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Cover: View of southern coastline of Gauss Halvø, showing eastern part of Smith Woodward Bjerg, Britta Dal and western part of Stensiö Bjerg

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Abstract

Henning Blom, Jennifer A. Clack and Per E. Ahlberg. Localities, distribution and stratigraphical context of the Late Devonian tetrapods of East Greenland. – Meddelelser om Grønland Geoscience 43. Copenhagen, Danish Polar Center, 2005. 50 pp.

The Devonian tetrapod-yielding localities of East Greenland are described in detail, giving new information on distribution and stratigraphical context. Three genera of tetrapods, *Ichthyostega*, *Acanthostega* and a third not yet described, are known from different localities on Gauss Halvø and Ymer Ø. On Ymer Ø, tetrapods have been found loose in talus on the north and south sides of Celsius Bjerg. Tetrapod localities on Gauss Halvø are distributed between Paralleldal and along the south coastline, and are represented both by talus-derived and *in situ* collected material. One *in situ* locality, yielding numerous *Ichthyostega* specimens, is located in the lower part of the Britta Dal Formation on Sederholm Bjerg in Paralleldal. An *Acanthostega* yielding *in situ* locality is located higher up in the Britta Dal Formation on Stensiö Bjerg on the south coast. Talus-derived material is reported from all areas and in both the Aina Dal Formation and the younger Britta Dal Formation. A review and summary of the detailed stratigraphy of the tetrapod-yielding succession on Gauss Halvø is presented for the first time and is based on old literature, specimen data, recent fieldwork, unpublished manuscripts and old field notes. Every recorded locality has been put in this stratigraphical framework in order to show a detailed distribution of specimens and enabling an assessment of this distribution.

Key words: *Acanthostega*, Devonian, distribution, East Greenland, *Ichthyostega*, localities, stratigraphy, tetrapod.

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Introduction

Although many new taxa and localities of Devonian tetrapods have been discovered from all over the world in recent years (Clack, 2002*a*), the largest collections and best-preserved material still originates from East Greenland. Two genera from East Greenland, *Ichthyostega* and *Acanthostega*, are known from virtually complete skeletons, whereas a third genus from East Greenland (description is being prepared by Clack, Ahlberg and Blom) and others from different regions, such as *Ventastega* (Ahlberg *et al*., 1994; Ahlberg and Luksevics, 1998), *Tulerpeton* (Lebedev and Clack, 1993; Lebedev and Coates, 1995), *Obruchevichthys* (Vorobyeva, 1977), *Elginerpeton* (Ahlberg, 1995; Ahlberg, 1998), *Metaxygnathus* (Campbell and Bell, 1977), *Hynerpeton* (Daeschler *et al*., 1994), *Sinostega* (Zhu *et al*., 2002) and an *Ichthyostega*-like specimen from Belgium (Clement *et al*., 2004), are fragmentary or known only from isolated elements. The material of *Ichthyostega* and *Acanthostega* is unique in not only providing detailed morphological and anatomical information (Clack, 2002*a*), but also for its potential for exploring taphonomy, stratigraphical distribution, and sedimentary and faunal context.

Vertebrate fossils from East Greenland were first discovered in Upper Devonian sedimentary rocks by Nathorst in 1899 during his rescue expedition for the Swedish balloonist Andrée, which also involved geological investigations (Nathorst, 1901). These fossils, represented by plates and scales, were sent to, and described by Woodward (1900). This fossil potential was not further explored until 1929 when Kulling brought home a great collection of vertebrates, mainly from the northern slopes of Celsius Bjerg (Koch, 1930; Kulling, 1930, 1931). The material was described by Stensiö (1931) who listed a number of species of the new placoderm, *Remigolepis*, as well as remains of *Holoptychius* and other indeterminable 'crossopterygians'. Although *Ichthyostega* specimens were among the material collected by Kulling, such as the ribs illustrated by Stensiö (1931, plate 36) and poorly preserved skulls, they were not recognised as such until well-preserved tetrapod skulls were collected in 1931 by Säve-Söderbergh and his team during the first season of Koch's Three-Year Expedition (1931-1934) in East Greenland (Säve-Söderbergh, 1932*a*,*b*). This expedition was the largest that had ever been sent out from Denmark, and although it was partly carried out in the spirit of using modern technology for research and Arctic exploration, it was also part of an effort by the Danes to assert sovereignty over East Greenland (Jarvik, 1996; Ries, 2002, 2003). The material that was collected in 1931 included 14 tetrapod specimens from which Säve-Söderbergh (1932*b*) described and illustrated seven different taxa; *Ichthyostega stensiöi* (*stensioei*), *I. watsoni*, *I. eigili*, *I.*? *kochi*, ichthyostegid sp. a, *I.*? sp. b and *Ichthyostegopsis wimani*. At that time, and for many decades to come, these were the earliest known tetrapods and almost the sole representatives of transitional forms between fish and land vertebrates. Therefore East Greenland suddenly became of significance to the geological-palaeontological community. This increase in interest was the starting point for more detailed studies in the Devonian of East Greenland, and additional tetrapod material, as well as other vertebrates, were regularly collected between 1933 and 1955 by different Swedish and Danish expeditions led by Säve-Söderbergh and Jarvik, among others (Jarvik, 1996). In 1952, Säve-Söderbergh's species were complemented by *Acanthostega gunnari* Jarvik, 1952 which was described in a paper that also included new postcranial material of *Ichthyostega* (Jarvik, 1952). From the increasing amount of data available, Jarvik (1980) later published more details of the limbs and the pelvic girdle. However, it was not until 1996 that he published a monographic work presenting a new reconstruction together with detailed anatomical descriptions and illustrations of the most significant and best preserved specimens. In the meantime, *Acanthostega*, had become the best known Devonian tetrapod and provided a great deal of understanding and new views of the origin of tetrapods (Clack, 1989, 1990, 1992, 1993, 1994*a,b*, 1998, 2002*a,b*; Clack and Coates, 1993, 1995; Coates, 1996; Ahlberg and Clack, 1998). This set of work was based on almost complete skeletal material from a locality initially collected by Nicholson in 1970 (Nicholson and Friend, 1976) and subsequently more extensively during an expedition in 1987 by a team from the University Museum of Zoology, Cambridge and the Geological Museum, Copenhagen (Clack, 1988*a,b*; Bendix-Almgreen *et al.*, 1990). The latest 'tetrapod' expedition in 1998 organised from the University of Cambridge (Clack and Neininger, 2000) collected further new and interesting tetrapod material, predominantly of *Ichthyostega*.

Jarvik (1996) illustrated and discussed many aspects of *Ichthyostega*'s anatomy, but the interpretation of many of these, such as the braincase and the vertebral column, still remained to be explored (Clack, 1998, 2002*a*). Furthermore, many questions related to the taxonomic, stratigraphical and sedimentological context of *Ichthyostega* have also remained unanswered (Clack and Neininger, 2000). The morphological and anatomical aspects of *Ichthyostega* are in the process of being reviewed and recently, a uniquely specialised ear was recognised from previously highly problematic anatomical structures (Clack *et al.*, 2003). The recent recognition of morphologically different assemblages of *Ichthyostega* has led to a taxonomic revision and recognition of three different *Ichthyostega* species (Blom, 2005), the distribution of which is of potential taphonomic, stratigraphical and palaeoenvironmental interest. Apart from that, very little has been published on the localities, distribution and environments of tetrapods, and the general faunal composition of Devonian vertebrates in East Greenland. Bendix-Almgreen *et al.* (1990) described the ecological and environmental context of *Acanthostega* from the *in situ* locality on Stensiö Bjerg (Clack, 1988*a,b*; Bendix-Almgreen *et al.*, 1990), and Spjeldnæs (1982) discussed the palaeoecology of *Ichthyostega* based on "*Ichthyostega*-material itself, the accompanying fauna and the enclosing sediments". Both works are slightly out of date and these observations need to be tested against the new anatomical, faunal and environmental data available through the ongoing review of *Ichthyostega* and its faunal and sedimentological context.

Although a series of papers have described the localities and the stratigraphical distribution of vertebrates from the Devonian of East Greenland (Säve-Söderbergh, 1932*a*, 1933, 1934; Johansson, 1935), the detailed description of tetrapod localities, sedimentological context and the stratigraphical relationship have never really been properly explored or summarised.

In the present paper, focus is placed on the localities, distribution and stratigraphical context of the tetrapods from East Greenland, providing a review of what is known from the literature and what can be extracted from the collections themselves, unpublished manuscripts and field notes. This also includes information from more recent fieldwork and interpretations of the stratigraphical framework. This summarises all the localities known from 1929 and onwards, and how they fit in to the overall picture as well as a detailed stratigraphical framework. Together, this forms an excellent basis for future studies of local as well as global biostratigraphy, palaeogeography and palaeoenvironment.

Geological setting

The geology of East Greenland from latitudes 70º to 82º is characterised by a fold belt that occupies most of the rocks exposed between the coast and the permanent ice cap. It forms part of a major Caledonian structure, which occurs on both sides of the North Atlantic Ocean and in East Greenland is dominated by metamorphic crystalline complexes as well as low-grade or non-metamorphic late Precambrian and Lower Palaeozoic sediments. In central East Greenland, continental clastic deposits of Devonian to Permian age are represented by successions of considerable thickness deposited in a series of continental basins. The Devonian sedimentary rocks generally rest unconformably on Cambrian and Ordovician carbonates and older rocks, and overlaid by Upper Palaeozoic and Mesozoic deposits.

The East Greenland tetrapod localities are situated on Ymer Ø and Gauss Halvø, in the central part of the continental Devonian basin that is exposed in an almost 100 km wide north-south belt, extending some 200 km from Hudson Land in north to Traill Ø in the south, with small outliers in Canning Land and on Wegener Halvø further south (Fig. 1). During its Mid and Late Devonian evolution, an over 8 km thickness of continental clastic sediments was deposited in various facies and environments. Vertebrates are known almost all the way through the succession and includes representatives of most major groups of early fossil vertebrates, including heterostracans, placoderms, acanthodians, chondrichthyans, actinopterygians, lungfishes, porolepiforms, 'osteolepiforms' and tetrapods (Blom *et al.*, in press).

Tetrapods are known from the Upper Devonian Celsius Bjerg Group, which is subdivided into seven formations: the Agda Dal, Elsa Dal, Aina Dal, Wimans Bjerg, Britta Dal, Stensiö Bjerg and Obrutschew Bjerg formations (Fig. 2). The whole group is characterised by silt- and sandstones, most of which contain vertebrate fossils that indicate a Famennian age. The tetrapods, however, are restricted to two formations in the middle part of the Celsius Bjerg Group, in which the Britta Dal Formation, the uppermost and most productive interval, is clearly separated (on Gauss Halvø) from the slightly poorer Aina Dal Formation by the almost unfossiliferous Wimans Bjerg Formation (Fig. 2). These three formations have been collectively referred to by the informal name 'Remigolepis Series', a useful shorthand to vertebrate palaeontologists.

The age of these deposits has been problematic and most recently Hartz *et al*. (1997, 1998) argued for a Carboniferous age based on 40Ar/39Ar plagioclase ages from basalts. Stemmerik and Bendix-Almgreen (1998) challenged this Carboniferous age, on the basis of lithostratigraphical correlation between the basalts and sediments dated by spores. Marshall *et al*. (1999) used new detailed palynological data and concluded that the deposits are Late Devonian in age.

The Aina Dal Formation, formally described by Nicholson and Friend (1976), consists of predominantly cross-laminated dark red to grey or black, very fine and fine-grained sandstones and siltstones, representing a variably active meandering river and flood basin environment (Olsen and Larsen, 1993). It reaches a maximum thickness of about 90 m at its type section on Stensiö Bjerg and towards Paralleldal, whereas the thickness decreases eastwards and to-

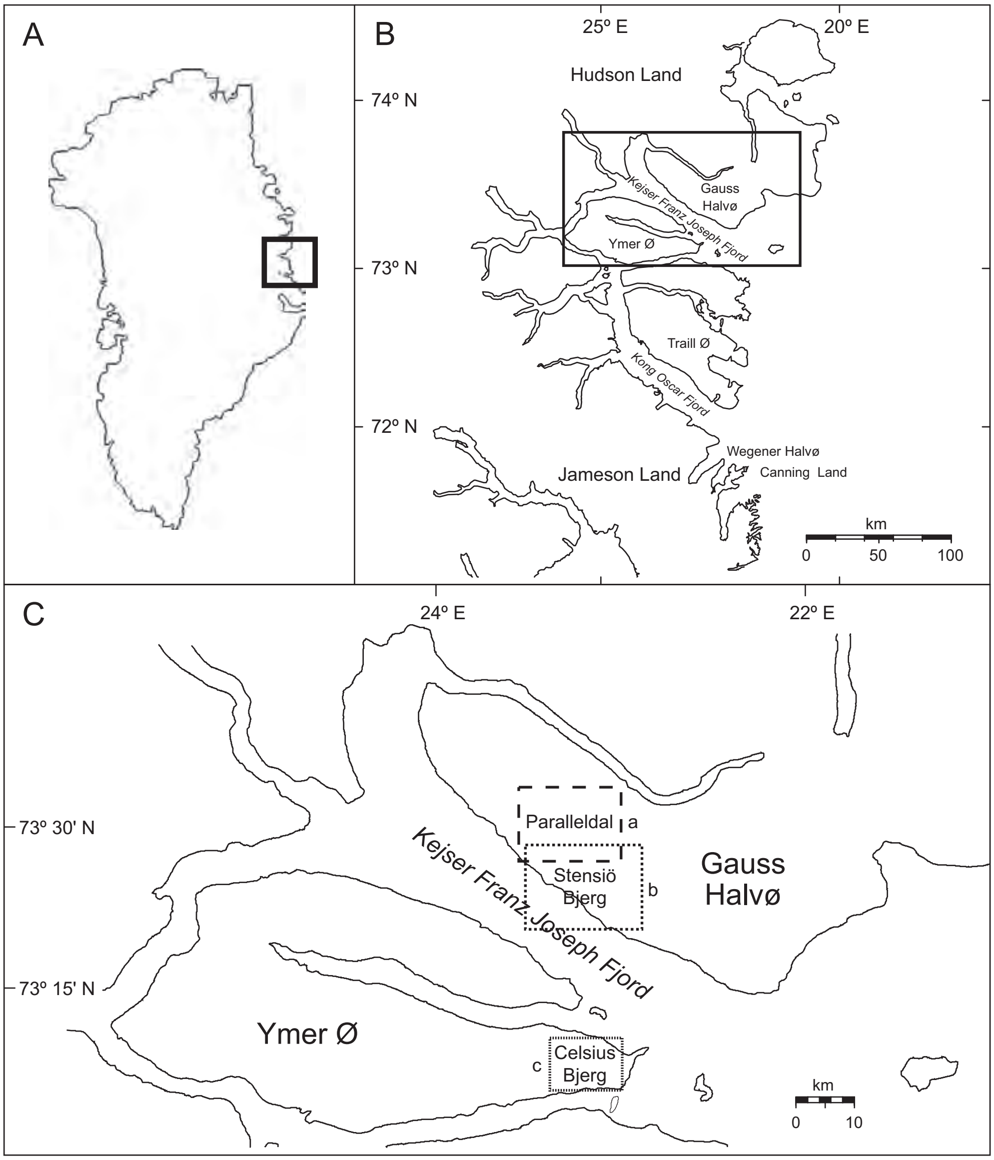

Fig. 1. Map of Greenland and areas of interest, showing area position (A), general extent of Devonian outcrops (B) and close up on the area where tetrapods have been found (C). Indicated areas (a-c) are represented by maps in figures 3, 7 and 9 respectively.

wards the southern exposures on Celsius Bjerg.

The Wimans Bjerg Formation, formally described by Nicholson and Friend (1976), conformably overlies the Aina Dal Formation, and is, apart from trace fossils and possible rare vertebrates, almost unfossiliferous. It is composed of 100-150 m of grey and red muddy siltstones alternating with grey coarse siltstone beds, which Olsen and Larsen (1993) interpreted as deposited in a lacustrine/playa mudflat environment.

