, while *Gyroptychius* species occur both in the Eifelian and Givetian (Dineley & Metcalf 1999).

The second assemblage comprises the taxa from the lower parts of the Kap Kolthoff Group. Since the thickness of the Kap Kolthoff Group varies depending on its position within the basin, and is possibly diachronous, is it difficult to correlate individual localities. This not only makes the validity of this assemblage problematic, but also its relation to the first assemblage. As noted above, *Asterolepis* is the only taxon that shows overlap with the assemblage of the Nathorst Fjord and Vilddal groups. The assemblage also includes taxa such as *Holoptychius*, *Spodichthys buetleri*, *Clarkosteus halmodeus?* and *Thursius? minor*, as well as an undetermined arthrodire and the problematic *Remigolepis? tuberculata* (Stensiö 1931; Jarvik 1985). The possible occurrence of *Holoptychius* is noteworthy since this would be the first instance of a taxon that is distributed throughout the whole upper

part of the East Greenland succession. This is the only genus showing such substantial distribution in East Greenland and it would be of great interest in the future to study whether there is morphological and taxonomic variation through the sequences indicating a succession of species as in other genera. Resolution of this problem would require detailed and difficult work on usually disarticulated, intractable and often poorly localised material, meaning that further, dedicated, collecting of this genus would be required.

The taxonomic status of *Clarkosteus balmodeus*? has been questioned by Miles (1966), and *Thursius? minor* has only been assigned to that genus based on similarities with the skull of the Scottish species, although the genus is diagnosed by the position of the fins (Jarvik 1985). This problem of taxonomic affinity aside, both genera are known from Givetian strata in North America and Scotland respectively (Denison 1978; Dineley & Metcalf 1999). *Spodichthys*, although endemic to East Greenland, appears to be a primitive tristichopterid similar to *Tristichopterus* (late Givetian) or *Eusthenopteron* (early Frasnian) (PEA pers. obs.).

Bothriolepis jarviki characterises a third assemblage from the uppermost part of the Kap Kolthoff Group, previously referred to as the “*Phyllolepis* Series, lower part” (Jarvik 1961). The assemblage also contains *Holoptychius* and some chondrichthyan teeth and spines of undetermined affinities. Jarvik (1961) suggested that this vertebrate fauna is early Famennian in age. However it could equally well be of Frasnian age since both *Bothriolepis* and *Holoptychius* are also known from the Frasnian of various places such as Scotland, East European Platform and Australia (Dineley & Metcalf 1999; Young 1999; Esin *et al.* 2000). The stratigraphical context of this assemblage could be affected if Bütler (1959) and Hartz *et al.* (1997) were correct in their view of boundary definitions. In their opinion this part of the succession would belong to the Kap Graah Group, rather than the uppermost part of Kap Kolthoff Group (Hartz *et al.* 1997)

The fourth assemblage corresponds to the “*Phyllolepis* Series, upper part” (Jarvik 1961) and is equivalent to both the Kap Graah Group and the Agda Dal Formation. Characteristic taxa of this

assemblage are *Bothriolepis groenlandica* and *Phyllolepis orvini*, which are complemented by *Holoptychius*, *Nielsenia nordica* and ?*Soederberghia* sp. The specimen of the latter is too poor for identification, but it clearly cannot be assigned to *Soederberghia* (MF pers. obs.). The genus *Soederberghia* occurs throughout the Frasnian and Famennian in other parts of the world (Ahlberg *et al.* 2001).

