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Vertebrate remains from Upper Silurian – Lower Devonian beds of Hall Land, North Greenland

Henning Blom

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Cover

Transitional scale of *Thulolepis striaspina* gen. et sp. nov., a new small thelodont species from the lowermost Devonian of North Greenland. SEM photograph of the holotype, MGUH VP 3510, found in an acetic acid residue of GGU sample 319264. The sample is from a limestone bed in the Chester Bjerg Formation at the top of Monument, an inselberg-like hill in central Hall Land (see Fig. 1). Length of the scale is 0.26 mm.

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Abstract

Blom, H. 1999: Vertebrate remains from Upper Silurian – Lower Devonian beds of Hall Land, North Greenland.

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Vertebrate microscopic remains of twenty-six taxa of thelodonts, heterostracans, osteostracans, anaspids, acanthodians and chondrichthyans are described from limestone beds in two localities of Late Silurian – Early Devonian age of the Chester Bjerg Formation, Hall Land, North Greenland. The limestone beds form a minor part of a monotonous calcareous sandstone–siltstone–mudstone sequence at the top of the Franklinian Basin succession.

Stratigraphical recognition using several thelodont and acanthodian taxa, supported by regional geological and structural trends, suggests a Silurian–Devonian boundary interval between beds of the Halls Grav and Monument localities. This possible resolution of the previous problematic correlation between the two distant sections of monotonous nature demonstrates the potential biostratigraphic utility of thelodonts in Silurian–Devonian marine successions.

The Chester Bjerg Formation thelodont assemblage is unique with several new endemic taxa, but *Loganellia* cf. *L. tuvaensis* is very similar to the type material of the Tuva region south of Siberia, Russia and indicates a Late Silurian age for the beds of the Halls Grav locality. *Canonina* cf. *C. grossi* suggests an Early Devonian age for the Monument locality, since *Canonina* is so far only found in Lower Devonian marine strata of Arctic Canada and Russia. Fragments of cosmopolitan acanthodian genera such as *Poracanthodes*, *Gomphonchus* and *Nostolepis* are found together with heterostracans, osteostracans, anaspids and chondrichthyans at both localities but do not give a more exact age determination than Late Silurian – Early Devonian. New thelodont taxa are *Loganellia almgreeni* sp. nov., *Paralogania foliala* sp. nov., *Praetriorlogania grabion* gen. et sp. nov. and *Thulolepis striaspina* gen. et sp. nov. *Nostolepis halli* sp. nov. is a new acanthodian species.

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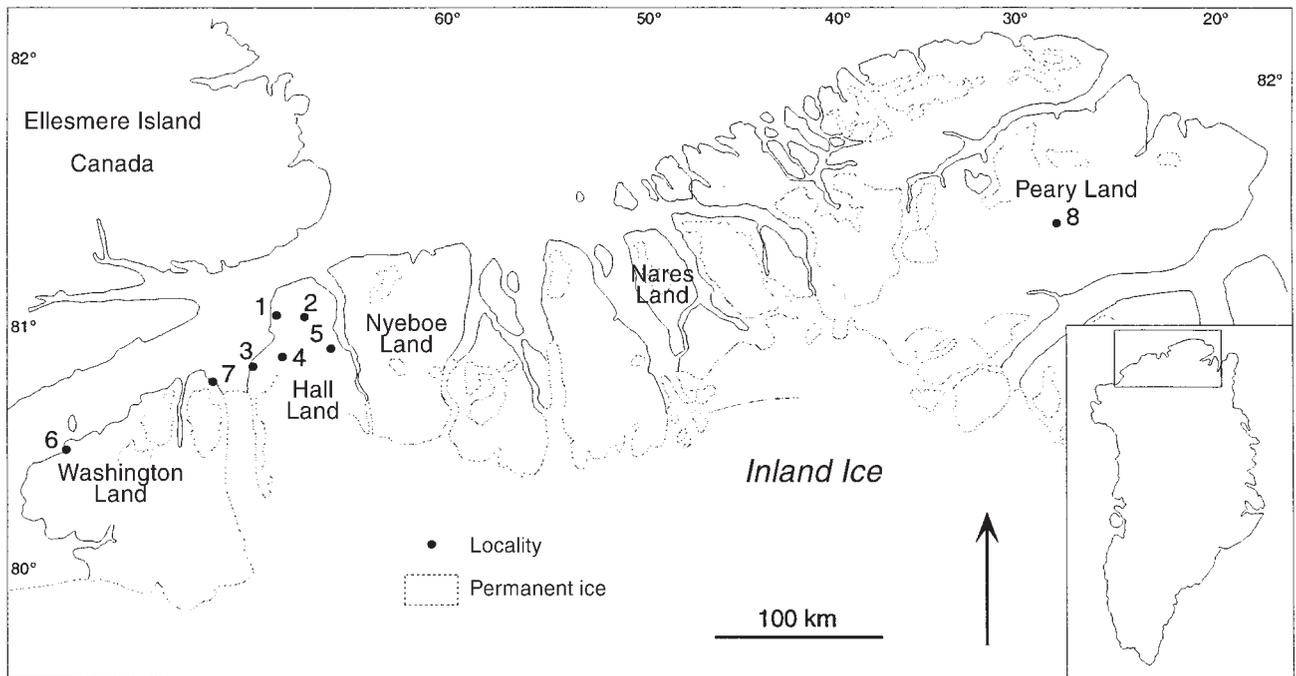