The Britta Dal Formation was also formally described by Nicholson and Friend (1976). It has been interpreted as alternating siltstones and very fine to fine-grained sandstones deposited in extensive flood basins and sandstones as point bars in shallow meandering fluvial channels (Bendix-Almgreen *et al.*, 1990; Olsen and Larsen, 1993). Recent stratigraphical and sedimentological studies may, however, challenge previous interpretations against a new hypothesis of periodic sheet flood origin for most of the main sandstone bodies (T. R. Astin

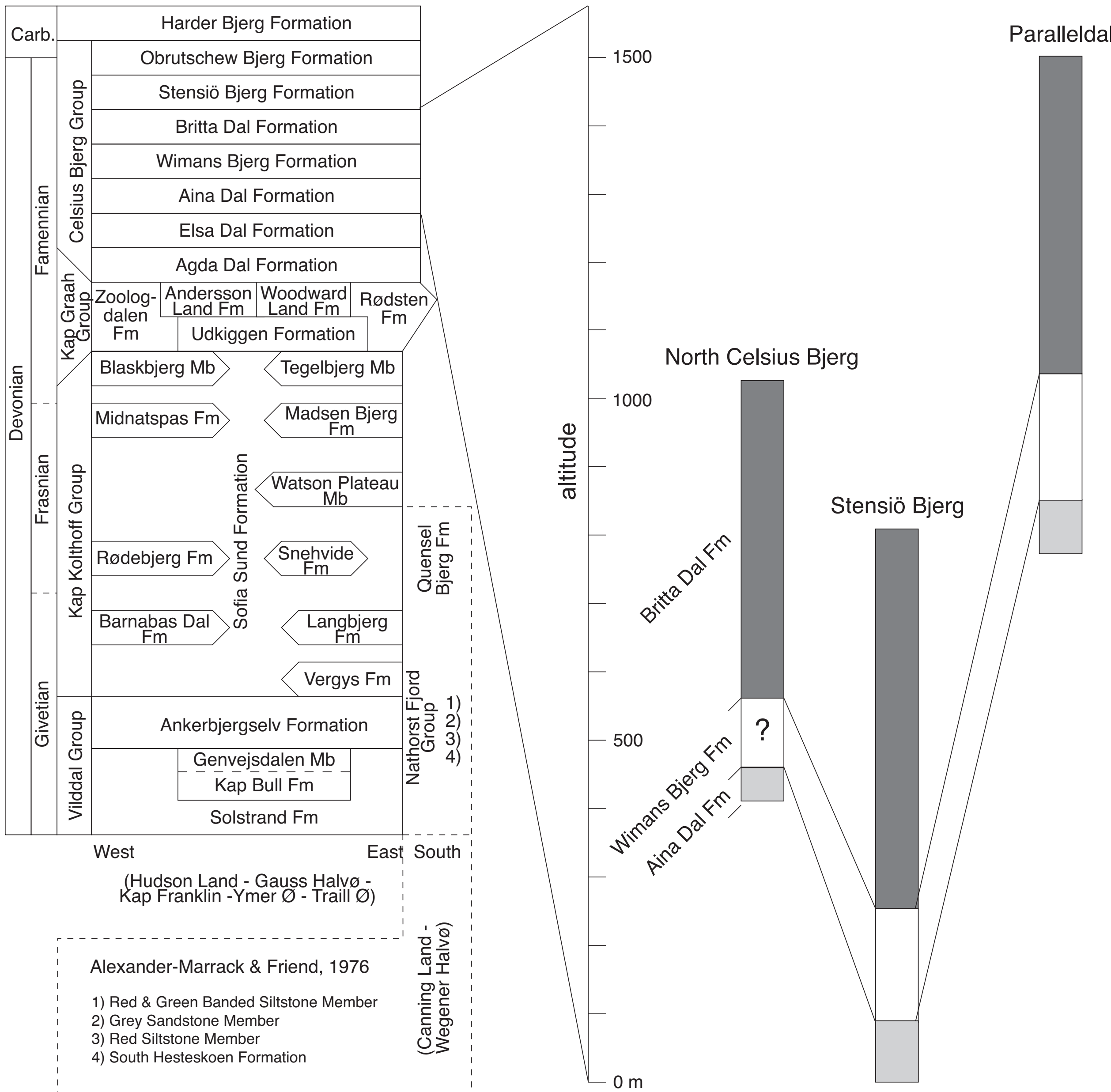

Fig. 2. Stratigraphical scheme of the Devonian subdivisions of East Greenland assembled from Alexander-Marrack and Friend (1976) and Olsen and Larsen (1993) with generalised sections of the tetrapod yielding formations in three key areas. Observe that the given thickness of Wimans Bjerg Formation on Celsius Bjerg originate from Olsen and Larsen (1993). The question mark indicates the thickness uncertainty of the Wimans Bjerg Formation, emphasised by Nicholson & Friend (1976), since they considered the formation absent in Celsius Bjerg.

and J. E. A. Marshall personal communication, 2004). The alternation of sandstone bodies and siltstones, nevertheless, characterise the whole stratigraphical extension of the formation, which in areas can reach about 500 m in thickness. The Britta Dal Formation is also thickest on the south coast of Gauss Halvø and becomes thinner towards north, east and south.

In a sedimentary basin analysis of the continental Devonian successions in East Greenland, Olsen (1993) recognised four tectonostratigraphic basin stages, of which the Celsius Bjerg basin stage (= Celsius Bjerg Group) is characterised by northward draining alluvial plains and lakes. Meandering rivers terminating in a flood basin characterise the alluvial plain of the Aina Dal Formation. These rivers were initially characterised by perennial flow with a gradual change towards increased ephemerality. Such possible seasonality is even more pronounced in the subsequent depositional system of the Wimans Bjerg Formation, in which ephemeral lakes periodically flooded featureless mud flats. In the original basin analysis, Olsen (1993) compared the depositional system of the Britta Dal Formation with the upper part of the Aina Dal Formation system, and interpreted the sediments as ephemeral meandering river sandstones and flood basin mudstones. The massive sandstones in the Britta Dal Formation may in fact represent periodic flooding and deposition of sands in an otherwise anastomosing system of river channels (T. R. Astin and J. E. A. Marshall personal communication, 2004).

Material and methods

There is no precise figure for the total number of tetrapod specimens or individuals in collections, but there are more than 550 block specimens sometimes preserving remains of more than one individual. There are about 200 *Acanthostega* specimens, more than 300 *Ichthyostega* specimens, at least two specimens of a new genus, and a number of specimens that are only recognised as tetrapods but without further assignment. Most material belong to the Geological Museum, Copenhagen, but some specimens collected by Nicholson in 1970 and by the team in 1987 are registered in the University Museum of Zoology, Cambridge and Sedgwick Museum, Cambridge. Most *Ichthyostega* specimens and a few *Acanthostega* specimens collected between 1929 and 1955 have Geological Museum, Copenhagen collection numbers (MGUH VP). Some specimens including those collected in 1970, 1987 and 1998 have either Geological Museum, Copenhagen field numbers (MGUH f.n.) or University Museum of Zoology, Cambridge numbers (UMZC T). Table 1 lists the large number of expeditions with the main participants that have worked on East Greenland tetrapods.

One of the major objectives of this paper has been to review and assemble all available information and give a detailed account for tetrapod localities and distribution in East Greenland. Despite the impression given by previous publications (e.g. Jarvik, 1996),

Table 1. Tetrapod-yielding expeditions carried out in East Greenland.

	Team	Areas of relevance studied	Comments
1929	0. Kulling	Ymer Ø	Koch expedition
1931	G. Säve-Söderbergh, E. Nielsen, H. Leth-Pedersen and D. Laursen	Ymer Ø	Danish Three Year Expedition
1932	G. Säve-Söderbergh, E. Johansson (Jarvik), G. Lindgren and T. Säve-Söderbergh	Ymer Ø, Gauss Halvø	Danish Three Year Expedition
1933	G. Säve-Söderbergh, G. Wängsjö, E. Ohlsson, B. Granström and T. Säve-Söderbergh	Gauss Halvø	Danish Three Year Expedition
1934	E. Johansson (Jarvik), G. Wängsjö, S. Hansson, O. Harder Jensen and R. Nielsen	Gauss Halvø	
1936	G. Säve-Söderbergh and team	Gauss Halvø	
1947	E. Jarvik and a Danish assistant	Ymer Ø	
1948	E. Jarvik, G. Wängsjö and teams	Ymer Ø	
1949	G. Wängsjö and two Swedish assistants	Gauss Halvø	
1951	E. Jarvik, G. Wängsjö and team	Gauss Halvø	
1954	E. Jarvik and two Swedish students	Ymer Ø	
1955a	E. Nielsen, S. E. Bendix-Almgreen and S. Molbech	Gauss Halvø	
1955b	E. Jarvik, H. C. Bjerring & J. Fabricius	Gauss Halvø	
1970	J. Nicholson	Gauss Halvø	
1987	S. E. Bendix-Almgreen, J. Clack, P. E. Ahlberg, R. Clack and B. Jørgensen	Gauss Halvø, Ymer Ø	
1998	J. Clack, S. Finney, S. Neininger and B. Hitchin	Gauss Halvø, Ymer Ø	

there is quite good locality data available for the specimens. Almost all tetrapod specimens have details given on their labels, including locality and altitude. Even the stratigraphical level is often indicated by *in situ* collection or original secondary assignment in the field. When stratigraphical level has not been indicated, it has still been possible to assign specimens to at least gross stratigraphical horizon using a detailed stratigraphical framework extracted from previous publications, unpublished manuscripts and field notes. In a few cases, comparison of sedimentological composition, using surface characters and thin sections, have also been used to identify the origin of specimens.

Stratigraphical framework

In order to be able to present details about the localities and distribution of tetrapods in East Greenland, it is important to establish the stratigraphical framework at a general as well as a local basis. Tetrapods are restricted to two major geographical areas; Gauss Halvø and Ymer Ø (Fig. 1). These in turn are divided into smaller parts, each representing several localities. The Paralleldal and south coastline areas on Gauss Halvø and south and north side of Celsius Bjerg on Ymer Ø, are all slightly different in their stratigraphical context and are therefore discussed individually. It is important to address these differences in order to recognise where in the stratigraphical framework many of the tetrapod specimens have been collected.

This review may also serve as a basis for future work on biostratigraphy of other vertebrate groups from East Greenland. This information is summarised in a number of maps and stratigraphical columns (Table 2, Figs 3-9) and is mainly based on literature rather than personal observations in the field.

Gauss Halvø

Paralleldal area

Paralleldal comprises the large valley extending from Franz Joseph Fjord in the west across the central part of Gauss Halvø to Moskusoksefjord in the east (Fig. 1, 3). Despite the area's importance as one of the major sources for *Ichthyostega* material, only restricted descriptions of the stratigraphy of the outcrops in this large valley were published by Säve-Söderbergh (1934) and Jarvik (Johansson, 1935). However, in 1936, Säve-Söderbergh investigated the area with the aim of describing its stratigraphy in detail, based on the changes in the placoderm genus *Remigolepis* through the 'Remigolepis Series' (Jarvik, 1996). These plans were never fulfilled, but parts of Säve-Söderbergh's unpublished manuscripts are available and form together with the descriptions by Säve-Söderbergh (1934) and Jarvik (Johansson, 1935), a foundation for this detailed review of the local stratigraphy.

Only two sections were initially measured and described by Säve-Söderbergh (1934), one on the south slope of Sederholm Bjerg (Figs 3, 5, section 15) and one on Remigolepis Ridge (Figs 3, 6, section 34). He defined some of the boundaries between the 'Lowermost, dark-red, marly division' (Aina Dal Formation), 'Middle, dark greyish division' (Wimans Bjerg Formation) and 'Upper reddish division' (Britta Dal Formation) and indicates a few major fossil horizons.

Jarvik's (Johansson, 1935) work was much more extensive with seven sections measured on the slopes of Sederholm Bjerg (Figs 3-5, sections 2, 6, 8-11, 20) and about ten on the northern slopes of Smith Woodward Bjerg and Remigolepis Ridge (Figs 3, 6, sections 26-33, 35-37). Several of these sections are not complete through the Aina Dal, Wimans Bjerg and Britta Dal formations, which he refer to as 'Lowermost red', 'Middle grey' and 'Upper reddish' divisions respectively, but a few key sections, 'Profile 1 and 4' (Figs 3-5, sections 20 and 11), were completed with all relevant boundaries. Jarvik (Johansson, 1935) also described characteristic beds and major fossil horizons, including those where *Ichthyostega* was collected.

The most detailed information on the

Table 2. List of sections measured on Gauss Halvø, East Greenland.

Profiles	Source	Location	Comments
A	Olsen & Larsen 1993	Smith Woodward Bjerg	
B	Nicholson & Friend 1976	Stensiö Bjerg	
C	Säve-Söderbergh 1933	Stensiö Bjerg	
D	Säve-Söderbergh 1933	Wiman Bjerg	
E	Säve-Söderbergh 1933	Wiman Bjerg	
F	Säve-Söderbergh 1934	Nathorst Bjerg	
G	Säve-Söderbergh 1934	Nathorst Bjerg	
H	Säve-Söderbergh 1934	Nathorst Bjerg	
I	Olsen & Larsen 1993	Agda Dal	
1	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 29/Crossopterygian Ravine
2	Jarvik (Johansson 1935)	Sederholm Bjerg	Profile 2
3	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 28
4	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 27
5	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 25
6	Jarvik (Johansson 1935)	Sederholm Bjerg	Broad Ridge
7	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 26
8	Jarvik (Johansson 1935)	Sederholm Bjerg	Narrow Ridge
9	Jarvik (Johansson 1935)	Sederholm Bjerg	Ridge east of Narrow Ridge
10	Jarvik (Johansson 1935)	Sederholm Bjerg	Ridge west of Profile 4
11	Jarvik (Johansson 1935)	Sederholm Bjerg	Profile 4
12	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 7
13	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 6
14	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 5
15	Säve-Söderbergh 1934	Sederholm Bjerg	Ridge east of Profile Ravine
16	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 4
17	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 9
18	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 8
19	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 10
20	Jarvik (Johansson 1935)	Sederholm Bjerg	Profile 1
21	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 11
22	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 12
23	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 13
24	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 19
25	Säve-Söderbergh (manuscript)	Sederholm Bjerg	S 20
26	Jarvik (Johansson 1935)	Smith Woodward Bjerg	
27	Jarvik (Johansson 1935)	Smith Woodward Bjerg	
28	Jarvik (Johansson 1935)	Smith Woodward Bjerg	
29	Jarvik (Johansson 1935)	Smith Woodward Bjerg	
30	Jarvik (Johansson 1935)	Smith Woodward Bjerg	Profile 3
31	Jarvik (Johansson 1935)	Smith Woodward Bjerg	
32	Jarvik (Johansson 1935)	Smith Woodward Bjerg	
33	Jarvik (Johansson 1935)	Remigolepis Ridge	
34	Säve-Söderbergh 1934	Remigolepis Ridge	
35	Jarvik (Johansson 1935)	Remigolepis Ridge	
36	Jarvik (Johansson 1935)	Circus Bjerg	
37	Jarvik (Johansson 1935)	Circus Bjerg	Profile 5

stratigraphy in the area has been gathered through a number of sections measured in 1936 by Säve-Söderbergh and his team. Some of that information is available from an unpublished manuscript held at the Department of Palaeozoology, Swedish Museum of Natural History, Stockholm, which unfortunately is not complete and only contains information from the sections measured on Sederholm Bjerg. Since no field notes are available, the only record of the sections measured on the south side of Paralleldal, are those from labels of specimens collected in 1936. However, they cannot provide details on altitude for boundaries.

Säve-Söderbergh worked out a detailed stratigraphy of the 'Remigolepis Series', especially in the 'Upper reddish division' (Britta Dal Formation), from 18 sections (17 included here) on Sederholm Bjerg. The south slope of Sederholm Bjerg is divided by ravines into a series of ridges, which form the basis for most of the sections. In his unpublished manuscript, Säve-Söderbergh used the division of the 'Remigolepis Series' with the abbreviations R1, R2 and R3 for the 'Lowermost red' (Aina Dal Formation), 'Middle grey' (Wimans Bjerg Formation) and 'Upper reddish' (Britta Dal Formation) divisions respectively.

In Paralleldal, the Aina Dal Formation ('Lower red division') is easily distinguished from the underlying strata and overlying Wimans Bjerg Formation. In contrast to the Wimans Bjerg and Britta Dal formations, the Aina Dal Formation is not as distinctly stratified. The sandstones and siltstones are greyish red but in the upper part darker reddish brown to black. The Aina Dal Formation is characterised by a few fossiliferous horizons that can be recognised in several different sections on both sides of the valley. Most of these horizons come from the upper part of the formation and Jarvik (Johansson, 1935) argued that the level at 842 m, 890 m, 921 m and 965 m in different parts of Sederholm Bjerg are all part of one continuous horizon. He also believed that the 754 m and 762 m levels on Smith Woodward Bjerg and Remigolepis Ridge respectively were continuous with that horizon on Sederholm Bjerg (Figs 3-6). Säve-Söderbergh also recognised in his fieldwork in 1936 a number of fossiliferous beds that he thought could belong to this particular horizon described by Jarvik (Johansson, 1935).

Before the detailed study by Säve-Söderbergh in 1936, very little of the stratigraphy of the Wimans Bjerg Formation ('middle grey') was noted. Its boundaries were mainly referred to only because they also form the boundaries of the above and overlying formations. Jarvik (Johansson, 1935), however, noted that the uppermost part of the unit was characterised by "banks [that] are made up of thin layers of bluish limestone with whitish hue of weathering, alternating with thin layers of marl, which weathers into white dust". Säve-Söderbergh likewise recognised the light band of weathered rock at the top of the 'division' during his fieldwork in 1936, but he also divided the Wimans Bjerg Formation into a darker lower part (R2a) and a lighter upper part (R2b). Furthermore, he recorded in the upper part, three very distinct hard banks, each about a metre thick, which can be recognised in several of the sections measured in Paralleldal.

There are some uncertainties regarding the boundary beds between the Aina Dal and Wimans Bjerg formations. On Sederholm Bjerg, Jarvik (Johansson, 1935) reported a dark grey fossiliferous bank at 933 m in the section on Broad Ridge (herein this is section 6), with *Remigolepis* specimens of *R. kochi* type, which he considered to be of the 'middle grey division' (Wimans Bjerg Formation). He noted also that these were the only fossils known from that formation. Säve-Söderbergh reported a horizon of similar character with *Holoptychius* and *R. kochi* which he also considered to be of the 'middle grey division' (Wimans Bjerg Formation). This horizon is at 884 m just west of section 21 (S11 in Säve-Söderbergh's unpublished manuscript). Because occurrence of fossils from the Wimans Bjerg Formation would otherwise be unique, it is unclear whether the horizon is correctly identified or whether it is in fact the Aina Dal Formation. Nevertheless it is at the boundary and the question remains as to whether the horizon lies at the top of the Aina Dal Formation or the bottom of the Wimans Bjerg Formation. Olsen and Larsen (1993) defined the lower boundary of the Wimans Bjerg Formation on Stensiö Bjerg at the base of the first wave-ripple laminated coarse siltstone bed. This may be the same bed mentioned by Jarvik (1935) and Säve-Söderbergh, and shows that the basal bed of the Wimans Bjerg Formation in fact contains fossils such as *Holopthychius* and *Remigolepis*.