The taxa of this assemblage have previously only been referred to as coming from the “*Phyllolepis* Series”, which makes it very difficult to be certain of the exact formation from which they derive: Rødsten, Zoologdalen or Agda Dal formations are all possible. In some areas, the Agda Dal Formation has an identical lithology to the uppermost part of the Kap Graah Group and is only distinguishable by slight differences in palaeocurrents. However, all the specimens of *Bothriolepis groenlandica* and *Phyllolepis orvini*, reported by Stensiö (1948) and Säve-Söderbergh (1934) respectively, must originate from the Agda Dal Formation since strata lower than this are not exposed in the areas of the localities in the Paralleldal area from which they collected their specimens (Stensiö 1948; Säve-Söderbergh 1934; Olsen & Larsen 1993). Other localities yielding *Bothriolepis* and *Phyllolepis* from the Rødsten and Zoologdalen formations show the complete range of this assemblage (Bütler 1935, 1940, 1954, 1959, 1961; Alexander-Marrack & Friend 1976; Friend *et al.* 1976a, b; Nicholson & Friend 1976; Yeats & Friend 1978; Friend *et al.* 1983; Olsen 1993; Olsen & Larsen 1993). As with assemblage three, Jarvik (1961) suggested that this vertebrate fauna is early Famennian in age, but *Bothriolepis* and *Phyllolepis* are known from the Frasnian of Scotland and Australia respectively (Dineley & Metcalf 1999; Young 1999).

The fifth assemblage is the largest and corresponds to the “*Remigolepis* Series”, well known for its tetrapods and named after and defined by the antiarch found frequently within the succession. This old subdivision includes the Aina Dal, Wimans Bjerg and Britta Dal formations, of which the Wimans Bjerg Formation has yielded only very few vertebrate specimens. Although not being formal, the term “*Remigolepis* Series” or “*Remigolepis* Group” is still a useful shorthand for vertebrate workers since it

refers to a particular part of the East Greenland succession where tetrapods have been found. It is also useful for the sediments on Celsius Bjerg, where the relation between the Aina Dal, Wimans Bjerg and Britta Dal formations are somewhat uncertain, but still characterised by the typical *Remigolepis* fauna. Although the faunal composition on the generic level is quite similar throughout the assemblage, it is possible to separate it based on a more detailed species-level biostratigraphy. Such division is possible thanks to detailed work that has been done on these sediments in part as a result of the great interest in contextualising the early tetrapods found in them. Substantial information is available from previous publications, unpublished manuscripts by Säve-Söderbergh and ongoing research, and it is possible to revise the faunal composition based on both previously collected material and the collections made in 1987 and 1998 by Anglo-Danish expeditions (Clack 1988a, b; Bendix-Almgreen *et al.* 1990; Clack & Neiningen 2000).

The Aina Dal Formation assemblage is characterised by a unique fish fauna containing *Soederberghia groenlandica*, *Phyllolepis nielseni* and *Bothriolepis nielseni*. It may also be the case that the fauna shows a distinctive *Remigolepis* component, with *R. kullingi* and *R. kochi*, but the taxonomy of the group is somewhat unstable and is in need of revision before the biostratigraphical potential of these taxa can be explored. The fauna also contains *Holoptychius*, *Jarvika arctica*, a possible new species of *Eusthenodon* and perhaps a new tristichopterid (HB and MF pers. obs.), of which the two latter may be restricted to the Aina Dal Formation. The Aina Dal Formation is also famous for its tetrapods, of which *Ichthyostega* is more common than *Acanthostega*. In a recent review of the taxonomy of *Ichthyostega*, Blom (2005) shows that the Aina Dal Formation is represented by only one species, *Ichthyostega stensioei*. *Acanthostega*, on the other hand is only represented by one or two specimens from the Aina Dal Formation and only two locations definitively in the Britta Dal Formation, so species level differentiation is not possible.

Although the Wimans Bjerg Formation has been considered unfossiliferous for vertebrates, Olsen & Larsen (1993), Jarvik (see Johansson 1935), as

well as Säve-Söderbergh (unpublished manuscript), reported *Remigolepis kochi* from a Paralleldal area horizon at the base of the formation that otherwise only contains rare *Holoptychius* scales.