Fig. 1. **Above:** Silurian–Devonian vertebrate-bearing localities in North Greenland. **1:** Halls Grav (Observatory Bluff). **2:** Monument. **3:** Kap Tyson East outcrops. **4:** Sunmark Mountain. **5:** Kayser Bjerg. **6:** Kap Independence. **7:** Kap Lucie Marie. **8:** central Peary Land. **Below:** The inselberg-like hill Monument, central Hall Land, seen from the east (locality **2** above). The one sample from Monument used in this study (GGU 319264) was collected from the top of the hill from a limestone bed of Early Devonian age. The height of the hill above the lowland plain is about 150 m (see Fig. 2). Photo: P.R. Dawes, July 1965.

Introduction

Fossils of Palaeozoic vertebrates are often poorly preserved, showing only fragmentary or diffuse traces of the living animal. Smaller, often microscopic vertebrate remains of disarticulated skeletons, such as teeth, scales and bone may well complement the less abundant articulated material, and such microscopic remains, especially thelodont scales, have proved useful as biostratigraphical and palaeogeographical tools (e.g. Gross 1947, 1967a; Turner 1973; Karatajute-Talimaa 1978; Märss 1982, 1986a; Blicek *et al.* 1988, in press; Blicek & Janvier 1991; Märss *et al.* 1995). For a comprehensive review the reader is referred to Long (1993) and references therein.

The present paper builds on this biostratigraphic utility in describing several collections of vertebrate remains from the Chester Bjerg Formation of western North Greenland. The Chester Bjerg Formation is the youngest unit within the Greenland segment of the Franklinian Basin of the Canadian Arctic Archipelago. In a regional context, the described vertebrate fossils suggest a maximum age for the closure of the Franklinian Basin and the onset of the mid-Palaeozoic Ellesmerian Orogeny in North Greenland.

The vertebrate record from the North Greenland segment of the Franklinian Basin is very poor when compared to the famous Devonian vertebrate faunas of eastern Greenland (Bendix-Almgreen 1976 and ref-

erences therein). Norford (1972) noted two anaspid fragments which he collected in 1966 from Kap Tyson (Fig. 1), south-western Hall Land during Operation Grant Land (1965–1966), a joint field project between the geological surveys of Canada and Greenland (Dawes 1984, 1987). Bendix-Almgreen & Peel (1974) reported samples containing microscopic remains of vertebrates that were collected in 1965 during the same field programme by J.H. Allaart and P.R. Dawes. Bendix-Almgreen & Peel (1974) reported thelodont, heterostracan and acanthodian remains from a locality in western Hall Land, near Halls Grav (Figs 1, 2). Some of these were later illustrated by Bendix-Almgreen (1976). Thelodonts from North Greenland were described by Turner & Peel (1986). Bendix-Almgreen (1986) also described fragments of anaspids and heterostracans from strata close to the Wenlock–Ludlow boundary in Washington Land (Fig. 1).

The present description of the vertebrate fauna of the Chester Bjerg Formation includes this material earlier reported by Bendix-Almgreen & Peel (1974), Bendix-Almgreen (1976) and Turner & Peel (1986), but also additional material from the locality near Halls Grav (Observatory Bluff) and previously undescribed material from Monument (Figs 1, 2) in central Hall Land (see also Blom in press).