Säve-Söderbergh (unpublished manuscript) described the Britta Dal Formation ('Upper reddish division'or R3) as having rich hard, distinctly projecting banks between softer more easily crumbling sediments. These individual banks could be followed along the slopes of Paralleldal. He could thus correlate individual horizons between the different measured sections in the area. Consequently, he gave a much more detailed stratigraphical framework than the simple indication of the altitude of a fossiliferous horizon as described by Säve-Söderbergh (1934) and Jarvik (Johansson, 1935). Säve-Söderbergh (unpublished manuscript) denoted the lower part of the Britta Dal Formation as R3a, which is composed of rock-types very similar to the underlying R2 (Wimans Bjerg Formation), defined on the slightly more reddish colour when seen from a distance. Although R3a has some alternation of softer and harder horizons, it is distinguished from the rest of the formation by the absence of the very prominent hard banks seen higher in the formation. Säve-Söderbergh (1934, unpublished manuscript) and Jarvik (Johansson, 1935) both placed the lower boundary of the Britta Dal Formation above a very prominent yellowish-weathering band. 'R3b' and the rest of the Britta Dal Formation are sufficiently easily distinguished using the frequent occurrence of very distinct projecting hard banks, so that Säve-Söderbergh (unpublished manuscript) introduced a practical nomenclature, which he used in all the sections measured in 1936. Based initially on the conditions seen in his type section S4 (Figs 3, 5, section 16) he defined sequences of groups of one or several projecting banks. Each of these groups of banks with their underlying softer layers is regarded as a division or sequence and given a letter (Rb, Rc, Rd etc.) R3b differs from the other 'divisions' by lacking a softer layer below the banks and the lower boundary starts with the bank named R3b1. In each of the higher divisions, the hard banks were numbered from below (R3b1, R3b2, etc.). The banks above R3i were not systematised because they were too incompletely exposed in the measured sections. Fossils have been collected all through the formation, but are rare in R3a. All the material collected from the 1936 expedition is labelled with its level according to this nomenclature, but only a few tetrapods were found during this expedition (see below). Since the detailed information assembled by Säve-Söderbergh in 1936 is only available for the north side of Paralleldal, there is restricted information on how the south side fits into this pattern. For this area, only the original sections by Säve-Söderbergh (1934) and Jarvik (Johansson, 1935) were available (Fig. 3, 6). It should, however, be noted that there are additional vertebrate specimens, including a few tetrapods, collected in 1936 from the south side of Paralleldal. These speci-

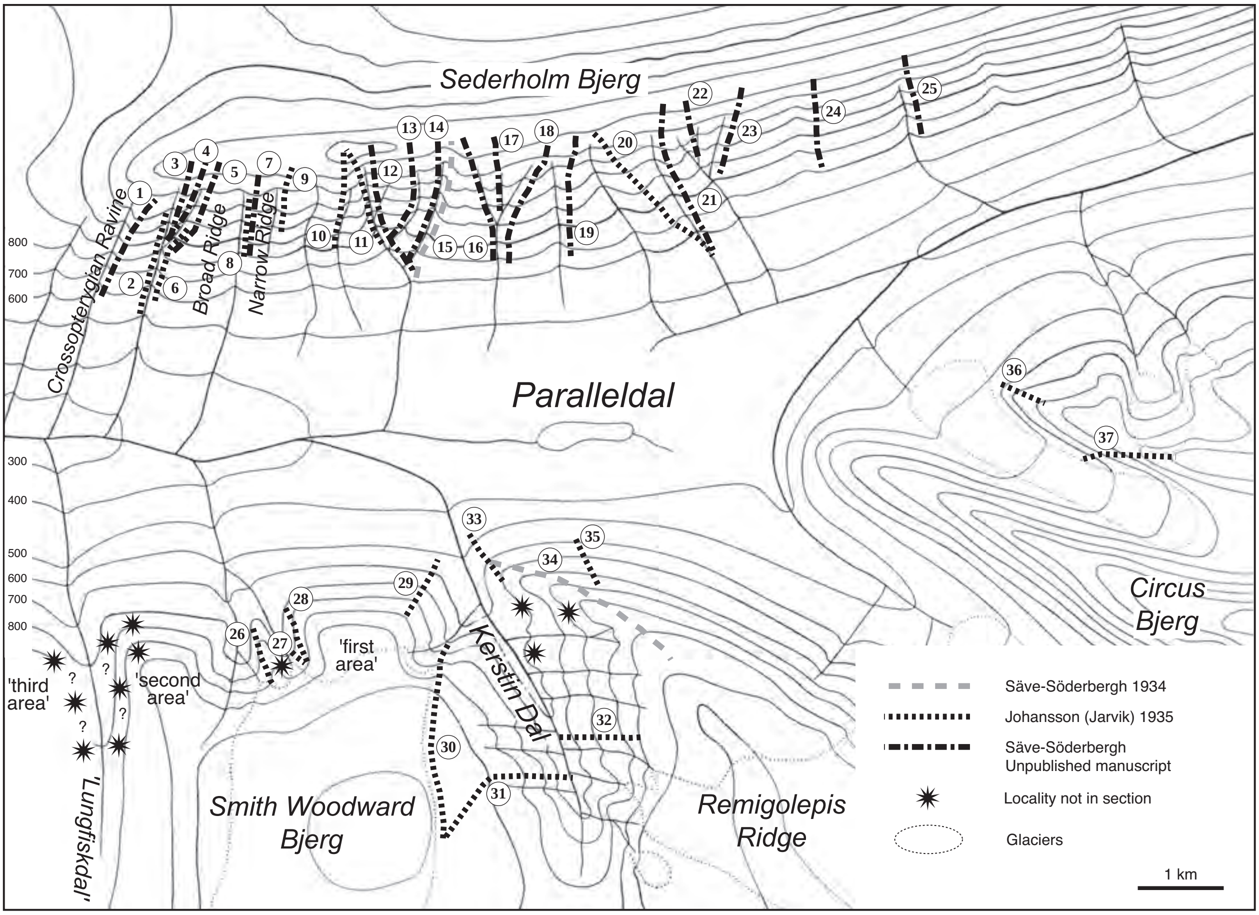

Fig. 3. Map of the Paralleldal area on Gauss Halvø, showing tetrapod localities and measured sections. Sections are illustrated in Figs 4-6.

mens, mostly still not unpacked, have details of locality, altitude and horizon using the nomenclature of Säve-Söderbergh. The information from this material could potentially be used for building up a better picture on the local stratigraphy of Smith Woodward Bjerg and Remigolepis Ridge (Fig. 3).

Successive expeditions used different techniques of nomenclature to log the sections yielding fossils, creating difficulties for cross-correlation. A good example of this is the 1174 m horizon on Sederholm Bjerg (Johansson, 1935) that has yielded numerous *Ichthyostega* specimens. Although it correlates with the 1208 m horizon in section 8 (Fig. 4) (Johansson, 1935), it is difficult to correlate it with any of the named horizons measured by Säve-Söderbergh in 1936. *Ichthyostega* is known from horizons of R3b and it could be argued, to judge from the sections in that area, that the 1174 m horizon is in fact one of the horizons from R3b (Fig. 4).

The assemblage information provided in sections from Paralleldal give an overall stratigraphical context for the area. The Aina Dal Formation has a maximum thickness of 90 m in the central parts of the north side of Paralleldal, but notably the thickness decreases eastwards over about 5 km to about 30 m. On the south side it seems nearer 70 m (Figs 4-6). The Wimans Bjerg Formation in the area varies between 150-200 m, and shows little lateral variation. Since the top of the Britta Dal Formation is not present on Sederholm Bjerg and the formation reaches to the top of the mountains, its thickness can only be estimated by comparison with other parts of Gauss Halvø. More than 400 m is nevertheless exposed in the most complete part of the

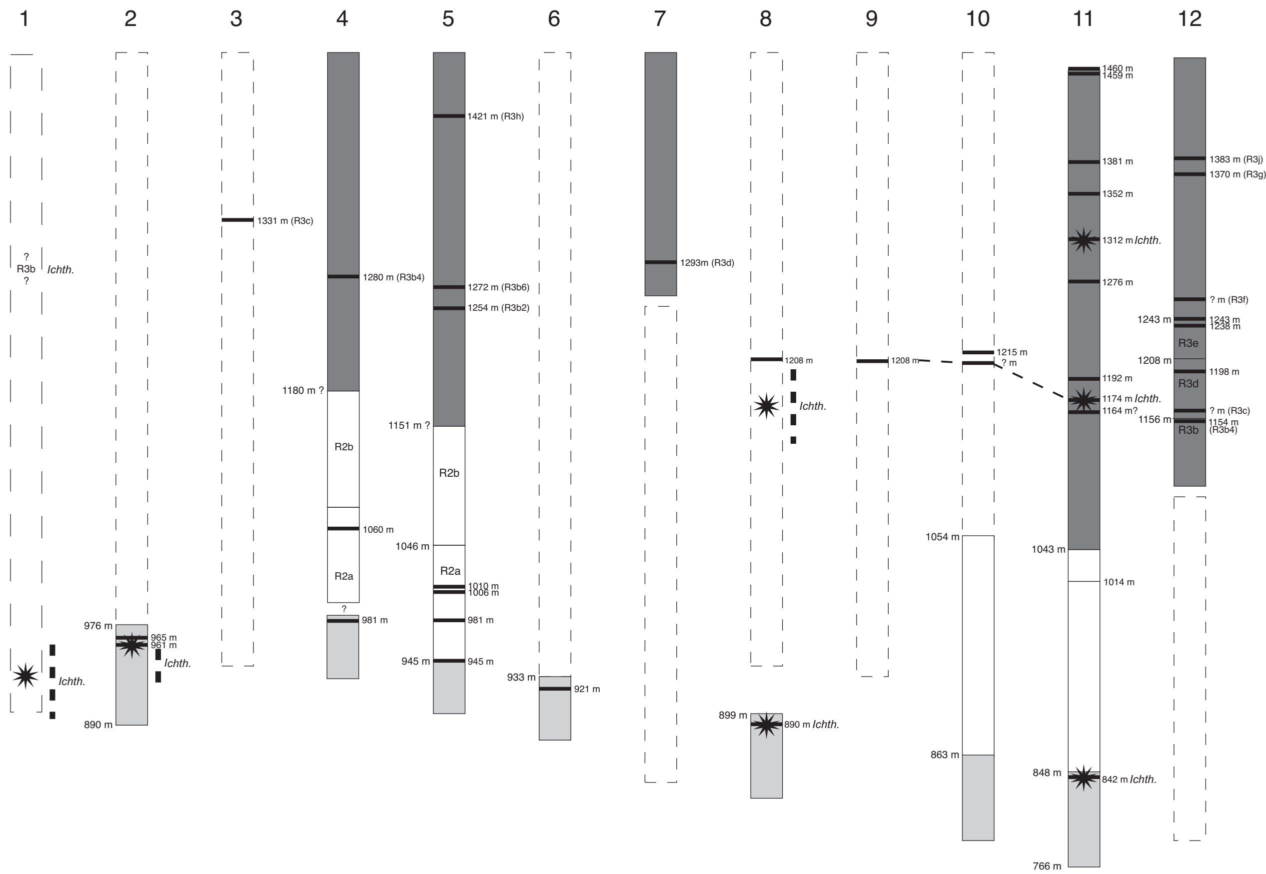

Fig. 4. Sections 1-12 measured on the north slope of Paralleldal, showing the Aina Dal (light grey), Wimans Bjerg (white) and Britta Dal (dark grey) formations. Thick black lines represent fossiliferous or otherwise significant horizons; tetrapod occurrences are indicated by stars and thick dashed lines.

succession (Fig. 4, section 11). On the south coastline the succession is more or less complete and the Britta Dal Formation is about 500 m thick, and it is therefore evident that a large part of the formation is truncated by erosion in Paralleldal.

South coastline area

The stratigraphy and sediments exposed on the south coast of Gauss Halvø have been described more recently than those of Paralleldal (Nicholson and Friend, 1976; Olsen and Larsen, 1993). Their work forms the basis for the formal definition of the Aina Dal, Wimans Bjerg and Britta Dal formations. Although a few measured sections were described by Nicholson and Friend (1976) and Olsen and Larsen (1993) (Fig. 7), a more detailed stratigraphy with descriptions of particular fossil horizons is available from older work by Säve-Söderbergh (1933, 1943) and Jarvik (Johansson, 1935). However, Säve-Söderbergh's work in Paralleldal in 1936 is still lacking in detail. Sections have recently been measured and sampled for spore and sediment analysis (Marshall *et al.*, 1999), and will form the basis for a more detailed stratigraphical description of the areas (T. R. Astin and J. E. A. Marshall personal communication, 2004).

At present, measured sections are available for the south slopes of Smith Woodward Bjerg, Stensiö Bjerg, Wiman Bjerg and Nathorst Bjerg (Figs 7-8). Olsen and Larsen's (1993) description of the Aina Dal, Wimans Bjerg and Britta Dal formations used a type section on Stensiö Bjerg (Figs 7-8, section B). Both this section and that presented by Nicholson and Friend (1976) are very

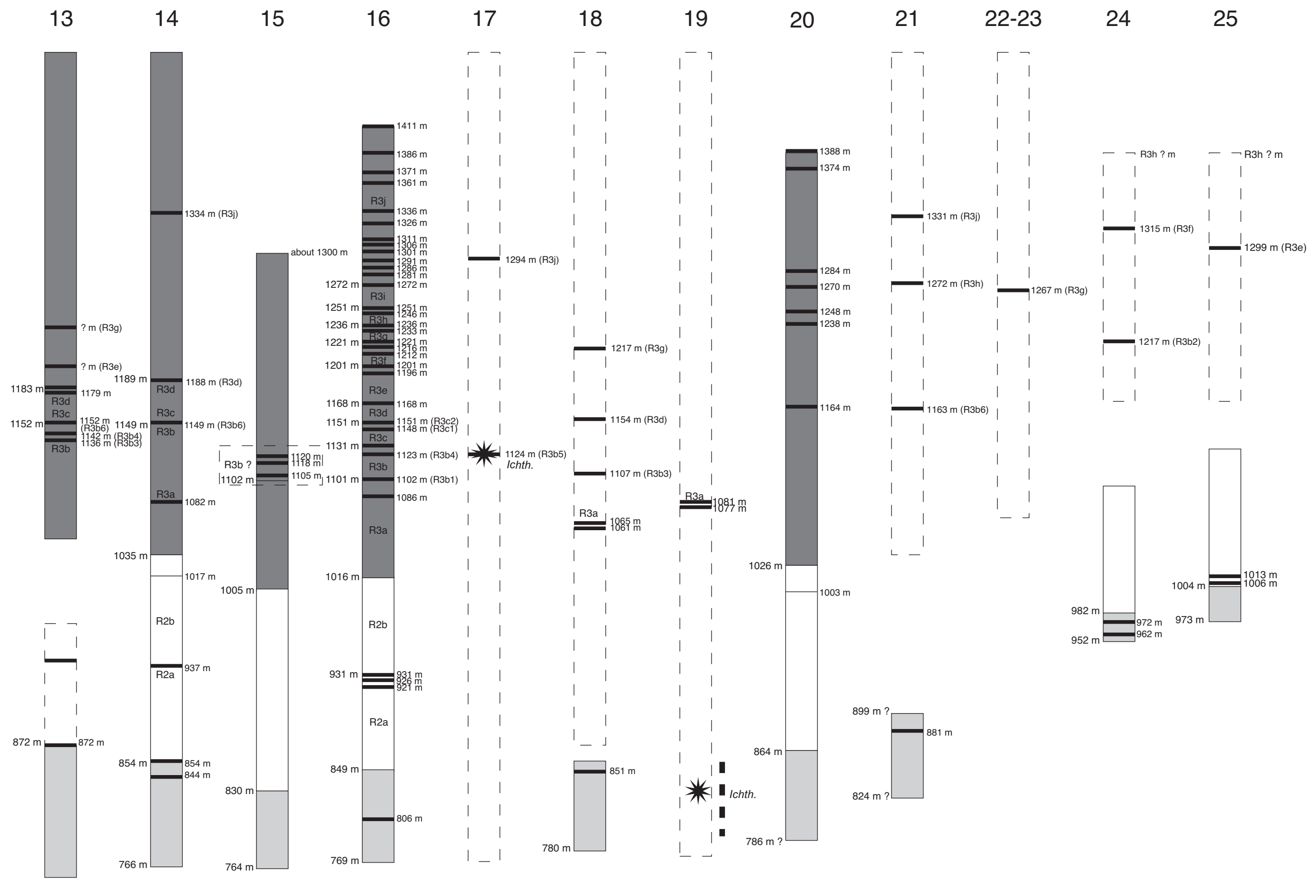

Fig. 5. Sections 13-25 measured on the north slope of Paralleldal, showing the Aina Dal (light grey), Wimans Bjerg (white) and Britta Dal (dark grey) formations. Thick black lines represent fossiliferous or otherwise significant horizons; stars and thick dashed lines indicate tetrapod occurrences.

general, with Säve-Söderbergh's (1933) section on Stensiö Bjerg a good supplement, indicating fossiliferous horizons in the Britta Dal Formation (Fig. 8).

On Wiman Bjerg and Nathorst Bjerg, Säve-Söderbergh (1933, 1934) focused on sections from lower parts of the succession, and recognised horizons that he believed could be correlated with the equivalent horizons mentioned by Jarvik (1935) and Säve-Söderbergh (unpublished manuscript) from Paralleldal.

The character and thickness of the Aina Dal Formation is not very different from that in Paralleldal. In the type area on Stensiö Bjerg, the Aina Dal Formation is generally about 80 m thick, but never exceeds 100 m. As in Paralleldal, the thickness decreases eastward. Although Olsen and Larsen (1993) formally described the formation, they gave few details of levels or boundaries in the type section. According to Olsen and Larsen (1993), the Wimans Bjerg Formation in southern Gauss Halvø around Stensiö Bjerg is approximately 150 m thick, and decreases in thickness to the east. The typical projecting hard banks are also visible in the Britta Dal Formation of this area, but until more detailed sections are described or measured it is very difficult to correlate these sequences with those of the Paralleldal. The full extent of the formation is preserved here and is about 500 m thick or slightly more.