At the generic level, the Britta Dal Formation assemblage is very similar to that of the Aina Dal Formation. The only unique genus is the lungfish *Oervigia nordica*, while at the species level the formation is characterised by *Ichthyostega watsoni*, *Ichthyostega eigili* and *Eusthenodon waengsjoei*, and potentially the more stratigraphically uncertain *Remigolepis acuta* and *Remigolepis incisa*. Other taxa represented are *Acanthostega gunnari* and *Holoptychius*, and perhaps *Jarvika arctica*: a few acanthodian spines have also been found in this formation on Gauss Halvø. A few taxa, such as *Remigolepis kochi*, *Remigolepis cristata*, possibly a new lungfish species (MF pers. obs.), and a new genus of a tetrapod have been collected mainly on Celsius Bjerg so that it is uncertain if they originate from the Aina Dal Formation or the Britta Dal Formation. The Famennian age usually given for this fauna has been confirmed by palynological data from above and below the formations of the “*Remigolepis* assemblage” (Marshall *et al.* 1999).

A detailed description of the localities, distribution and stratigraphical context of tetrapods from this part of the succession provides more details and a framework for further studies on vertebrate distribution in the “*Remigolepis* Series” (Blom *et al.* 2005).

The rest of the succession, which was formerly referred to as the “*Grönlandaspis* Series”, comprises the sixth assemblage and is characterised by *Groenlandaspis mirabilis* and *Holoptychius*. This assemblage is distributed within the three now formal lithostratigraphical units: Stensjö Bjerg, Obrutschew Bjerg and Harder Bjerg formations. The Obrutschew Bjerg Formation was stated to be unfossiliferous (Olsen & Larsen 1993), but this is refuted by the find of a basal actinopterygian from the black shale on Celsius Bjerg (Jarvik 1961; Nicholson & Friend 1976; Friedman & Blom 2006). *Groenlandaspis* has been reported from Givetian to Famennian strata from a number of continents, such as North America, Europe, Africa, Antarctica and Australia (Daeschler *et al.* 2003). A biostratigraphical sub-

division based on this assemblage, including both *Groenlandaspis* and *Holoptychius*, that apparently straddles the Devonian–Carboniferous boundary requires further study. The boundary is defined by spore assemblages located within the Obrutschew Bjerg Formation (Marshall *et al.* 1999). The potential presence of *Groenlandaspis* and *Holoptychius* both below and above that boundary is of particular interest, as neither of these taxa has previously been reported from the Carboniferous (Bendix-Almgreen 1976). Either the dating of the boundary, the identity of the material, or the stratigraphical occurrence of these taxa in other parts of the world could require revision.

CONCLUSIONS

This contribution has summarized the results of nearly a century of palaeontological collecting in the Devonian strata of East Greenland. Despite a perception that the vertebrate faunas from East Greenland are well documented, this study has revealed substantial problems with dating, distribution, and taxonomy of the constituents. Examination of existing literature, museum specimens, and newly collected material has provided an advance on previous reviews (Jarvik 1961; Bendix-Almgreen 1976). These earlier contributions lacked a firm lithostratigraphic foundation, but subsequent work (Alexander-Marrack & Friend 1976; Friend *et al.* 1976a, b; Nicholson & Friend 1976; Yeats & Friend 1978; Friend *et al.* 1983; Olsen & Larsen 1993) has provided the present study with a formalized framework in which to interpret faunal distributions.

While considerable strides have been made in evaluating the taxonomic and phylogenetic status of much of the fossil material from East Greenland, inadequate documentation of the stratigraphical context of most specimens remains an obstacle to a more comprehensive picture of faunal change throughout the Devonian of this region. In some cases (e.g., Celsius Bjerg), additional field work may be unable to resolve existing problems, but in other instances further collecting would undoubtedly be of great help in refining existing

stratigraphical data. This review has pointed out some of the outstanding problems to be tackled, including the fact that alpha-taxonomic studies to the species level are required for detailed correlations between formations and to other parts of the world.

As studies on the vertebrates of East Greenland shift from largely non-stratigraphical issues such as phylogeny to explicitly distributional ones, including the reconstruction of faunal assemblages and palaeoenvironment, careful investigation of stratigraphical context will become increasingly important. Future field-based efforts targeting persistent litho- and biostratigraphical problems will provide a refined framework in which to interpret the faunal assemblages reviewed here.

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