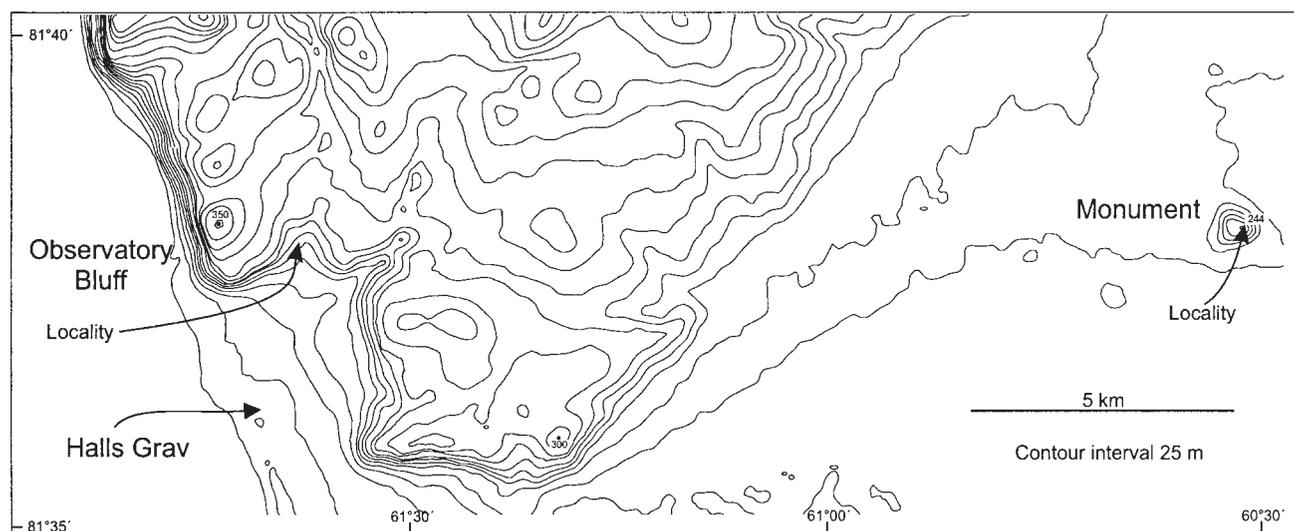


Fig. 2. Map showing two vertebrate-bearing localities from the Chester Bjerg Formation near Halls Grav in western Hall Land and at the top of Monument in central Hall Land (see Fig. 1). Modified from Dawes (1987).

Geological setting

North Greenland is characterized by sedimentary rock successions of Proterozoic to Cenozoic age (Fig. 3) deposited in several discrete sedimentary basins that crop out in an east–west belt, north of the central ice cap (Inland Ice) that covers most of Greenland (Peel & S nderholm 1991). During the early Palaeozoic a carbonate shelf – deep water basin system, the Franklinian Basin, extended across northern Ellesmere Island and North Greenland (Surlyk & Hurst 1984; Trettin 1991; Higgins *et al.* 1991a, b). The preserved succession is mainly of Cambrian–Silurian age although upper Proterozoic and lower Devonian strata may be present. The thickness of the sedimentary column reaches about 8 km and overlies a craton composed of Archaean and Proterozoic crystalline basement which, together with Middle and Upper Proterozoic sedimentary and volcanic rocks, is exposed to the south of the Franklinian Basin outcrop. The Franklinian Basin is unconformably overlain by Carboniferous and younger strata of the Wandel Sea Basin in northern and eastern areas of North Greenland (H kansson *et al.* 1991; Stemmerik & H kansson 1991).

For much of its early Palaeozoic history the Franklinian Basin succession of North Greenland (Fig. 3) is characterized by a carbonate-dominated shelf succession in the south, and a northern siliciclastic-dominated deep water basin (Higgins *et al.* 1991a, b). This scenario persisted until the late Silurian when the clastic succession of the southward expanding trough completely drowned the shelf (Hurst & Surlyk 1982; Higgins *et al.* 1991a, b).

The Chester Bjerg Formation described by Hurst & Surlyk (1982) as the uppermost lithostratigraphic unit of the Peary Land Group (Larsen & Escher 1985, 1987),

represents the last phase of basin deposition. It overlies and interfingers with the Nyeboe Land Formation and has an estimated thickness of 500–800 m (Dawes 1976; Hurst & Surlyk 1982). It outcrops from Hall Land, in the west, to Nares Land, in the east (Fig. 1; Larsen & Escher 1985, 1987).

In its type area in the northern cliffs of Chester Bjerg, northern Hall Land, the Chester Bjerg Formation is characterized by laminated light green mudstone with sandy streaks and increasing abundance of laminated siltstone up-section. Primary sedimentary structures in northern outcrops are difficult to discern due to the strong Ellesmerian deformation which closed the Franklinian Basin in the mid-Palaeozoic. Starved and climbing ripples, however, are found in the mudstone and are common together with slumped sand. In some areas trace fossils are abundant. The formation includes the youngest preserved sediments of the Franklinian Basin, deposited from very dilute turbidity currents in a distal basinal plain (Higgins *et al.* 1991a, b).

Regional geological considerations suggest that the Chester Bjerg Formation can be no older than Ludlow (late Silurian) at its base (Hurst & Surlyk 1982). The age of the upper part, however, is the subject of discussion. Graptolites of *Monograptus transgrediens* type indicate a late Pridoli (latest Silurian) age (Berry *et al.* 1974; Hurst & Surlyk 1982) but a substantial thickness of strata occurs above the graptoliferous levels. The microremains of vertebrates described here occur within these higher strata and with their description this paper aims to evaluate the age of the fauna, following earlier studies by Bendix-Almgreen & Peel (1974) and Turner & Peel (1986).