An overall stratigraphical picture of the Celsius Bjerg Group on Gauss Halvø and Celsius Bjerg was presented in five stratigraphical columns by Olsen and Larsen (1993, fig. 89). Their boundaries between the Aina Dal, Wimans Bjerg and Britta Dal formations on Gauss Halvø do not correlate perfectly with

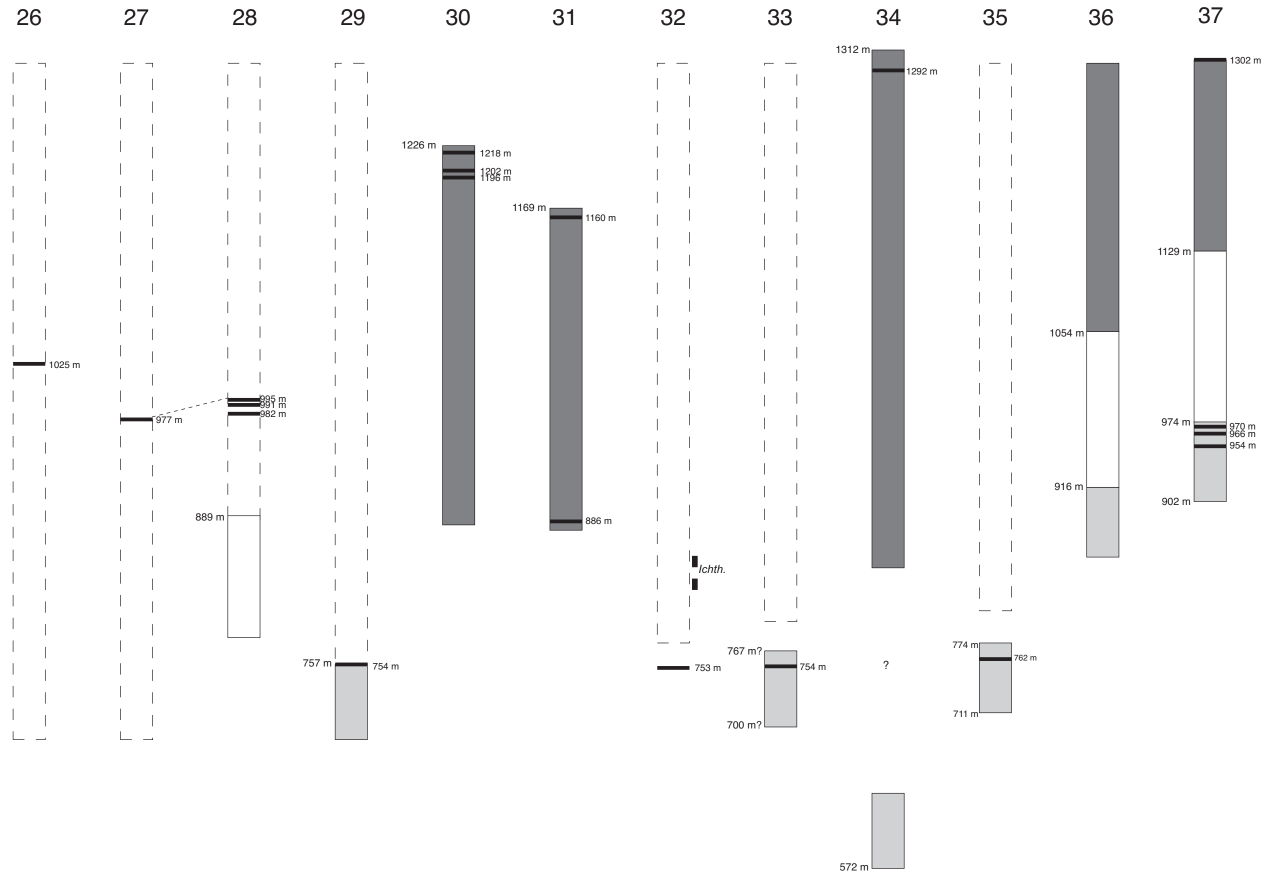

Fig. 6. Sections 26-36 measured on the southern slope of Paralleldal, showing the Aina Dal (light grey), Wimans Bjerg (white) and Britta Dal (dark grey) formations. Thick black lines represent fossiliferous or otherwise significant horizons; stars and thick dashed lines indicate tetrapod occurrences.

detailed levels given by Säve-Söderbergh, particularly in the Nathorst Bjerg area (Fig. 8). The scheme by Olsen and Larsen (1993) seems to present a general correlation in the area rather than absolute boundary indication. It should also be mentioned that major faults in the Nathorst Bjerg area could affect the altitude of boundaries between different sections. No indication of such structural disturbance has been reported, and it is likely that the discordance in the altitude of boundaries is due to simplification in the scheme by Olsen and Larsen (1993).

As seen in the sections (Fig. 8), the whole succession containing the Aina Dal, Wimans Bjerg and Britta Dal formations dip to the west and hence rises towards the east. Towards the west this is also a general character, but more notably is that the exposure of the Aina Dal Formation makes a sharp uplifted kink in the eastern part of Smith Woodward Bjerg. This has been loosely suggested to be related to a major fault running from that point towards the east of the exposed cliff on Stensiö Bjerg (Olsen and Larsen, 1993, fig. 101). However, as there is no disturbance in the Aina Dal, Wimans Bjerg and Britta Dal formations on Smith Woodward Bjerg, this seems rather unlikely. At the same time the thickness of the Wimans Bjerg Formation is substantially less on Smith Woodward Bjerg. It is, therefore, more likely that this is due to common basin architecture with infill and boundary fault compensation at the basin margin. As the sediments thicken, the boundary fault has more movement and you get an open fold at the basin margin. Most important for the distribution of tetrapod localities is, nevertheless, the fact

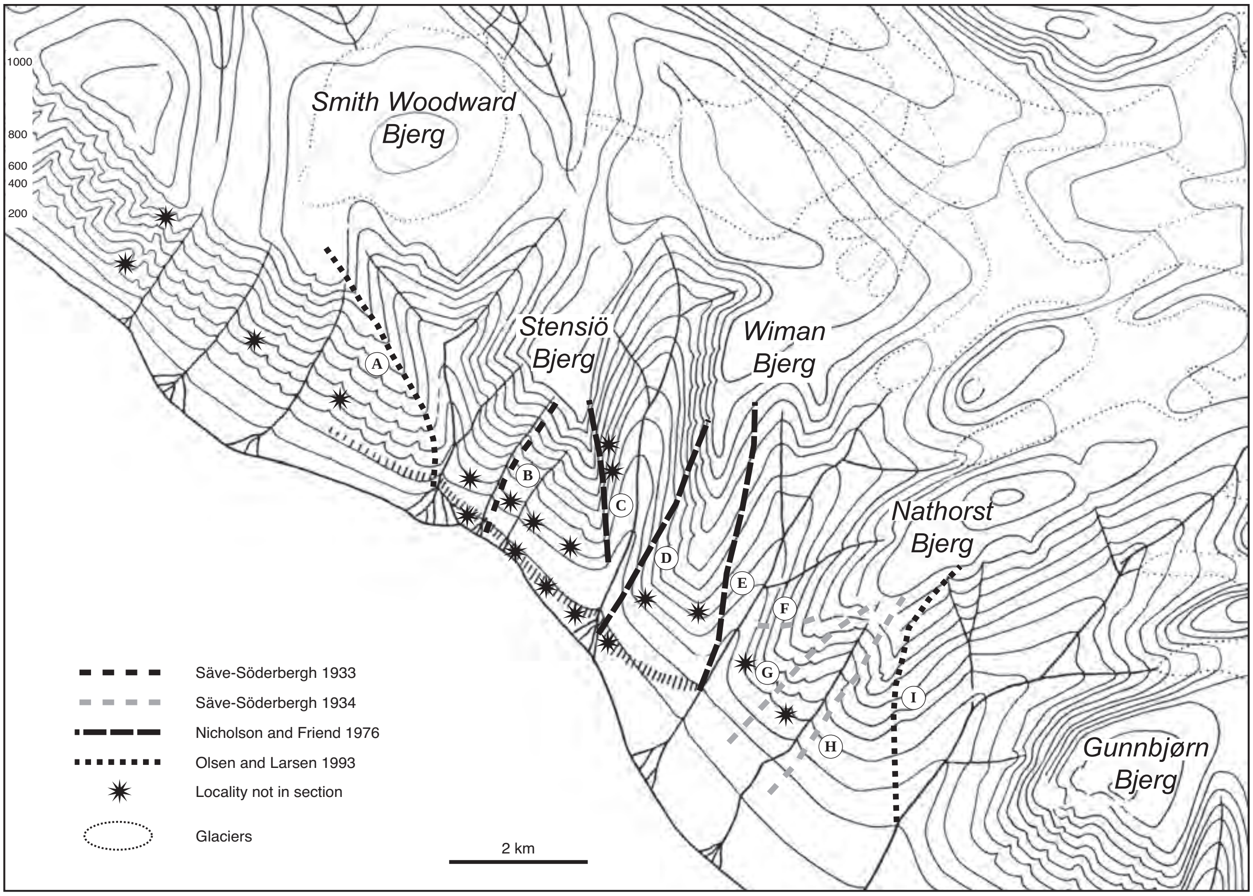

Fig. 7. Map of the south coastline area on Gauss Halvø showing tetrapod localities and measured sections. Sections are illustrated in Fig. 8.

that the exposure on Smith Woodward Bjerg of the Aina Dal Formation is higher and the Wimans Bjerg Formation thinner than elsewhere along the coastline.

Ymer Ø

Celsius Bjerg

Although Celsius Bjerg was one of the first places on East Greenland where Devonian vertebrates were found and the local stratigraphy studied, there are major problems with the stratigraphical context in the area, in particular in relation to the distribution of the tetrapod-yielding Aina Dal, Wimans Bjerg and Britta Dal formations. In early work, the sediments in question were described only as belonging to the 'Remigolepis Series' and not subdivided as on Gauss Halvø (Säve-Söderbergh, 1932*a*; 1933). Nicholson and 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, no absolute values for the boundaries were given, only relative thickness and sample groups. However, using their geological sketch map of the Celsius Bjerg area, it is possible to obtain a general idea about the possible position of the base of the Aina Dal Formation (Nicholson and Friend, 1976, fig. 22). On the north slopes of Celsius Bjerg, the lower boundary varies from about 200 m to 400 m between the most western part of western Celsius Bjerg and the Western Circus Valley (Fig. 9). Further east the boundary appears to rise even higher

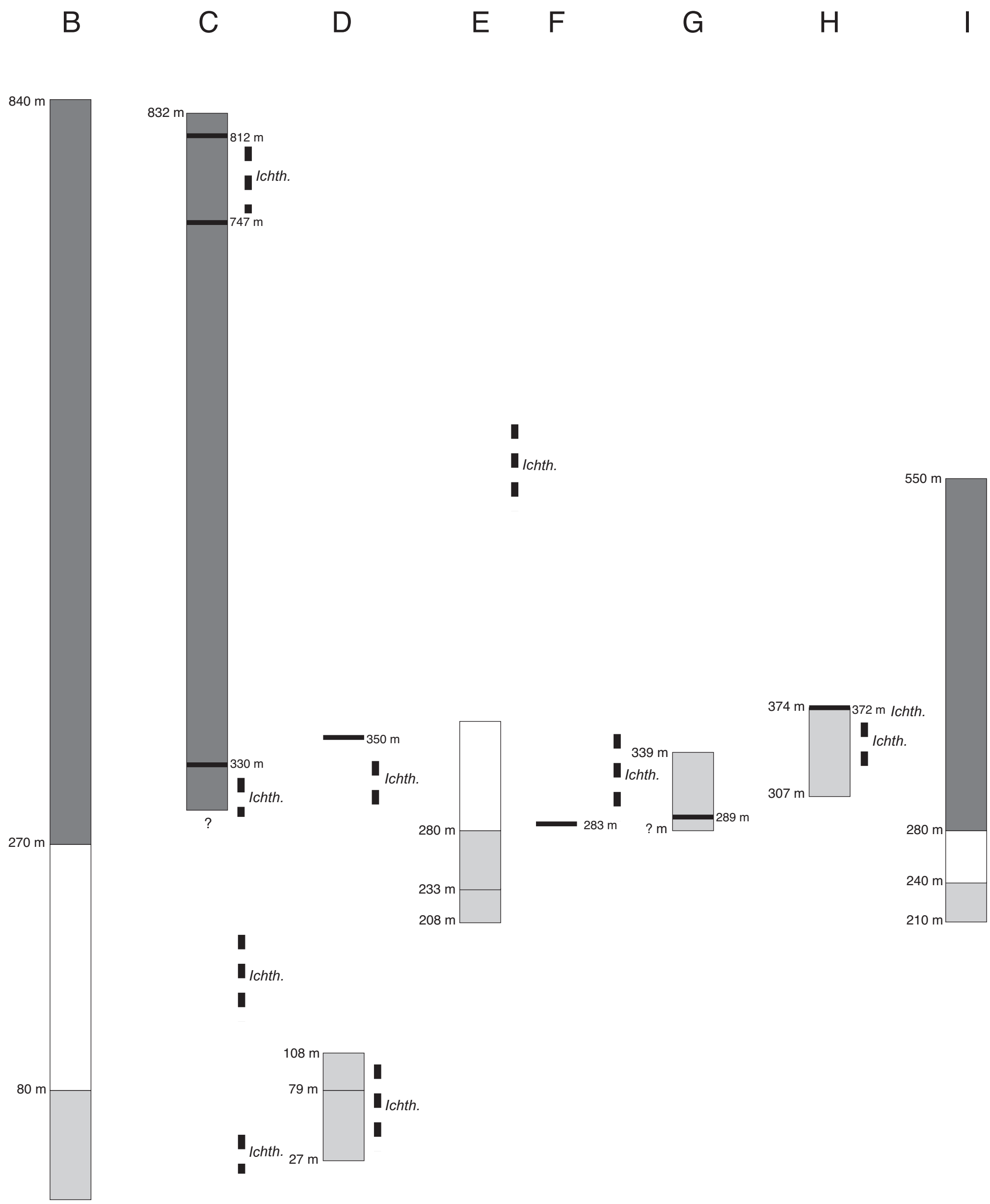

Fig. 8. Sections A-I measured along the south coastline on Gauss Halvø, showing the Aina Dal (light grey), Wimans Bjerg (white) and Britta Dal (dark grey) formations. Thick black lines represent fossiliferous or otherwise significant horizons; stars and thick dashed lines indicate tetrapod occurrences.

and may even reach an altitude of 700 m. Equivalently on south Celsius Bjerg, the lower boundary of the Aina Dal Formation varies from about 150 m in the westernmost end to about 800 m in the east close to a major fault (Nicholson and Friend, 1976, fig. 22).

Olsen and Larsen (1993), however, recognised and reported the occurrence of Wimans Bjerg Formation on Celsius Bjerg. They also used a reference section on southeast Celsius Bjerg to define the Wimans Bjerg Formation, but that part is very poorly exposed in this area and the boundaries not clearly defined. They also presented a section from southwest Celsius Bjerg, which although not specifying boundaries between Aina Dal, Wimans Bjerg and Britta Dal formations indicates a base for the Aina Dal Formation at about 300 m.

Summarizing all the information on Celsius Bjerg, the detailed stratigraphy of both sides of Celsius Bjerg is still very

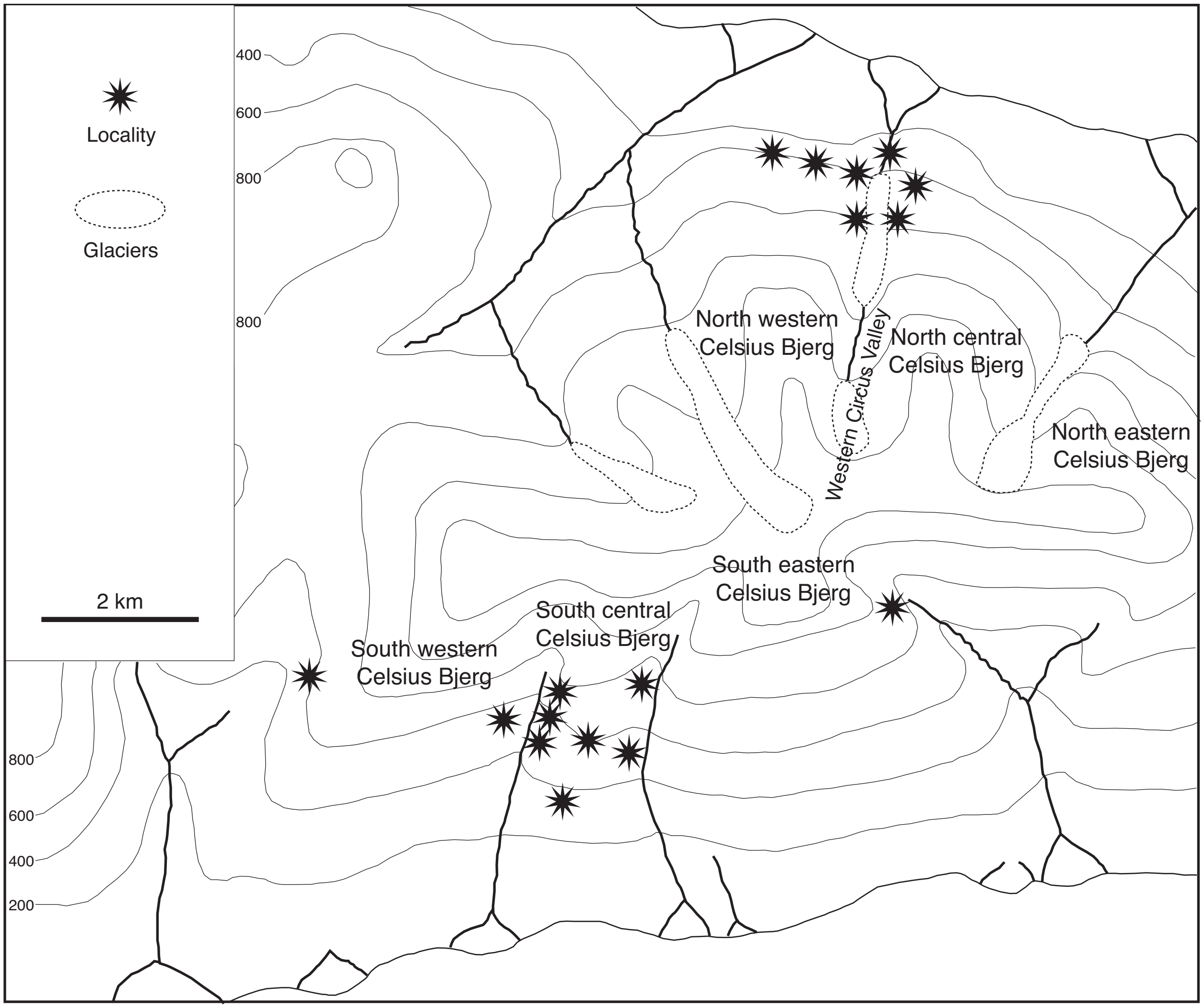

Fig. 9. Map of the Celsius Bjerg area showing tetrapod localities.

uncertain and it is not possible to define boundaries between the formations of interest. No sections are therefore illustrated and localities only will be indicated in the map with their stratigraphical context a subject for speculation and further discussions.

Localities and tetrapod distribution

Gauss Halvø

Paralleldal area

The north and south sides of Paralleldal are among the most fossiliferous of all areas in East Greenland and the main source for *Ichthyostega*. No *Acanthostega* specimens have been collected from this area. As a result of the detailed stratigraphical work in 1936 by Säve-Söderbergh, there are also large collections of fish material still to be analysed from the numerous localities in the valley.

One of the more important sources for *Ichthyostega* specimens is the *in situ* Britta Dal Formation horizon at 1174 m on the south slope of Sederholm Bjerg, at the northern side of Paralleldal. The horizon was first detected in 1934 and described by Jarvik (Johansson, 1935) in the section that he originally called 'Profil 4' (Figs 3-4, 10, section 11). During that first field season, Jarvik and his team collected 11 *Ichthyostega* specimens from that particular horizon. In the same section, he also collected one from another Britta Dal Formation horizon at 1312 m and another from an Aina Dal Formation horizon at 842 m.

The 1174 m horizon, which was also subsequently collected in 1949, 1951 and 1955, has provided almost 50 well preserved specimens. Some of these are articulated with both skulls and associated postcrania (Fig. 11). Later collections were often referred to the 1174 m horizon on the ridge west of 'Profilravinen', which corresponds well, if not exactly, with Jarvik's 1935 'Profil 4' locality (Fig. 10, section 11). One spec-

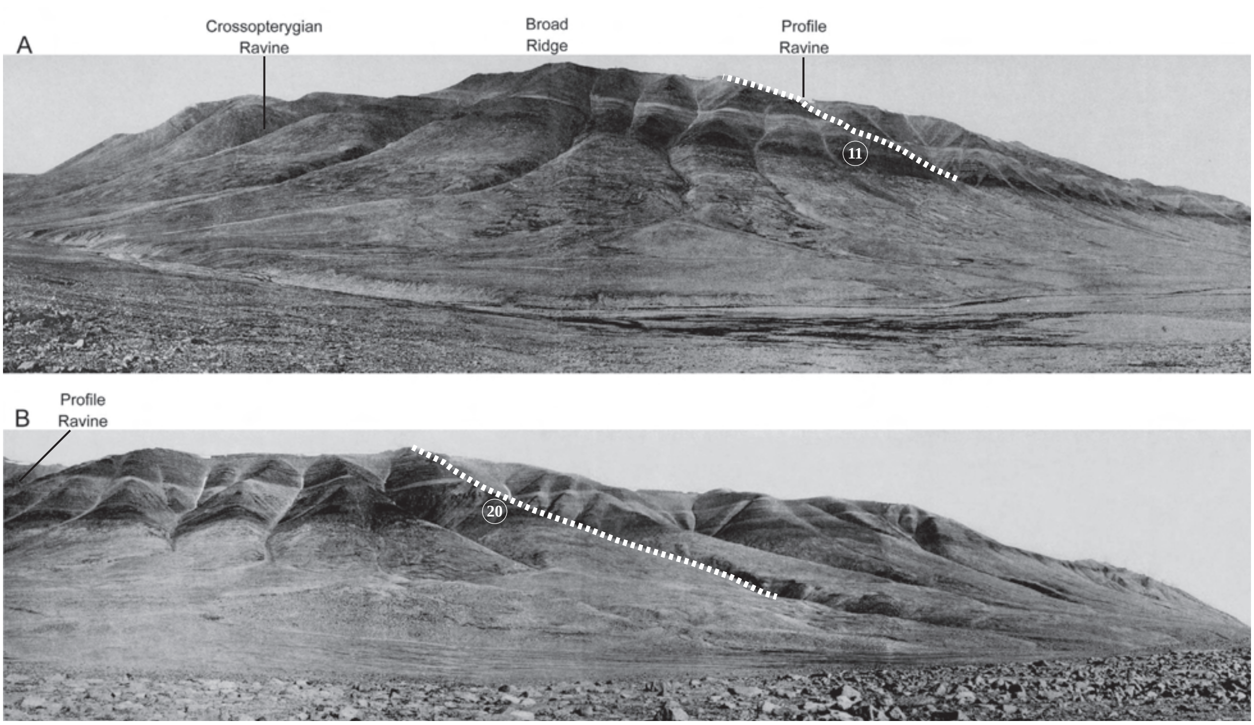

Fig. 10. View of the southern slope of Sederholm Bjerg in Paralleldal. A: Western part with section 11 indicated. B: Eastern part with section 20 indicated.

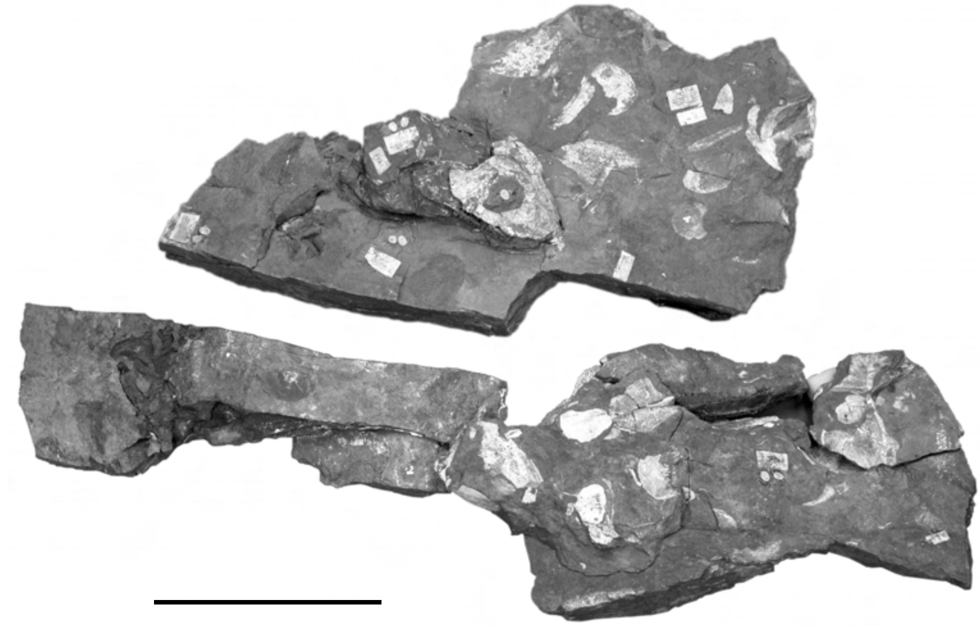

Fig. 11. Several blocks of Ichthyostega *specimen MGUH VP 6237 from horizon at 1174 m on Sederholm Bjerg. Scale bar equals 10 cm.*

imen, which was also found on this ridge in the talus, appears on the basis of matrix type to be of the Aina Dal Formation. Another Aina Dal Formation specimen was found in the talus of the next ridge to the west, a specimen labelled 'second ridge east of Narrow Ridge' (Figs 3-4, section 10).

Although the 1174 m horizon was recognised at 1208 m on the next ridge to the west (Figs 3-4, section 9), 'ridge east of Narrow Ridge' (Johansson, 1935), no *Ichthyostega* specimens were found there. One specimen was, however, found much lower in the talus of the Aina Dal Formation.

Between 1934 and 1951, 11 *Ichthyostega* specimens were collected from the distinct ridge named Narrow Ridge by Jarvik (Johansson, 1935) (Fig. 3). Five were collected from the local talus of the 890 m Aina Dal Formation horizon, and four from undefined parts of the same formation. Another two specimens are known from the Britta Dal Formation; below the horizon at 1208 m (Fig. 4), and in an undefined part of the talus. The latter is recognised as a Britta Dal Formation specimen by its matrix, which is generally coarser and more mica-rich than the matrix of specimens found from the Aina Dal Formation.

Broad Ridge, the large ridge west of Narrow Ridge (Fig. 3), has yielded three *Ichthyostega* specimens from the Aina Dal Formation, of which one is assigned in more detail to the local talus below 933 m. Although a large number of sections were measured on Broad Ridge (section 3-6), only two additional specimens were collected from the R3b6 horizon of the Britta Dal Formation.

The Aina Dal Formation has yielded twelve specimens from the ridge west of Broad Ridge. They originate from the local talus below the 965 m horizon near the top of the formation

The ravine furthest to the west of those measured and collected on Sederholm Bjerg is named Crossopterygian Ravine (Figs 3-4, 10). It has yielded six specimens from the Aina Dal Formation talus and one from the local talus of R3b in the Britta Dal Formation.

Although Jarvik in 1934 (Johansson, 1935) and more importantly Säve-Söderbergh in 1936 carried out substantial stratigraphical work and collecting in the ravines east of 'Profil 4' (section 11), very few *Ichthyostega* specimens were recognised from these strata. Their work, however, is still very useful for assembling a stratigraphical framework for the area that can be used in future biostratigraphical studies using other vertebrate groups (Figs 3-6). Three *Ichthyostega* specimens have, nevertheless, been collected from the local talus of R3b5 at 1124 m in section 17 (S9 in Säve-Söderbergh's unpublished manuscript). It is probable but not certain that this R3b5 horizon at 1124 m correlates with the significant horizon at 1174 m in section 11. Apart from this, only two specimens have been collected from the local talus of the Britta Dal Formation R3g horizon at 1217 m in section 18 (S8), and one from the Aina Dal Formation talus in section 19 (S10).

The south side of Paralleldal also yielded a number of *Ichthyostega* localities along the northern slopes of Smith Woodward Bjerg and Remigolepis Ridge (Fig. 3). A large number of specimens were collected in local talus in the northeastern part of the third area from the east on Smith Woodward Bjerg (Fig. 3). When four *Ichthyostega* were collected there in 1949, the material was assigned to the Wimans Bjerg Formation. A few years later when 15 other specimens were collected in the same area from a local talus at 980 m, they were recognised as an Aina Dal Formation assemblage. Considering the overlap in locality and sedimentological composition, it is evident that the previous material also originates from the Aina Dal Formation rather than the Wimans Bjerg Formation.

To the west of this area on Smith Woodward Bjerg, a larger valley, informally named 'Lungfiskdal', cuts deep into the mountain side. Ten *Ichthyostega* specimens were collected from the slopes of ridges that line the sides of the valley. A majority of those were collected from the Britta Dal Formation talus of the 'sixth ridge', presumably the sixth from the mouth of the valley. Only one of those is given a detailed altitude, of 1015-1020 m. The rest of specimens from 'Lungfiskdal' include one collected from the Britta Dal Formation talus on 'ridge one', and three with uncertain affinity from 'ridge four', 'Kröken' and 'north side' respectively.

East of 'Lungfiskdal' is the area referred to as the 'second portion from the east' on Smith Woodward Bjerg (Fig. 3). In its northwestern part, eight specimens were collected, equally divided between the Aina Dal and Britta Dal formations.

Between the second and first collecting areas to the east on Smith Woodward Bjerg, is a small keel-shaped promontory with ravines on each side. These were used for measuring a few sections (section 26-28) to give an idea about the local stratigraphy (Jarvik, 1935, fig. 3). However, only one *Ichthyostega* specimen was found in the Britta Dal Formation on the northeast side of the promontory.

The large valley between Smith Woodward Bjerg and Remigolepis Ridge is named Kerstin Dal (Fig. 3). Numerous ravines and ridges interrupt both sides of the valley and were used by Jarvik (Johansson, 1935) and Säve-Söderbergh (1934), as landmarks for their localities. These ridges yielded eight specimens collected from various slopes of both the Aina Dal and Britta Dal formations. The localities often refer to a ridge number, but it is unclear today, which ridge is referred to. It seems, however, reasonable to believe that ridges 1-6 refer to the eastern side of Kerstin Dal on the slope of Remigolepis Ridge, since the western side has fewer and less obvious ravines (Johansson, 1935). One Aina Dal Formation and three Britta Dal Formation (at about 967 m) specimens were collected on the first ridge from the mouth of the valley. Three Britta Dal Formation specimens originate from the second ridge. One of these, the famous and beautifully preserved skull MGUH VP 6064 (Fig.

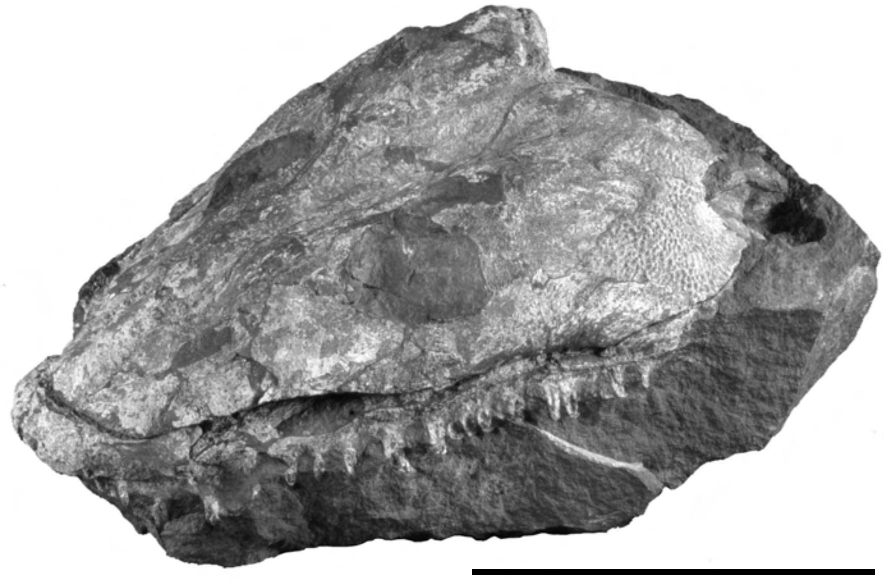

Fig. 12. Ichthyostega *specimen MGUH VP 6064, 'Salongstego-cephalen', from Remigolepis Ridge, Kerstin Dal. Scale bar equals 10 cm.*

12), is often referred to as the 'Salongstegocephalen' since it was exhibited lying on a blue velvet cushion in the saloon of the ship Gustav Holm on the way home from Greenland in 1934 (Jarvik, 1996). Although it was collected in the talus at 801 m (845 m in Johansson, 1935) at the level of the Wimans Bjerg Formation, it is evident that it had fallen there and actually originates from lower parts of the Britta Dal Formation (Johansson, 1935). One specimen was also collected from the talus of the fourth ridge without any clear indication of where its source.

Only two specimens from Paralleldal lack any details of provenance, although one is referred to as derived from 'Profile S23' which was one of the sections measured by Säve-Söderbergh in 1936 and should be somewhere on the south side of Paralleldal.

South coastline area

Tetrapods are only known from one *in situ* locality on the south coast of Gauss Halvø. This locality, which is well-known for providing the unique collection of *Acanthostega* specimens, was discovered by Nicholson in 1970 and excavated in detail in 1987 (Bendix-Almgreen *et al.*, 1988; Bendix-Almgreen *et al.*, 1990). About one hundred specimens containing both articulated and disarticulated *Acanthostega* material were collected *in situ* (Fig. 13), in an exposure close to the top of the Britta Dal Formation on the south-east slope of Stensiö Bjerg (Figs 7, 14). Another hundred *Acanthostega* specimens of various completeness have been collected in the talus below and around the fossil-yielding horizon. The outcrop was originally estimated to lie at an altitude of 733 m, but during more recent fieldwork in the area (Clack and Neininger, 2000), a more accurate 800 m level was measured for the locality. Although Säve-Söderbergh (1933) never found this horizon, it should fall within a close distance of his original section (Figs 7-8, section C). One tetrapod specimen has even been found just above the *Acanthostega in situ* locality and a few *Acanthostega* in the scree well below the locality at about 200 m. It is not possible to say whether these originate from the 800 m horizon or from lower levels within the succession. In the talus below 600 m, a patch of disarticulated spines was found in association with what

Fig. 13. Acanthostega in situ *outcrop at about 800 m on Stensiö Bjerg.*

seems to be a tetrapod interclavicle, suggesting that a larger predator, presumably a sarcopterygian such as *Eusthenodon*, might have regurgitated these remains (Blom *et al*., in press).

More than ten *Ichthyostega* specimens were found much lower in the Britta Dal Formation but on various levels in the big talus between about 100-300 m. Although this is at the level of the Wimans Bjerg Formation, they must originate from higher up in the Britta Dal Formation. Most of these are found in the middle part of Stensiö Bjerg, but a few were also collected further to the east and west.