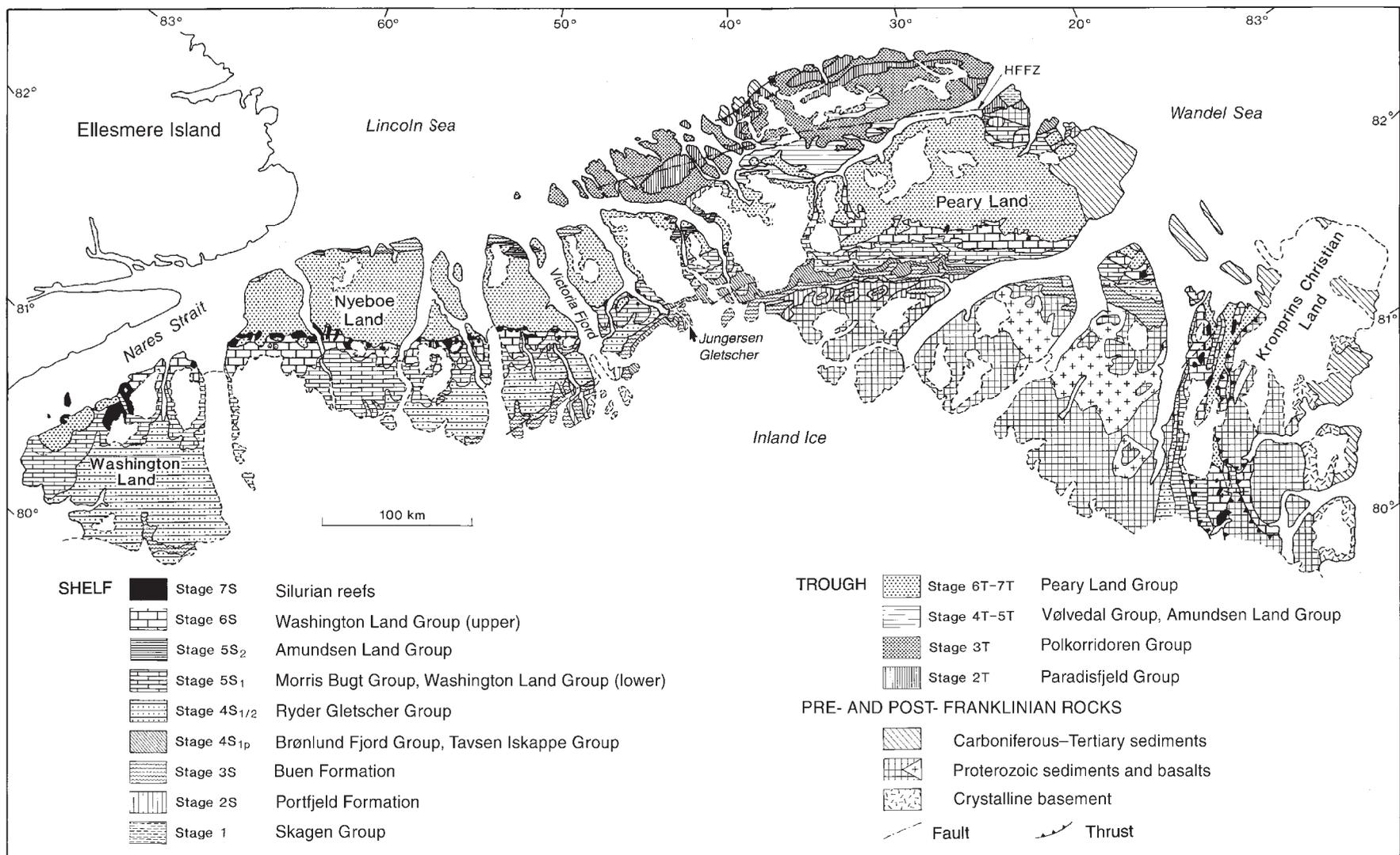


Fig. 3. Geological map of North Greenland. The map shows the major stratigraphic units of the Franklinian Basin corresponding to the basin evolutionary stages recognized by Higgins *et al.* (1991a). **HFFZ**: Harder Fjord fault zone. Slightly modified from Ineson & Peel (1997, fig. 2).

Localities

Halls Grav (Figs 1, 2)

In detail, the Halls Grav locality refers to hill slopes behind Observatory Bluff (Fig. 2), north-east of the notable historical site of C.F. Hall's grave (Dawes & Peel 1984). Charles F. Hall led the first scientific expedition to North Greenland, the U.S. North Polar Expedition 1871–73, and died on board the ship USS *Polaris* at the wintering site adjacent to his grave, western Hall Land (Dawes 1987).

Dawes & Peel (1984, pp. 31–32) have reported at least 200 m of “brown to buff weathering, thin-bedded monotonous sequence of grey, variously laminated mudstone with some calcareous siltstones and platy limestone and occasional darker weathering beds of fine-grained graywacke” in the cliffs at Observatory Bluff. Thin beds of limestone and limestone breccia occur in the upper parts of the cliffs.

The first vertebrate-producing samples (GGU 82734, 82736–38) were collected in 1965 by P.R. Dawes and J.H. Allaart during Operation Grant Land (1965–1966)

from one thicker limestone bed, at an altitude of about 215 m on the eastern side of Observatory Bluff, which lies 2 km north-east of Halls Grav. Other samples from the same section were collected in 1985 by J.S. Peel and M.R. Blaker during the North Greenland Project of the Geological Survey of Greenland (1978–85). Several samples from the GGU sample series 298937–68 have been processed and used in the present study. They were collected from talus clearly adjacent to fast outcrop; although the previous *in situ* locality was not found, they are from the same general area (J.S. Peel, personal communication 1999).

Monument (Figs 1, 2)

P.-H. Larsen collected GGU sample 319264 from a limestone bed in a monotonous sandstone–siltstone–mudstone sequence at the top of the prominent inselberg-like hill called Monument, central Hall Land, in 1985 during the North Greenland Project (1978–85).

Material and methods

Specimens with the prefix MGUH VP and all additional material are deposited in the Geological Museum, Copenhagen, Denmark. Samples and residues carrying the prefix GGU are the property of Grønlands Geologiske Undersøgelse (Geological Survey of Greenland, now amalgamated into the Geological Survey of Denmark and Greenland), Copenhagen, Denmark. Other material belongs to collections of the Geological Survey of Canada (abbreviated GSC) and the Institute of Geology of Lithuania (former Lithuanian Scientific Geological Research Institute with abbreviation LitNIGRI).

This study includes 11 residues from the Halls Grav locality and one from Monument (Figs 1, 2, 4), extracted through processing by dissolving in weak acetic acid. GGU samples 82734, 82736–8, 298953, 298960, 298963 were previously prepared at the former Geological Survey of Greenland. GGU samples 298937–38, 298950, 298954 from the Halls Grav locality and

parts of GGU 319264 from the Monument locality have been dissolved by the author, using the buffering method developed by Jeppsson *et al.* (1985). These four samples had a high carbonate content and were easily dissolved in the weak acid. The resulting residues were wet sieved into five fractions; larger than 1 mm, 1–0.5 mm, 0.5–0.25 mm, 0.25–0.125 mm. Smaller fractions were discarded. Each fraction was further extracted by heavy liquid density separation, following the method developed by Schøler (1989). All residues were very rich in vertebrate remains and other acid-resistant microfossils, differing only in their state of preservation. Samples collected in 1985 by J.S. Peel and M.R. Blaker from talus of the Halls Grav locality are often badly preserved, probably due to weathering of the rock. The poorest samples, yielding very few valuable specimens, were also less minutely picked. In addition to the vertebrates, conodonts, ostracods,

| Taxa | Halls Grav | | | | | | | | | | Monument | |
|--|------------|-------|-------|-------|--------|--------|--------|--------|--------|--------|----------|--------|
| | 82734 | 82736 | 82737 | 82738 | 298937 | 298938 | 298950 | 298953 | 298954 | 298960 | 298963 | 319264 |
| Thelodonti | | | | | | | | | | | | |
| Order Katoporida Karatajute-Talimaa 1978 | | | | | | | | | | | | |
| Family Loganiidae Karatajute-Talimaa 1978 | | | | | | | | | | | | |
| <i>Loganellia</i> cf. <i>L. tuvaensis</i> | x | x | x | x | x | x | x | x | x | x | x | ? |
| <i>Loganellia almgreeni</i> sp. nov. | | | | | | | | | | | | x |
| <i>Paralogania foliala</i> sp. nov. | | | | x | | | | | | | | |
| <i>Praetrilogania grabion</i> gen. et sp. nov. | x | x | | x | x | | | | | | | x |
| Order Thelodontida Kiær 1932 | | | | | | | | | | | | |
| Family Nikoliviidae Karatajute-Talimaa 1978 | | | | | | | | | | | | |
| <i>Nikolivia</i> sp. | | x | | x | x | | | | | | | ? |
| <i>Canonia</i> cf. <i>C. grossi</i> | | | | | | | | | | | | x |
| Family Incertae sedis | | | | | | | | | | | | |
| <i>Thulolepis striaspina</i> gen. et sp. nov. | | | | | | | | | | | | x |
| Thelodontida indet. | | | | x | | | | | | | | x |
| Heterostraci | | | | | | | | | | | | |
| Cyathaspidiformes indet. | | x | x | x | x | | | | | | | |
| Pteraspidiformes indet. | | | | | | | | | | | | x |
| Heterostraci indet., type A | | x | x | x | | | | | | | | |
| Heterostraci indet., type B | | | | | | | | | | | | x |
| Heterostraci indet., type C | | x | | x | | | | | | | | x |
| Heterostraci indet., type D | | x | | x | | | | | | | | |
| Heterostraci indet., type E | x | x | x | x | x | | | x | | | | x |
| Anaspida | | | | | | | | | | | | |
| Anaspida indet. | x | x | | x | x | | | | | | | x |
| Osteostraci | | | | | | | | | | | | |
| Osteostraci indet. | | x | | x | | | | | | | | x |
| Osteostraci? indet. | | | | x | | | | | | | | x |
| Chondrichthyes | | | | | | | | | | | | |
| Chondrichthyes indet. | | | | | | | | | | | | x |
| Acanthodii | | | | | | | | | | | | |
| Order ClimaTiida Berg 1949 | | | | | | | | | | | | |
| Family ClimaTiidae Berg 1940 | | | | | | | | | | | | |
| <i>Nostolepis halli</i> sp. nov. | x | x | x | x | x | | | | | | | |
| ClimaTiida indet. | x | x | x | x | | | | | | | | |
| Order Ischnacanthida Berg 1940 | | | | | | | | | | | | |
| Family Ischnacanthidae Woodward 1891 | | | | | | | | | | | | |
| <i>Gomphonchus</i> cf. <i>G. sandelensis</i> | x | x | x | x | x | | | | | | | x |
| <i>Poracanthodes</i> cf. <i>P. punctatus</i> | x | x | x | x | x | | | | | x | | x |
| <i>Poracanthodes</i> cf. <i>P. porosus</i> | x | x | x | x | x | | | x | x | x | x | x |
| Acanthodii indet. | | | | | | | | | | | | |
| Spine fragments | x | x | x | x | x | | | | x | | x | x |
| Dental elements | x | x | x | x | x | | | x | x | x | x | x |
| Incertainae sedis | | | | | | | | | | | | |
| | x | x | x | x | x | x | x | x | x | x | x | x |