More than 30 specimens of *Ichthyostega* and one of *Acanthostega* have been collected from the Aina Dal Formation on Stensiö Bjerg (Figs 15-16). They were collected in 1987 and 1998 in what has been labelled as the 'scree below camp-

Fig. 14. View of eastern part of Stensiö Bjerg, separated from Wiman Bjerg by Aina Dal. Acanthostega in situ *outcrop is indicated by arrow.*

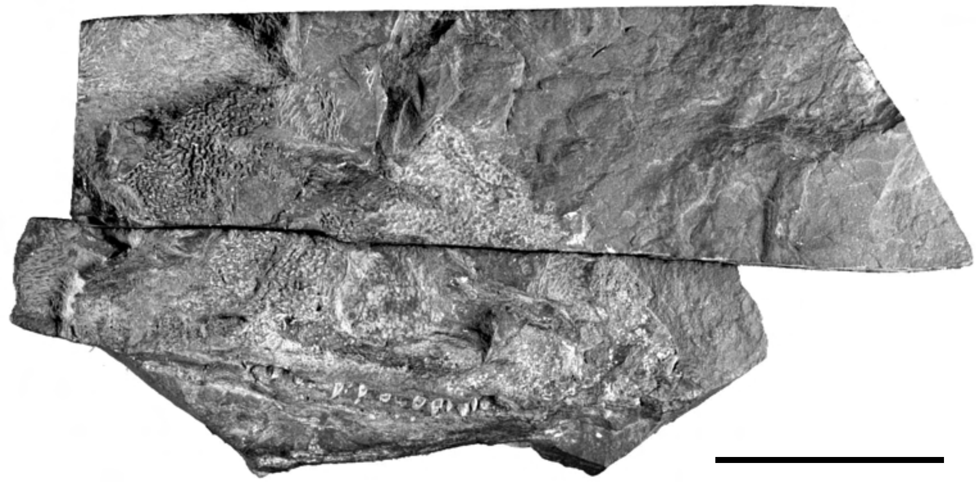

Fig. 15. Ichthyostega *specimen MGUH f.n. 1398 from the Aina Dal Formation of the locality 'loose in scree below campsite' on Stensiö Bjerg. Scale bar equals 5 cm.*

site', which means different levels (0-80 m) within the talus below the cliff and the plateau (Fig. 17) used as camp site for 1987 and 1998 expeditions, which forms the top of the Aina Dal Formation, and immediately west of the Aina Dal waterfall (Figs 14, 17). This locality also relates to the more general reference of a few *Ichthyostega* specimens collected during earlier expeditions in the 1940's. These Aina Dal Formation specimens have been labelled 'bottenterrassen', 'Stensiö Bjerg, western part', 'Ravin väster om västra grytan' and '74 m and talus below along the shore of Stensiö Bjerg'.

Fig. 16. Acanthostega *specimen MGUH f.n. 1330 (part + counter-part) from the Aina Dal Formation of the locality 'loose in scree below campsite' on Stensiö Bjerg. Scale bar equals 5 cm.*

Fig. 17. View of the Aina Dal Formation cliff surface and scree below camp site at Stensiö Bjerg. Observe one of the authors (P.E.A.) for scale.

There are also several finds of tetrapods from the slopes adjacent to that of Stensiö Bjerg. To the east, separated by a valley named Aina Dal, is Wiman Bjerg (Fig. 18), on which several tetrapods have been found, including the holotype of *Acanthostega* (MGUH VP 6033) (Fig. 19). It was found in 1932 in the southwest corner in the talus under the highly fossiliferous bed at 350 m (Säve-Söderbergh, 1933) (Figs 7, 8, section E), but was not recognised as a tetrapod until later (Jarvik, 1952). Another *Acanthostega* specimen and an *Ichthyostega* rib have also been found at this site, which exposes rocks of the Britta Dal Formation. In 1998 an unidentifiable tetrapod fragment was collected on the same side of the mountain towards Aina Dal, but from talus of the Aina Dal Formation.

On the southeast corner of Wiman Bjerg, towards Elsa Dal, several tetrapods have been collected from a large loose block of the Britta Dal Formation at 520 m (Figs 7-8, section E). Most of these are recognised as probable *Acanthostega*, including numerous fragments of at least two juveniles.

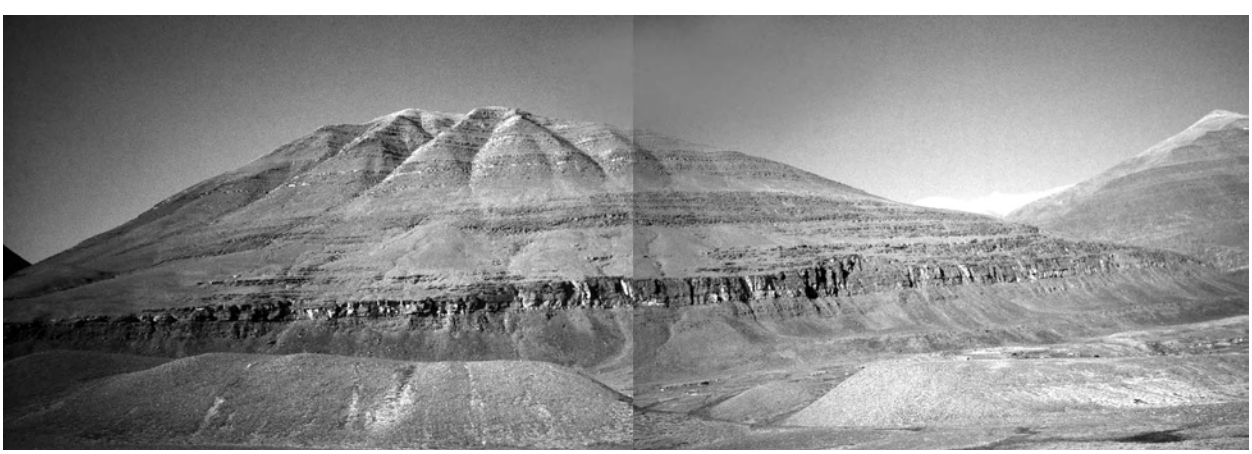

Fig. 18. View of the south slopes of Wiman Bjerg.

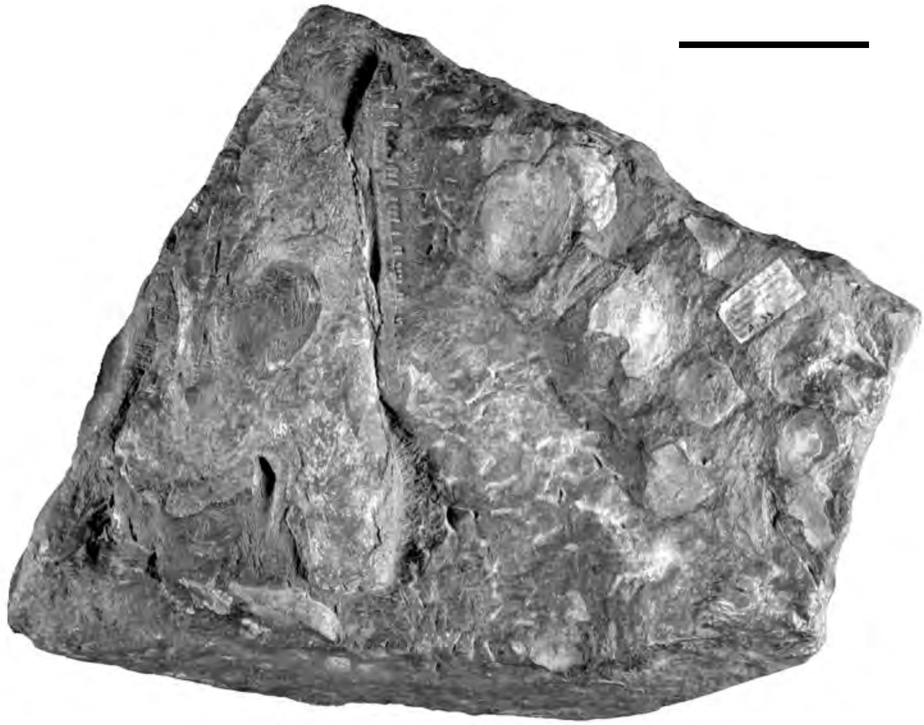

Fig. 19. The holotype of Acanthostega, *MGUH VP 6033, from local talus below 350 m on Wiman Bjerg. Scale bar equals 5 cm.*

Fig. 20. View of eastern part of Smith Woodward Bjerg, divided from the western part of Stensiö Bjerg by Britta Dal.

Nathorst Bjerg, which is located east of Wiman Bjerg, provided three *Ichthyostega* specimens collected in 1933 and 1948. Two were collected from the talus of the fossiliferous Aina Dal Formation horizon at 372 m, in the middle part of

Fig. 21. The well-preserved Ichthyostega *specimen MGUH VP 6115 from the western part of Smith Woodward Bjerg.*

Nathorst Bjerg (Säve-Söderbergh, 1934) (Figs 7-8, section H). The third specimen was collected in an equivalent talus in the western part (Fig. 7, section F).

From the slopes of Smith Woodward Bjerg, to the west of Stensiö Bjerg (Fig. 20), about 15 *Ichthyostega* specimens were collected at different levels 'below the high slope'. Since the south slope of Smith Woodward Bjerg extends far along the coastline and the locality description is no more detailed than 'east', 'middle' or 'west', it is quite difficult to determine the correct locality. It is, however, evident that specimens originate from both the Aina Dal and Britta Dal formations. One of the well-preserved *Ichthyostega* specimens, MGUH VP 6115 (Fig. 21), was collected from about 370 m on the eastern part of the western part and may in fact have been collected *in situ* (Jarvik, personal communication to J.A.C., 1990). Considering its altitude and sedimentological composition it certainly originates from the Aina Dal Formation. Another *Ichthyostega* specimen found at 832 m from the same slope originates from the Britta Dal Formation.

Ymer Ø

North Celsius Bjerg

The slopes on the north side of Celsius Bjerg (Fig. 22) were the first to yield tetrapods, including the type material of *Ichthyostega*. To date, about 80 specimens of *Ichthyostega* have been collected, varying considerably in the amount of detail provided about locality. The north side has yielded only *Ichthyostega* specimens and not, as on the south side, *Acanthostega* and the new tetrapod genus currently under description by the authors.

Perhaps the most significant locality is East Plateau which, according to Säve-Söderbergh (1933), is limited to the eastern part of western North Celsius Bjerg where the type material was collected in 1931 (Fig. 23). At least six specimens were collected from East Plateau, including the holotypes of *Ichthyostega stensioei*, *Ichthyostega watsoni*, *Ichthyostega*? *kochi* and *Ichthyostegopsis wimani* (Säve-Söderbergh, 1932). The other two taxa named by Säve-Söderbergh (1932), *Ichthyostega eigili* and ichthyostegid sp. A, were found above the slope down to the East Plateau, at the eastern boundary

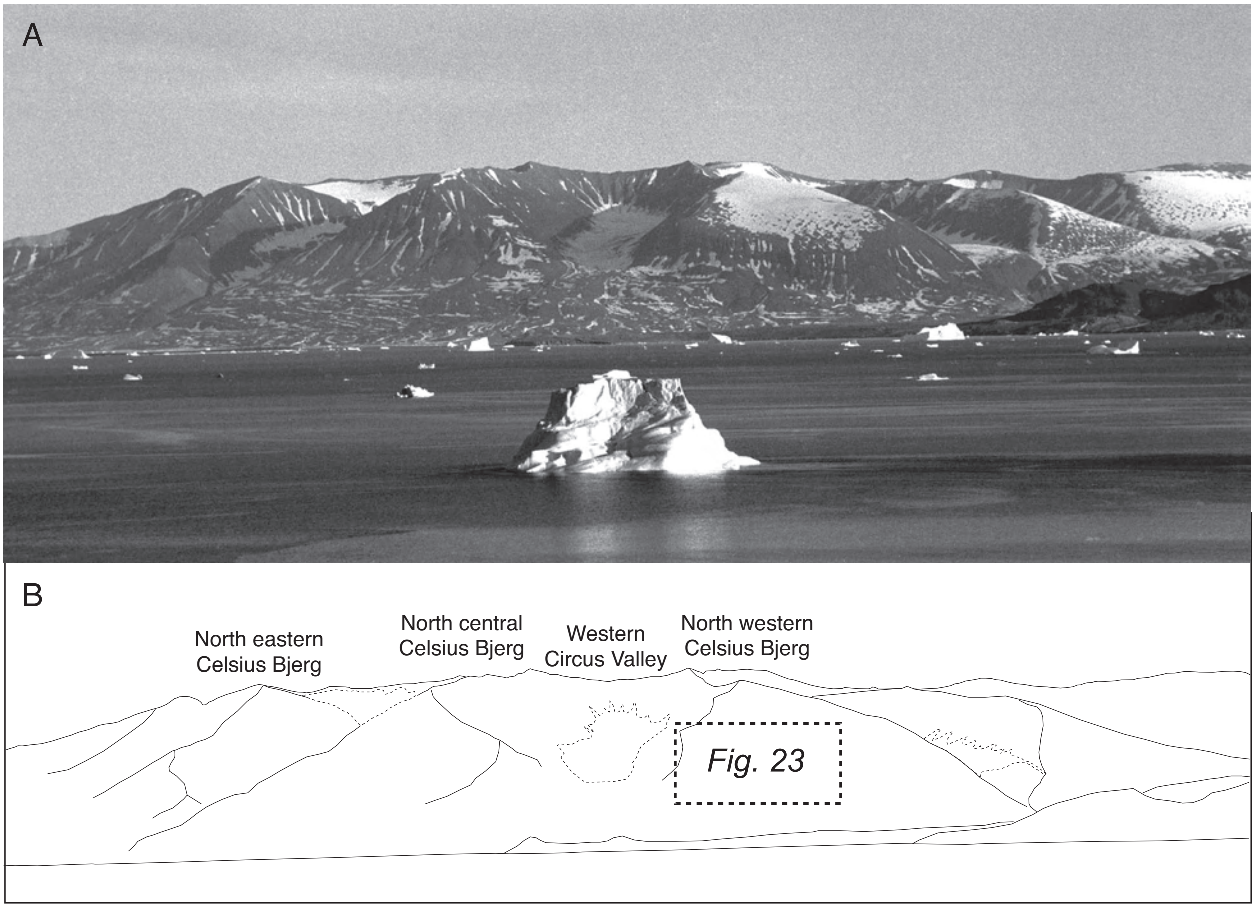

Fig. 22. Photograph of north face of Celsius Bjerg taken from Gauss Halvø.

of the Eastern Upper Terrace (Fig. 23). Of these original taxa only three, *I. stensioei*, *I. eigili* and *I. watsoni*, are still considered valid (Blom, 2005). In 1987, three *Ichthyostega* specimens were collected in the scree at 380 m, 400 m and 450 m below the East Plateau. There are also a number of specimens with poor locality data that still may originate from East Plateau. These are referred to as 'East Plateau, Coulisses' or just 'northern slope of Celsius Bjerg'. Another significant locality that has been referred to as East Plateau is 'Stora raset' above Topmost Coulisse. That refers to the large talus behind and above Topmost Coulisse (Fig. 23). About 10 specimens have collected over the years from this locality, which has also been referred to as Eastern Upper Terrace.

Another part of the north side of Celsius Bjerg that has provided numerous *Ichthyostega* specimens is what, in general terms, was simply called the Coulisses. They are two large down-faulted blocks exposed west of Lower Terrace, which runs below East Plateau (Fig. 23). During the first two field seasons, and occasionally also later, these two coulisses were not distinguished from each other. Ten specimens were collected there and not given any further details on the label than around the Coulisses. Later, however, more details were given and the Coulisses were divided in into 'western' and 'eastern' (Säve-Söderbergh, 1932). Five *Ichthyostega* specimens were found in the talus behind the 'western Coulisse' and one simply in talus at the 'western Coulisse'.

According to Säve-Söderbergh (1933), the fossil locality 'Behind the Western Coulisse' is bounded to the east by a sharp ridge. This ridge was called Kochi

Ridge and has yielded a few *Ichthyostega* specimens. There are also a few localities closely related to those mentioned, but they are not assigned more details than 'Gully on north facing scree, east of Kochi-Ridge, approximately *in situ*', 'small Coulisse west of Western Coulisse, stuck in brook' and 'Älven west of fault, Kitteln'.

Other significant localities on north Celsius Bjerg are those linked with Western Circus Valley (Figs 9, 22). This valley divides the western part of North Celsius, with its East Plateau etc, from the central part according Säve-Söderbergh (1932). It holds a glacier covered with so much rubble that ice can be seen only in major crevasses. There could be some confusion related to the name Western Circus Valley, since Nicholson and Friend (1976) used the name North Central Circus Valley for the same valley. Nicholson and Friend (1976) also used a completely different terminology from that of Säve-Söderbergh (1932, 1934) for the different parts of Celsius Bjerg (Nicholson and Friend, 1976, fig. 22). Herein we use the original names given by Säve-Söderbergh (1932, 1934), as used also by the majority of people collecting in the area, so that geographical names can be compared to those on labels.

A majority of about 20 specimens collected in the Western Circus Valley originate from the western side. Details are,

Fig. 23. Close-up of north western Celsius Bjerg.