Fig. 4. Occurrence of vertebrate taxa in different GGU samples from the Chester Bjerg Formation.

coprolites, internal moulds of gastropods, bryozoans?, conularids and rare brachiopods also occur.

Microscope studies with transmitted light were made on standard thin sections or objects immersed in aniseed oil to make the bone transparent. The small and fragile scales were imbedded in plastic resin for the preparation of thin sections. Photographic illustrations of non-histological specimens were prepared by scanning electron microscopy (SEM). Most fragments and all scales have been photographed with SEM detec-

tion, or the visible effect of light, perpendicular to the length axis, to best elucidate the crown sculpture. Most scales and fragments have been oriented with the anterior to the left. Sketches and drawings of scales and other fragments were made using a camera lucida attached to a standard stereo-microscope, which also was used during general studies and picking. All photographs and drawings were stored and treated digitally.

Correlation and biostratigraphy

The exact ages of the lower and upper boundaries of the Chester Bjerg Formation are not clearly defined and the age of the formation is subject to debate (Bendix-Almgreen & Peel 1974; Berry *et al.* 1974; Bendix-Almgreen 1976; Hurst & Surlyk 1982; Armstrong & Dorning 1984; Dawes & Peel 1984; Larsen & Escher 1985, 1987; Turner & Peel 1986). A record of the graptolite *Pristiograptus dubius* (?) *ludlowensis* from north-eastern Nyeboe Land indicates an early Ludlow age and is the oldest recorded fossil from the formation (Larsen & Escher 1985, 1987). The upwards extension of this uppermost unit of the Franklinian Basin succession in Greenland is controversial and it has been suggested that it reaches the top of the Silurian or even into the Early Devonian.

Graptolites from the lower parts of the cliffs east of Halls Grav were referred by Berry *et al.* (1974) to *Monograptus* sp. of *M. transgrediens* type, suggesting a late Pridoli (Silurian) age. A specimen referred to *Monograptus* cf. *M. aequabilis* suggested an earliest Devonian age but was redetermined by H. Jaeger as *Monograptus* cf. *M. transgrediens* of Pridoli age (Hurst & Surlyk 1982; Dawes & Peel 1984). The vertebrate yielding limestone beds of the Halls Grav area occur above the graptolite horizon.

Bendix-Almgreen & Peel (1974) and Bendix-Almgreen (1976) considered the vertebrate fauna to be of Late Silurian – Early Devonian age, showing no contradiction to the earlier age interpretation mainly based on the identification of the graptolites. The thelodont fauna was further compared by Turner & Peel (1986) with Late Silurian faunas of Arctic Canada and Tuva, south of Siberia in Russia. Palynomorphs from one of these vertebrate-yielding samples were considered to be of Wenlock or Early Ludlow age by Armstrong & Dorning (1984) but the possibility of reworking is neither supported by their palynomorphs nor by the studied vertebrate assemblage. None of the other fossil groups associated with the vertebrate remains have yet been used to clarify the age relationships, but study of conodonts may add information of importance. A new species of the trilobite *Hemiarges* found in an erratic block, believed to belong to the Chester Bjerg Formation, also suggests a Late Silurian age (Lane *et al.* 1980; Dawes & Peel 1984) and *Hemiarges* does occur in samples collected near Halls Grav by J.S. Peel and M.R. Blaker in 1985.

The present study of Chester Bjerg Formation vertebrates has improved our knowledge of the composition and taxonomy of the vertebrate fauna, especially with regard to the better preserved thelodonts and acanthodians. Correlation around the Silurian–Devonian boundary based on heterostracans is unreliable, since many of the important groups appeared earlier in Canada than in Europe (Dineley & Loeffler 1976). Moreover, the fragmental nature of the heterostracans from North Greenland also makes correlation based on this group uncertain.

Isolated scales of thelodonts are biostratigraphically important, mainly because they are found in most biogeographical provinces and are widespread in the Silurian and early Devonian. However, few of the taxa from the Chester Bjerg Formation are directly comparable with taxa known from other areas and none of the Greenland thelodont species are identical with species from other areas. *Loganellia* cf. *L. tuvaensis* is very similar to scales described by Karatajute-Talimaa (1978) from the Pridoli of Tuva, south of Siberia in Russia. The rest of the thelodont assemblage in Tuva, on the other hand, is completely different with several species of *Helenolepis* Karatajute-Talimaa 1978 as the only complementary taxa to *Loganellia tuvaensis* Karatajute-Talimaa 1978. The other similar taxon, *Loganellia incompta* Karatajute-Talimaa 1990, is found as the only taxon in the Pridoli of the West Siberian Plate (Karatajute-Talimaa 1990; Talimaa in press). *Canonina grossi* Vieth 1980 is only found in Lower Devonian strata from provinces all around the world, but the Chester Bjerg Formation occurrence is not considered identical.

This apparently conflicting occurrence of co-existing Silurian and Devonian forms can possibly be solved by looking separately at each locality and its fauna. Together with the abundant occurrence of *L. cf. L. tuvaensis* in the Halls Grav material, several specimens have been found of the genus *Nikolivia* Karatajute-Talimaa 1978. *Nikolivia* has been regarded as a typical Devonian taxon and a detailed subdivision of Lochkovian deposits in Eurasia has been made with *Nikoliviid* thelodonts (Talimaa in press). *Nikolivia elongata* Karatajute-Talimaa 1978, however, has also been found in late Pridoli strata of Severnaya Zemlya (Karatajute-Talimaa *et al.* 1986; Karatajute-Talimaa & Märss 1997; Talimaa in press). *Nikoliviids* are also found in Cana-

dian rocks of latest Silurian or early Devonian age (Dineley & Loeffler 1976; Vieth 1980), and it cannot be excluded that nikoliviids may reach as low as the Pridoli in Greenland as well.

The thelodont assemblage of Monument includes several new taxa and *Canonina* cf. *C. grossi*. *Canonina grossi* is so far only found in Lochkovian strata from eastern Arctic Canada, Severnaya Zemlya, Timan-Pechora Province, Podolia and Nevada (Vieth 1980; Turner & Murphy 1988; Talimaa in press). A few poorly preserved scales found in residues from Monument may have affinity with *L.* cf. *L. tuvaensis* and *Nikolivia*.

P.R. Dawes reports (personal communication 1999) that the monotonous nature of the Chester Bjerg Formation in Hall Land, without characteristic regional marker beds, prevents precise correlation of distant sections like Monument and Observatory Bluff (Fig. 2). Monument, however, is closer to the centre of the asymmetric synclinorium of Hall Land (Dawes 1987, fig. 48), and since there is no clear evidence of major tectonic disturbance of the regional deposition of rock units, a younger age for the Monument strata is suggested. This is supported by the thelodonts and it may be implied that the Silurian–Devonian boundary lies somewhere between these vertebrate-bearing horizons of Monument and Halls Grav, suggesting that *Canonina* may play an important role in stratigraphical interpretations. If this suggestion is correct, the new thelodont taxa *Thulolepis striaspina* gen. et. sp. nov. and *Loganellia almgreeni* sp. nov. that occur together with *Canonina* cf. *C. grossi* may be potential indicators of a Devonian age in future biostratigraphic schemes. *Praetrigonia grabion* gen. et sp. nov. is present in both assemblages and its distribution would therefore extend across the Silurian–Devonian boundary. Loganiiids such as *Paralogonia foliala* sp. nov. from the Halls Grav vertebrate fauna may be typically Pridoli in age.

Vertebrate biostratigraphy around the Silurian–Devonian boundary is poorly understood, since few known vertebrate-yielding sections cover that period. Märss (1997) compared the vertebrates from Silurian–Devonian boundary successions in some Eurasian regions. She found that the boundary is well marked by the appearance of *Turinia pagei* (Powrie 1870) and '*Traquairaspis*' ssp. but this has not been demonstrated in the boundary stratotype in the Barrandian Basin, Bohemia (Martinsson 1977). The stratotype contains only a few poorly preserved acanthodian scales, including genera such as *Gomphonchus* Gross 1971 and *Nostolepis* Pander 1856 (Märss 1997). The Chester Bjerg

Formation has an acanthodian fauna comparable to the known faunas of Europe but several of the late Silurian and early Devonian taxa need revision before they can offer a good possibility for correlation between Europe and arctic North America. *Gomphonchus sandelensis* (Pander 1856), for example, is a well distributed taxon which offers no more exact precision than a Late Silurian – Early Devonian correlation between Europe and Arctic Canada (Gross 1947, 1957, 1971; Vieth 1980; Märss 1986a, 1997). *Poracanthodes punctatus* Brotzen 1934 is also recognized from lower Pridoli – Lower Devonian strata of Europe and the Canadian Arctic (Gross 1947, 1957, 1971; Märss 1986a, 1997; Burrow *et al.* 1997; Vergoossen in press). *P.* cf. *P. punctatus* from both vertebrate-yielding localities of the Chester Bjerg Formation is similar to punctatiform scales from the lowermost Pridoli of the Baltic, referred to as *P. aff. P. punctatus* (Märss 1986a).