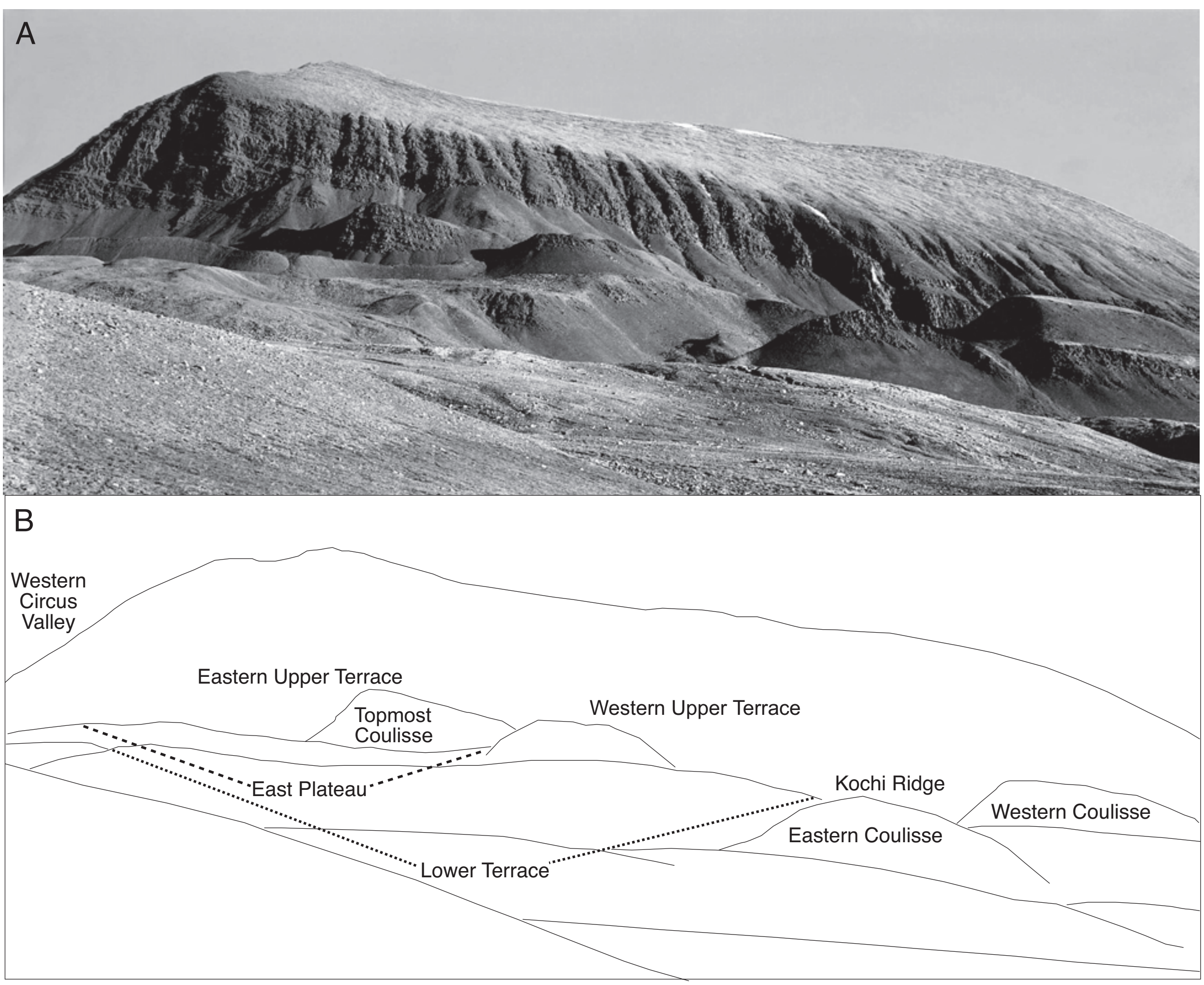

Fig. 24. View of the central part of the south side of Celsius Bjerg, showing two localities collected at about 400 m and 360 m in 1998 (see Clack & Neininger, 2000).

however, scarce and few specimens are given greater details than just 'inner part', 'lower part', or just simply 'western side'. Furthermore, vague locality details also characterise specimens from the rest of the valley, which has yielded one specimen from the 'eastern side', five from the 'moraines', three from the 'delta' and one from the 'plateau in the north end'.

In the western part of central north Celsius Bjerg, towards the Western Circus Valley, five *Ichthıyostega* specimens were collected from the talus of 'Double Ravine'.

There are also specimens with very little detail, such as 'north side of Ymer Ø, hill about 6 km northwest of Kap Graah, 100 m above sea level' and just 'north Celsius Bjerg'.

As shown above, the stratigraphical context of north Celsius Bjerg is somewhat problematic, and it is therefore quite difficult to assign the different localities to any formation with certainty. Although the geological sketch map of Nicholson and Friend (1976, fig. 22) may provide an indication of the lower boundaries of Aina Dal Formation in the area, the implications of this uncertainty will be discussed later in this paper.

South Celsius Bjerg

Only about 40 tetrapod specimens have been collected on the south side of Celsius Bjerg, and most were collected during the latest field expedition in 1998. The majority of these have been found in the central part. Several were collected at the western end in the scree between 460 and 725 m (Fig. 9). They includes numerous *Ichthyostega* specimens and two *Acanthostega*. There are also several *Ichthyostega* specimens from the talus in the central part in horizons between 360 and 600 m. Tetrapods have also been collected from central South Celsius Bjerg, either just referred to as the 'eastern end 500-800 m' or Eastern Terrace ('Östra läktaren' according to Säve-Söderbergh (1933)). In addition, the latter has also yielded a specimen of a new tetrapod, currently under description by the authors. A better specimen of the same new genus (Fig. 25) has also been collected at the eastern end of the western part, an area in which a few *Ichthyostega* specimens have been collected in talus at about 600 m. Only one tetrapod specimen has been found in the eastern part of South Celsius Bjerg, in the eastern corner at 885 m.

Since the stratigraphical context of south Celsius Bjerg is somewhat prob-

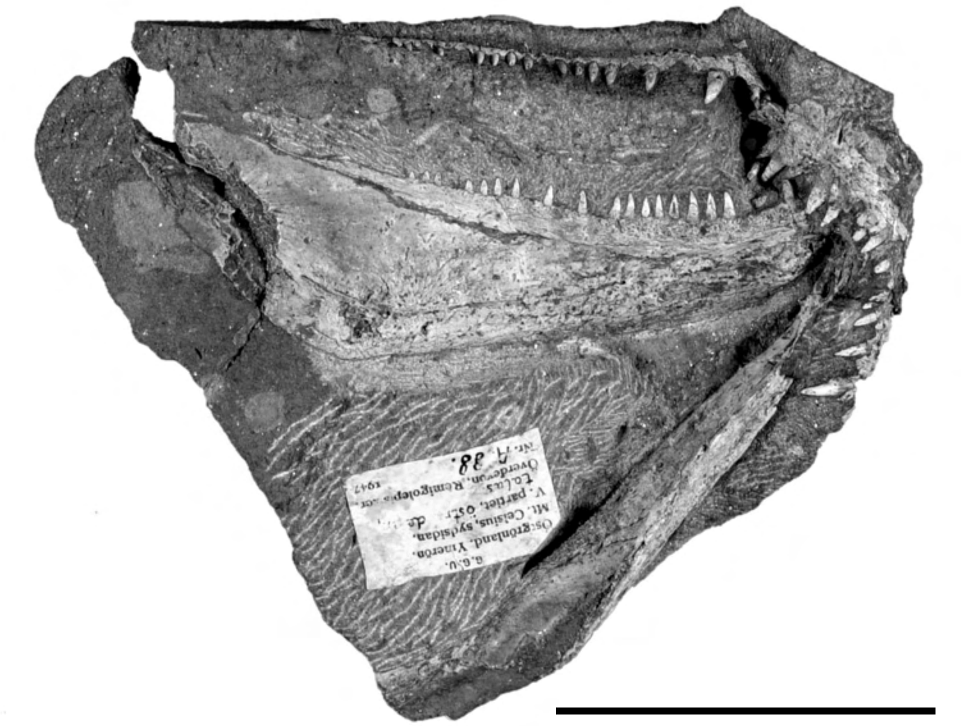

Fig. 25. Specimen MGUH VP 6088 of a new tetrapod genus from the easternmost talus of the western part of the south side of Celsius Bjerg.

lematic, it is quite difficult to confidently assign the different localities to formations. However, if the geological sketch map of Nicholson and Friend (1976, fig. 22) is correct, then most specimens originate from talus at the level of Aina Dal Formation or higher and could certainly contain Britta Dal Formation material as well.

Table 3. List of tetrapod-yielding localities in East Greenland with references to specimens, altitude, collecting year (see Table 1), section (see Table 2) and level (referring to the various stratigraphical units represented at the localities. R1, Aina Dal Formation; R3, Britta Dal Formation; CN, undifferentiated units on north Celsius Bjerg; CS, undifferentiated units on south Celsius Bjerg.

Locality	Taxa content	Specimens	Altitude	Collecting year	Section	Level
Nathorst Bjerg, south side, talus from horizon 372 m	2 *Ichthyostega*	222, 6106	372 m	1948, 1933	H	R1?
Nathorst Bjerg, south side, western part, talus along the base of the 'Remigolepis series'	1 *Ichthyostega*	6036		1933	F?	R1
North Celsius Bjerg,	*Ichthyostega*	6094		1948	Specimens not relatable to any measured sections	CN
North Celsius Bjerg, Älven W. of fault, Kitteln.	*Ichthyostega*	6011		1931		CN
North Celsius Bjerg, behind western Coulisse	3 *Ichthyostega*	6100, 6224, 6226		1948, 1954		CN
North Celsius Bjerg, behind western Coulisse, north face of mountain, loose in scree east of main waterfall	*Ichthyostega*?	1627	ca 430 m	1987		CN
North Celsius Bjerg, central part, talus	*Ichthyostega*	6168		1948		CN
North Celsius Bjerg, Coulisses,	6 *Ichthyostega*	6009-6010, 6014, 6141, 6262-6263		1929, 1931, 1949		CN
North Celsius Bjerg, Eastern Plateau	6 *Ichthyostega* + *Ichthyostegopsis* wimani	6002, 6007, 6012, 6013, 601, 6001, 6005		1931		CN
North Celsius Bjerg, Eastern Plateau, Above East Plateau	Ichthyostegid sp. A	6006		1931		CN
North Celsius Bjerg, Eastern Plateau, Above East Plateau, eastern margin of estern upper plateau	*Ichthyostega eigili*	6004		1931		CN
North Celsius Bjerg, Eastern Plateau, Coulisses	*Ichthyostega*	6008		1931		CN
North Celsius Bjerg, Eastern Plateau and large talus above topmost Coulisse	10 *Ichthyostega*	871, 887, 6104-6105, 6109, 6225, 6227-6228, 6242, 6245		1948, 1954, 1955b		CN
North Celsius Bjerg, Eastern Plateau, scree below	?Tetrapod?	1657	ca 450 m	1987		CN
North Celsius Bjerg, Eastern Plateau, scree below	*Ichthyostega*	1617	ca 380 m	1987		CN
North Celsius Bjerg, Eastern Plateau, scree below	*Ichthyostega*	1618	ca 400 m	1987		CN
North Celsius Bjerg, Eastern Plateau, western part, 'Kochiryggen', above Coulisses	2 *Ichthyostega*	809, 6098		1948		CN
North Celsius Bjerg, Gully on north facing scree East of Kochi Ridge, approximately *in situ*	Tetrapod?	1612	ca 280 m	1987		CN
North Celsius Bjerg, middle part, 'dubbelravinen', east branch of double Ravine, loose in scree west of stream	Tetrapod?	1633	ca 770 m	1987		CN
North Celsius Bjerg, middle part, 'dubbelravinen'	4 *Ichthyostega*	6028, 6031-6032, 6101		1932, 1948		CN

Table 3. Continued.

Locality	Taxa content	Specimens	Altitude	Collecting year	Section	Level
North Celsius Bjerg, Upper Coulisse	*Ichthyostega*	6171		1948	Specimens not relatable to any measured sections	CN
North Celsius Bjerg, Upper Plateau, western part behind Coulisse, loose	2 *Ichthyostega*	6017-6018		1932		CN
North Celsius Bjerg, Upper Plateau, western part, loose	3 *Ichthyostega*	6016, 6019-6020		1932		CN
North Celsius Bjerg, Western Circus Valley, beside main stream flowing from Western Circus Valley, loose in scree	*Ichthyostega*	1650	240 m	1987		CN
North Celsius Bjerg, Western Circus Valley, delta	2 *Ichthyostega*	6099, 6103		1948		CN
North Celsius Bjerg, Western Circus Valley, eastern side, loose	*Ichthyostega*	6029		1932		CN
North Celsius Bjerg, Western Circus Valley, morain, lower part	5 *Ichthyostega*	6230, 6248, 6249, 6250, 5251		1954, 1955b		CN
North Celsius Bjerg, Western Circus Valley, north end of west side, loose in scree	Tetrapod	1660	ca 530 m	1987		CN
North Celsius Bjerg, Western Circus Valley, plateau at north end, loose in scree	? Tetrapod	1656	ca 520 m	1987		CN
North Celsius Bjerg, Western Circus Valley, western side	8 *Ichthyostega*	46, 78, 80, 6021-6025		1932, 1948		CN
North Celsius Bjerg, Western Circus Valley, western side, loose in scree at north end of valley	Tetrapod – *Ichthyostega*?	1653	530 m	1987		CN
North Celsius Bjerg, Western Circus Valley, western side, in lower part, talus	2 *Ichthyostega*	6246-6247		1955b		CN
North Celsius Bjerg, Western Circus Valley, western side, inner part, talus,	4 *Ichthyostega*	6095-6097, 6244		1948, 1955b		CN
North Celsius Bjerg, Western Circus Valley, western side, loose in scree about 100 m from north end of valley	Tetrapod?	1663	ca 590 m	1987		CN
North Celsius Bjerg, Western Circus Valley, western side, loose in scree about 100 m south of valley entrance	tetrapod – *Ichthyostega*?	1662	ca 590 m	1987		CN
North Celsius Bjerg, Western Coulisse, talus	Tetrapod	813		1948		CN
North Celsius Bjerg, western part, small Coulisse west of West Coulisse, *in situ*(?) at brook	*Ichthyostega*	6102		1948		CN
North side of Ymer Ø, hill about 6 km northwest Kap Graah, 100 m above sea level	*Ichthyostega*	6231		1954		CN
Paralleldal, Sederholm Bjerg, Broad Ridge	2 *Ichthyostega*	6127, 6206		1936, 1949, 1951	3-6	R1
Paralleldal, Sederholm Bjerg, Broad Ridge, west of ‘Profilravinen’, loose below 933 m	Tetrapod	718a		1934	3-6	R1
Paralleldal, Sederholm Bjerg, ‘Crossopterygieravinen’, loose	6 *Ichthyostega*	564, 6122-6126		1949	1	R1
Paralleldal, Sederholm Bjerg, first ridge east of Narrow Ridge, loose, R1	*Ichthyostega*	6219		1951	9	R1

Table 3. Continued.

Locality	Taxa content	Specimens	Altitude	Collecting year	Section	Level
Paralleldal, Sederholm Bjerg, Narrow Ridge	*Ichthyostega*	6128		1949	7, 8	R3
Paralleldal, Sederholm Bjerg, Narrow Ridge, R1	4 *Ichthyostega*	6188, 6212-6213, 6218		1951	7, 8	R1
Paralleldal, Sederholm Bjerg, Narrow Ridge, below fossil horizon at 1208 m, loose	*Ichthyostega*	6058	1208 m	1934	7, 8	R3
Paralleldal, Sederholm Bjerg, Narrow Ridge, west of 'Profilravinen', Narrow Ridge, local talus 890 m	5 *Ichthyostega*	713, 717, 6038, 6067, 6252	890 m	1934	7, 8	R1
Paralleldal, Sederholm Bjerg, 'Profil 4', fossil horizon 1174 m	11 *Ichthyostega*	6051-6057, 6060-6063	1174 m	1934	11	R3
Paralleldal, Sederholm Bjerg, 'Profil 4', fossil horizon 1312 m	*Ichthyostega*	6049	1312 m	1934	11	R3
Paralleldal, Sederholm Bjerg, 'Profil 4', fossil horizon 842 m	*Ichthyostega*	6050	842 m	1934	11	R1(P?)
Paralleldal, Sederholm Bjerg, 'Profil S10', horizon R1, loose	*Ichthyostega*	6080		1936	19	R1
Paralleldal, Sederholm Bjerg, 'Profil S29', horizon R3b, talus	*Ichthyostega*?	1155		1936	1	R3
Paralleldal, Sederholm Bjerg, 'Profil S8', horizon R3g, 1217 m, lokal talus.	2 *Ichthyostega*	1064, 6073	1217 m	1936	18	R3
Paralleldal, Sederholm Bjerg, 'Profil S9', rygg: southwest side, horizon R3b5, talus 1124 m	3 *Ichthyostega*	6070-6072	1124 m	1936	17	R3
Paralleldal, Sederholm Bjerg, 'Profil' S25, horizon R3b6, local talus	2 *Ichthyostega*	6077, 6084		1936	5	R3
Paralleldal, Sederholm Bjerg, ridge west om 'Profilravinen'	*Ichthyostega*	6185		1951	11	R1
Paralleldal, Sederholm Bjerg, ridge west om 'Profilravinen'	48 *Ichthyostega*	1)	1174 m	1949, 1951, 1955b	11	R3
Paralleldal, Sederholm Bjerg, ridge west of Broad Ridge, local talus about 965 m	12 *Ichthyostega*	6039-6048, 6065-6066	965 m	1934	2	R1
Paralleldal, Sederholm Bjerg, second ridge east of Narrow Ridge, loose	*Ichthyostega*	6116		1949	10	R1
Paralleldal, Smith Woodward Bjerg, 2 portion from east, west side, north part, loose	4 *Ichthyostega*	6117-6119, 6187		1949, 1951	Specimens not relatable to any measured sections	R3
Paralleldal, Smith Woodward Bjerg, 2 portion from east, west side, north part, Loose, R1	4 *Ichthyostega*	6207-6210		1951		R1
Paralleldal, Smith Woodward Bjerg, 3 portion from east, north east part Loose R2	4 *Ichthyostega*	6145-6148		1949		R2
Paralleldal, Smith Woodward Bjerg, 3 portion from east, northeast part, loose (980 m) R1	15 *Ichthyostega*	6189-6196, 6198, 6200-6205	980 m	1951		R1
Paralleldal, Smith Woodward Bjerg, east part, norteast side of 'västra kilformiga partiet' R3	*Ichthyostega*	6211		1951		R3

Table 3. Continued.

Locality	Taxa content	Specimens	Altitude	Collecting year	Section	Level
Paralleldal, Smith Woodward Bjerg, Kerstindal, north of first ravine, ca 967 m (r3)	3 *Ichthyostega*	6130, 6184, 6215	967 m	1949, 1951	Specimens not relatable to any measured sections	R3
Paralleldal, Smith Woodward Bjerg, Kerstindal, Remigolepis Ridge, second ridge, loose in talus about 801 m	*Ichthyostega*	6064	801 m	1934		R3
Paralleldal, Smith Woodward Bjerg, Kerstindal, Remigolepis Ridge, fourth ridge, Loose	*Ichthyostega*	6079		1936		R?
Paralleldal, Smith Woodward Bjerg, Kerstindal, Remigolepis Ridge, first ridge, loose on terrace	*Ichthyostega*	6076		1936		R1
Paralleldal, Smith Woodward Bjerg, Kerstindal, second ridge, loose on terrace	2 *Ichthyostega*	6078, 6214		1936		R3
Paralleldal, Smith Woodward Bjerg, Lungfiskdal, 'Kröken', talus	*Ichthyostega*	6082		1936		R?
Paralleldal, Smith Woodward Bjerg, Lungfiskdal, north side	Tetrapod	1122		1936		R?
Paralleldal, Smith Woodward Bjerg, Lungfiskdal, first ridge, horizon R3, 1030 m local talus	*Ichthyostega*	6068	1030 m	1936		R3
Paralleldal, Smith Woodward Bjerg, Lungfiskdal, fourth ridge talus	*Ichthyostega*	6081		1936		R?
Paralleldal, Smith Woodward Bjerg, Lungfiskdal, sixth ridge, talus,	5 *Ichthyostega*	862, 6216, 6074-6075, 6258		1936, 1951		R?
Paralleldal, Smith Woodward Bjerg, Lungfiskdal, sixth ridge, talus, (R3, 1015-1020 m)	*Ichthyostega*	6069	1015-1020 m	1936		R3
Paralleldal, Smith Woodward Bjerg, 'Profil 23', loose	*Ichthyostega*	6083		1936		R?
Paralleldal, unknown	*Ichthyostega*	6257		1955b		R?
Smith Woodward Bjerg, south side, east part, talus below high slope	9 *Ichthyostega*	139, 6107- 6108, 6110, 6169, 6232, 6239-6240, 6256		1948, 1955a, 1998		R3
Smith Woodward Bjerg, south side, middle part, talus below high slope	*Ichthyostega*	6111		1948		R3
Smith Woodward Bjerg, south side, western part, east part below high slope, talus	3 *Ichthyostega*	881, 6112, 6243		1948, 1955a		R3
Smith Woodward Bjerg, south side, western part, east part below high slope, talus	*Ichthyostega*	6115	ca 370 m	1948		R3
Smith Woodward Bjerg, south side, western part, east part below high slope, talus	*Ichthyostega*	839	ca 832 m	1948		R3
South Celsius Bjerg, central part?, below 'Östra läktaren', loose	Tetrapoda sp. (new genus & species), 2 *Ichthyostega*	6026-6027, 6220		1932		CS

Table 3. Continued.

Locality	Taxa content	Specimens	Altitude	Collecting year	Section	Level
South Celsius Bjerg, central part, east end, scree	Tetrapod	185	500 m	1998	Specimens not relatable to any measured sections	CS
South Celsius Bjerg, central part, east part Loose below 800 m	*Ichthyostega*	6087	<800 m	1947		CS
South Celsius Bjerg, central part, east slope	*Ichthyostega*	6223		1954		CS
South Celsius Bjerg, central part, middle scree	2 tetrapod	172-173	ca. 600 m	1998		CS
South Celsius Bjerg, central part, scree	2 Ichthyostega, tetrapod	196, 200, 301	500 m	1998		CS
South Celsius Bjerg, central part, scree	2 Tetrapod	302-303	360 m	1998		CS
South Celsius Bjerg, central part, west end, scree	16 *Ichthyostega*	174-181, 186-187, 190-195	460 m	1998		CS
South Celsius Bjerg, central part, west end, scree	Tetrapod	183	600 m	1998		CS
South Celsius Bjerg, central part, western slope	2 *Acanthostega* + tetrapod	877, 6085-6086		1947, 1954		CS
South Celsius Bjerg, central part, western slope, 725 m	Tetrapod	785	725 m	1947		CS
South Celsius Bjerg, eastern part, eastern corner, 885 m	Tetrapod	784	885 m	1947		CS
South Celsius Bjerg, western part, eastern part, talus	Tetrapoda sp. (new genus & species)	6088		1947		CS
South Celsius Bjerg, western part, near outcrop bands	Tetrapod	198	<600 m	1998		CS
South Celsius Bjerg, western part, west end, talus 500-630 m	*Ichthyostega*	6229	500-630 m	1954		CS
Stensiö Bjerg, Acanthostega site outcrop, *in situ*	100 *Acanthostega*	2)	800 m	1987	C	R3
Stensiö Bjerg, at beach, talus	*Ichthyostega*	823		1948	?	R?
Stensiö Bjerg, eastern part, above bottenterrassen, talus	*Ichthyostega*	6089		1948	?	R3
Stensiö Bjerg, fossil bearing strata just north of and corresponding to Acanthostega site outcrop	3 *Acanthostega*	1253, 1256-1266	773 m	1987	?	R3
Stensiö Bjerg, loose in scree	2 *Acanthostega*	?, 271	ca. 200 m	1987	?	R3
Stensiö Bjerg, loose in scree near Acanthostega *in situ* horizon	6 *Acanthostega*	147-149, 152-154	800 m	1998	C	R3
Stensiö Bjerg, loose in scree above Acanthostega site outcrop	Tetrapod	158	800 m	1998	C	R3
Stensiö Bjerg, loose in scree below Acanthostega *in situ*, below 600 m	Tetrapod?	155	600 m	1998	C	R3
Stensiö Bjerg, loose in scree below camp site	28 *Ichthyostega* + *Acanthostega*	3)	0-80 m	1987, 1998	?	R1
Stensiö Bjerg, loose in scree just below Acanthostega in situ horizon	93 *Acanthostega*	4)	800 m	1987, 1998	C	R3
Stensiö Bjerg, loose in scree on south east ridge just at camp	*Ichthyostega*	278	90 m	1987	C	R3?
Stensiö Bjerg, lowest part of "bottenterassen"	3 *Ichthyostega*	278, 414, 6034		1947	?	R1
Stensiö Bjerg, middle part, 'Stora raset', talus	10 *Ichthyostega*	177, 185, 1204, 6035-6036, 6092-6093, 6167, 6254, 6253	100-300 m	1932, 1933, 1948	B	R3

Table 3. Continued.

Locality	Taxa content	Specimens	Altitude	Collecting year	Section	Level
Stensiö Bjerg, western part, above bottenterassen, talus	*Ichthyostega*	6241		1955a	?	R3
Stensio Bjerg, western part, 'Ravin vaster om vastra grytan', 74 m and talus below	3 *Ichthyostega*	835, 6113-6114	74 m	1948	?	R1
Unknown	10 Ichthyostega	?, 53, 109, 6015, 6030-6131, 6217, 6259- 6261			?	R?
Wiman Bjerg, Aina Dal end	Tetrapod?	110	<100 m	1998	D	R1
Wiman Bjerg, ovan bottenterrassen, talus	*Acanthostega*	6090		1948	D	R1
Wiman Bjerg, south east ridge loose in scree	2 *Acanthostega* juveniles, 3 *Acanthostega*	138, 1399-1400, 1499, 1607	ca 520 m	1987, 1998	E	R3
Wiman Bjerg, southwest corner, local talus below 350 m	*Acanthostega* (holotype) + Ichthyostega	6033, 6255	<350 m	1932	D	R3

1) 6132, 6134-6140, 6143-6144, , 6149-6153, 6155-6166, 6172-6182, 6186, 6221, 6233-6238
2) 150-151, 156-157, 159-160, 215-231, 233-270, 272-274, 276-277, 279-295, 1209-1210, 1218, 1220,1222, 1224, 1226-1228, 1231-1245, 1248-1255, 1257-1258, 1261-1265, 1267-1269, 1272- 1274, 1284-1288, 1290-1294, 1299-1302, 1304-1310, 1312-1318, 1320-1324, 1350-1352, 1354-1359, 1361-1362, 1364-1370, 1373-1380, 1601-1604
3) 102-104, 107, 125, 131-132, 141, 144-145, 1276, 1327, 1330, 1333, 1339, 1343-1344, 1346, 1381, 1384, 1386, 1388-1389, 1392-1396, 1398
4) 156-157, 159-160, 215-231, 233-274, 276-277, 279-295, 1209-1210, 1218, 1220, 1222, 1224, 1313, 1320, 1322, 1323, 1373, 1366

Discussion

The detailed record of tetrapod localities, and their distribution within the stratigraphical framework presented here, demonstrates unique information previously not thought to be available. A subject of particular importance is that of the stratigraphical source of individual specimens originate in terms of stratigraphical level. Although Jarvik (Johansson, 1935; Jarvik, 1996) clearly stated that a large number of *Ichthyostega* specimens were collected from an *in situ* locality on Sederholm Bjerg at 1174 m, this information has never really been recognised by the geological-palaeontological community. This confusion is probably related to the fact that a majority of *Ichthyostega* specimens were actually found loose in talus and were therefore previously considered to be of uncertain provenance. This misconception can now be eliminated, and the detailed stratigraphical framework and distribution of tetrapod specimens now available can be used to establish whether there are any morphological differences between specimens of different ages. Blom (2005) has suggested that three of the species erected by Säve-Söderbergh (1932*b*) are distributed differently within the succession, and that the other taxa are junior synonyms of these three. Furthermore, the detailed stratigraphical framework presented herein can now be used for similar studies of the other known vertebrates within the same strata. Potentially suitable taxa for that kind of work are *Remigolepis* and *Holoptychius*, which are both well-distributed within that part of the succession and are well represented in collections (Blom *et al*., in press).

Although we have greatly improved our understanding of the distribution of tetrapods in East Greenland, there are a few issues that need to be addressed before a fully reliable picture can be obtained. One immediate problem is the difficulty in correlating strata between Celsius Bjerg and Gauss Halvø. This problem, which has been emphasised herein, relates to the lack of detailed stratigraphical information available for the Celsius Bjerg successions. Most efforts have been carried out on a larger scale (Nicholson and Friend, 1976; Olsen and Larsen, 1993) and have not provided any clear solution to the position of in the boundaries of the different tetrapod-yielding formations the succession. Blom (2005) has tried to clarify some of these questions by comparing individual specimens of *Ichthyostega* from North Celsius Bjerg with those of Gauss Halvø. Blom (2005) demonstrates that two different assemblages on Gauss Halvø, from the Aina Dal and Britta Dal formations respectively, are morphologically different from each other. These assemblages are then compared with the type material of Celsius Bjerg in terms of these morphological characteristics, as well as sedimentological data observed from the matrix surrounding the specimens. The results show that the *Ichthyostega* specimens from north Celsius Bjerg in general, and East Plateau in particular, seem to represent mixed assemblages (Blom, 2005). This can easily be understood and explained by reference to the local topography and how rocks are exposed in the area. Comparison of Nicholson and Friend's (1976) geological sketch map with the outcrop photograph of the East Plateau area (Figs 9, 23), leads to the reasonable inference that the base of the Aina Dal Formation is at the approximate level of the East Plateau.

The cliff above should then, according to Nicholson and Friend (1976) represent only the Britta Dal Formation, but no strata of the Wimans Bjerg Formation. From their interpretation of the stratigraphy, the talus on and around East Plateau could potentially contain rocks and specimens of both formations. If Olsen and Larsen (1993) are correct in their interpretation, about 100 m or less of this at least 300 m high steep cliff (Fig. 23) should consist of the Wimans Bjerg Formation. Specimens found on and around East Plateau could thus still originate from either the Aina Dal or Britta Dal formations. The question of whether the Wimans Bjerg Formation is present on Celsius Bjerg or not, is relevant for discussion of variation in formation boundaries in different parts of the basin. The possibility that the formations are diachronous may ultimately also have an effect on the distribution of taxa. The type of mixed assemblage seen on North Celsius Bjerg may potentially also be seen among other vertebrate groups that show taxonomical variation within the succession often referred to as the 'Remigolepis Series'. The best candidate for such a pattern is *Remigolepis* itself which was originally described from North Celsius Bjerg, and like *Ichthyostega* was said to include several different species (Stensiö, 1931). Some of these *Remigolepis* taxa have been suggested to show successional distribution, which can be compared with that of *Ichthyostega* (Johansson, 1935; Säve-Söderbergh, unpublished manuscript; Blom *et al*., in press). Some questions remain concerning the validity of the different *Remigolepis* species (M. Holten Petersen personal communication, 2003). However, it is important to know whether it shows a similar pattern of species distribution to *Ichthyostega*. If it shows clear species separation on Gauss Halvø but a mixed assemblage on Celsius Bjerg, it could mean either that the formations of the 'Remigolepis Series' are indistinct on Celsius Bjerg, or that we see a mixed population of *Remigolepis* morphologies there.

East Greenland, with its two well-known tetrapod genera, *Ichthyostega* and *Acanthostega*, and a third genus being described by the authors shows together with the Catskill Formation fauna (Shubin *et. al.,* 2004), a much higher diversity than any other known Devonian tetrapod-yielding area (Clack, 2004). This diversity, however, is neither geographically nor stratigraphically homogeneous within East Greenland.

First, the tetrapod assemblages from the south side of Celsius Bjerg show potentially a higher diversity than those of the closely located north side, as well as the more remote localities on Gauss Halvø. South Celsius Bjerg yields three genera: *Ichthyostega*, *Acanthostega* and the third genus. North Celsius Bjerg on the other hand has yielded only *Ichthyostega* specimens. Paralleldal has similarly yielded only *Ichthyostega*, whereas the south coastline of Gauss Halvø has yielded both *Ichthyostega* and *Acanthostega*. This variation in diversity is probably not a simple sampling effect since south Celsius Bjerg with its 'higher' diversity has provided fewer specimens than any of the other areas. Alternatively, the distribution may relate to how different taxa lived within the basin, but discussions on environmental constraints will remain speculative until a better sample size and more significant patterns of taxa distribution are available.

Ichthyostega is the taxon showing the most consistent distribution with occurrences in all areas and in both the Aina Dal and Britta Dal formations. However, *Ichthyostega* specimens from the Britta Dal Formation are restricted to the lower parts. Since *Acanthostega* on Gauss Halvø is known from the Aina Dal Formation and higher up in the Britta Dal Formation it shows, at least locally, a longer range than *Ichthyostega*. Bearing that in mind, it is curious that there is no clear evidence of *Acanthostega* from the lower parts of the Britta Dal Formation. The Aina Dal Formation has yielded only two specimens, so it is as yet impossible to test whether *Acanthostega* is morphologically more conservative through time than *Ichthyostega*.

The absence of *Acanthostega* from the Britta Dal Formation in Paralleldal may not be surprising: the *in situ Acanthostega* horizon on Stensiö Bjerg lies above the preserved part of the succession on, for example, Sederholm Bjerg (Figs 4, 5). However, it serves to emphasise the curious fact that *Acanthostega* is absent in the lower parts of Britta Dal Formation. The absence of *Acanthostega* from the Aina Dal Formation in the same area may result from a simple sampling effect of what was then a rare taxon.

The absence of *Acanthostega* in the lower parts of the Britta Dal Formation in all the areas, at a time when they are known to have existed suggests taphonomic and environmental restrictions on tetrapod taxa in East Greenland and may explain their inconsistent preservation. The Aina Dal and Britta Dal formations have both been interpreted as deposited in active meandering river systems. Although interpreted as being laid down in similar environmental conditions, their sedimentology shows significant differences (Olsen and Larsen, 1993; Olsen, 1993). These differences are further emphasised by the development of a recent hypothesis challenging previous interpretations of active river depositions for the Britta Dal formation. A new interpretation of sheet flood origin for the *Acanthostega*-bearing sandstones has been suggested (T. R. Astin and J. E. A. Marshall personal communication, 2004). Analysis of differences in depositional history between the two tetrapod-yielding formations, their taxonomic composition, and variations in distribution of taxa within may give some constraints, that in turn may inform us about the particular environment in which different taxa are found. Another set of constraints might be available from direct studies of the taphonomic and sedimentological context of the individual localities. This type of data could, for example, be collected from additional fieldwork on the *Ichthyostega in situ* horizon at 1174 m. Since the precise locality of these *Ichthyostega* specimens is known, it should be possible to explore the sedimentological context of that particular horizon and its specimens. The depositional history of the sediments and a detailed taphonomic analysis should allow us to accumulate new data on the environment in which *Ichthyostega* is preserved. Although a similar approach has been made to the *Acanthostega in situ* site on Stensiö Bjerg (Bendix-Almgreen *et al.*, 1990), its sedimentological context may be challenged (as noted above, T. R. Astin and J. E. A. Marshall personal communication, 2004). It would, therefore, be particular useful revisit the two *in situ* localities. A detailed analysis of their taphonomic and sedimentological context in an attempt to clarify the relation the specimens have to the depositional environment. One objective would be to confirm whether tetrapod specimens were deposited in their natural environment or had been transported from elsewhere. Knowledge of this site could then more carefully be used in the more general context of palaeoecological, sedimentological, environmental and faunal studies.

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The invasion of the land by vertebrates is a key episode in the history of life, and is marked by an evolutionary transformation often referred to as the fish-tetrapod transition. The Late Devonian tetrapods Ichthyostega and Acanthostega from East Greenland are among the earliest tetropods known. They are also the best preserved tetrapods of the Devonian period and are therefore of crucial importance for our understanding of how fishlike animals evolved, for example, limbs with fingers and toes, characters usually closely associated with the adaptation of walking on land.

This monograph provides detailed information on the Late Devonian (Famennian) localities of East Greenland from which these important tetrapods originate. It also gives new information on the distribution and stratigraphical context of these fossils, facilitating discussions of regional stratigraphy, environmental constraints and global comparison with other tetrapod-yielding localities.

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