The revision of poracanthodid acanthodians is especially relevant for the porosiform scales which in this study include a wide variety of scale types referred to as *Poracanthodes* cf. *P. porosus*. *P. porosus* Brotzen 1934 appears earlier in the Silurian than *P. punctatus* and ranges into the Lower Devonian. Some *P.* cf. *P. porosus* from North Greenland are similar to very poorly preserved porosiform poracanthodid acanthodians from the Late Silurian of Cornwallis Island, Arctic Canada (Burrow *et al.* 1997). Within the *P.* cf. *P. porosus* type of scale a distinct morphological type exists which is similar to *P. menneri* Valiukevicius 1992. *P. menneri* has been described from an articulated specimen from the Lochkovian of Severnaya Zemlya (Valiukevicius 1992) while isolated scales of probable *P. menneri* affinity have also been recorded from the uppermost Silurian and lowermost Devonian of the Kaliningrad district of the eastern Baltic, as well as the Lower Devonian of the Central Urals (Märss 1997). Some porosiform scales are also similar to *P. subporosus* Valiukevicius 1998, which in eastern Baltic and Byelorussia has a stratigraphical distribution from Pridoli to Lochkovian (Valiukevicius 1992). The establishment of finer biostratigraphical zonation, based on the taxonomical revision of poracanthodiform acanthodians, may solve many of the age-dating problems that appear in Silurian–Devonian boundary strata.

The thelodont and acanthodian faunas from the Silurian–Devonian boundary of North Greenland should have their closest affinity with forms from the equivalent Franklinian Basin succession in Arctic Canada. Loganiid scales from the Pridoli Douro Formation of Devon Island described by Vieth (1980) are

morphologically quite variable, but include a few scales that resemble *Loganellia* cf. *L. tuvaensis* from the Halls Grav locality. The Lochkovian Drake Bay Formation of Prince of Wales Island has a few taxa which can be compared with the Chester Bjerg Formation fauna, including *Canonina grossi*, *Nikolivia* and *Gomphonchus sandelensis* (Vieth 1980). The differences, however, between the faunal composition of the Chester Bjerg Formation and the fauna of similar age in the Baillie–Hamilton and Cornwallis Island sections are striking (author's observations of the material of Märss *et al.* 1997, 1998).

In conclusion, the thelodont assemblages seem to be the most age diagnostic remains from the vertebrate-yielding localities of the Chester Bjerg Formation. The Halls Grav locality contains *Loganellia* cf. *L. tuvaensis* and *Nikolivia* sp., indicating a Late Silurian age for this assemblage which also shows new thelodont taxa such as *Paralogania foliala* sp. nov.

Systematic palaeontology

Most of the major clades listed in Figure 4 are considered monophyletic and reflect the latest studies of interrelationships of the Craniata (Janvier 1996a, b). Thelodonts were excluded from this classification due to their questionable validity as a separate clade (Janvier 1981, 1996a, b; Wilson & Caldwell 1998), but Turner (1991) has argued for their monophyly based on evidence from scale morphology. New material has revealed greater variation in body morphology than previously thought (Wilson & Caldwell 1998), but the true affinity and relationship of thelodonts and their typical scales still remains open. Thelodonts are here described initially as a separate group, within the classification of the better known craniate clades. Classification of higher thelodont taxa is based on works by Karatajute-Talimaa (1978, 1997).

Several different thelodont classifications of morphological scale varieties within a species have been used. The traditional head, transitional and body (trunk) scale classification was re-defined by Märss (1982, 1986b) to oral, cephalo-pectoral, postpectoral, precaudal and pinnal scale types, based on studies of articulated specimens of *Phlebolepis elegans*. Further knowledge about

and *Praetriorlogania grabion* gen. et sp. nov. *Canonina* cf. *C. grossi* from Monument suggests an Early Devonian age and the fauna is complemented by the new taxa *Loganellia almgreeni* sp. nov., *Praetriorlogania grabion* gen. et sp. nov. and *Thulolepis striaspina* gen. et sp. nov. It is possible that the apparent succession of faunas from Halls Grav to Monument may prove to be of biostratigraphic utility in the Silurian–Devonian boundary interval. The acanthodians, including one new species of *Nostolepis*, one problematic climatiid, one species of *Gomphonchus* and variable poracanthodiforms, cannot give a more precise age than Late Silurian – Early Devonian for both localities, although future taxonomical revision of the poracanthodiforms may change that. The heterostracans, osteostracans and anaspids from the Chester Bjerg Formation are not useful age determinants, since they are poorly preserved and are not yet reliable for comparison of Circum-Arctic strata.

the scale variation in comparison with the position on the body has been achieved by studies on the squamation of articulated thelodonts from the Silurian of Scotland by Märss & Ritchie (1998). In the present study, head, transitional and trunk scale classification has been used as a basis, with complementary classification when possible. Acanthodian taxonomical classification follows Denison (1979) with some modification at the generic level.

Thelodonti

Order Katoporida Karatajute-Talimaa 1978

Family Loganiidae Karatajute-Talimaa 1978

Genus *Loganellia* Turner 1991

Type species. *Thelodus scoticus* Traquair 1898; Lower Silurian (Llandovery), Patrick Burn Formation, Logan Water, Lesmahagow, Lanarkshire, Scotland. Later designated as type species for genus *Logania* by Gross (1967a). The diagnosis for *Loganellia scotica*, includ-