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

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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

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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. *Canonia* cf. *C. grossi* suggests an Early Devonian age for the Monument locality, since *Canonia* 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., *Praetrilogania 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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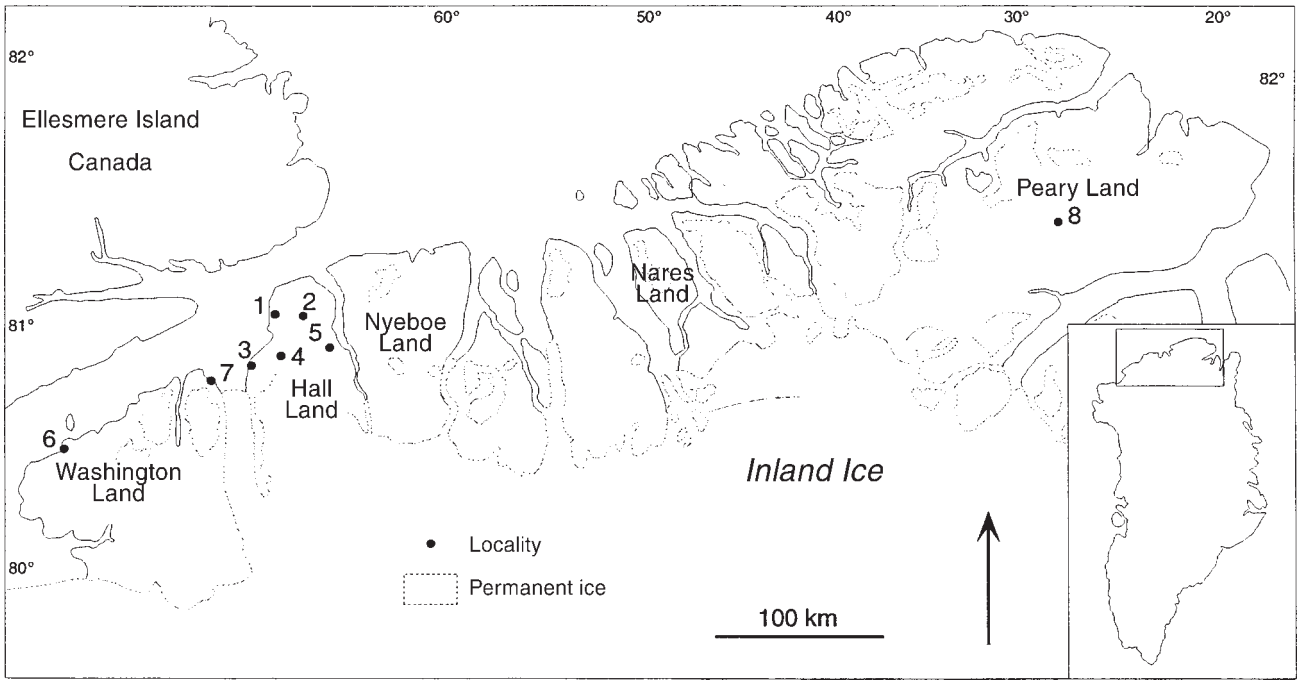

Fig. 1. **Above**: Silurian–Devonian vertebrate-bearing localities in North Greenland. **1**: Halls Grav (Observatory Bluff). **2**: Monument. **3**: Kap Tyson East outcrops. **4**: Sunmark Mountain. **5**: Kayser Bjerg. **6**: Kap Independence. **7**: Kap Lucie Marie. **8**: central Peary Land. **Below**: 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; Blieck *et al*. 1988, in press; Blieck & 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 references 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).

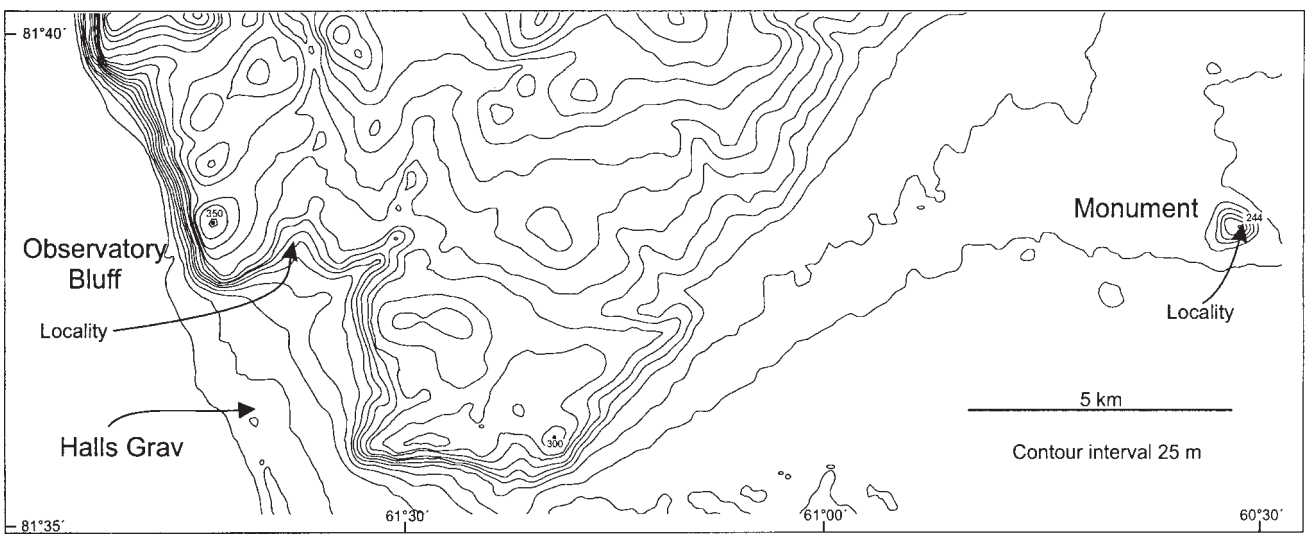

Fig. 2. Map showing two vertebrate-bearing localities from the Chester Bjerg Formation near Halls Grav in western Hall Land and at the top of Monument in central Hall Land (see Fig. 1). Modified from Dawes (1987).

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 & Sønderholm 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 unconformally overlain by Carboniferous and younger strata of the Wandel Sea Basin in northern and eastern areas of North Greenland (Håkansson *et al*. 1991; Stemmerik & Håkansson 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).

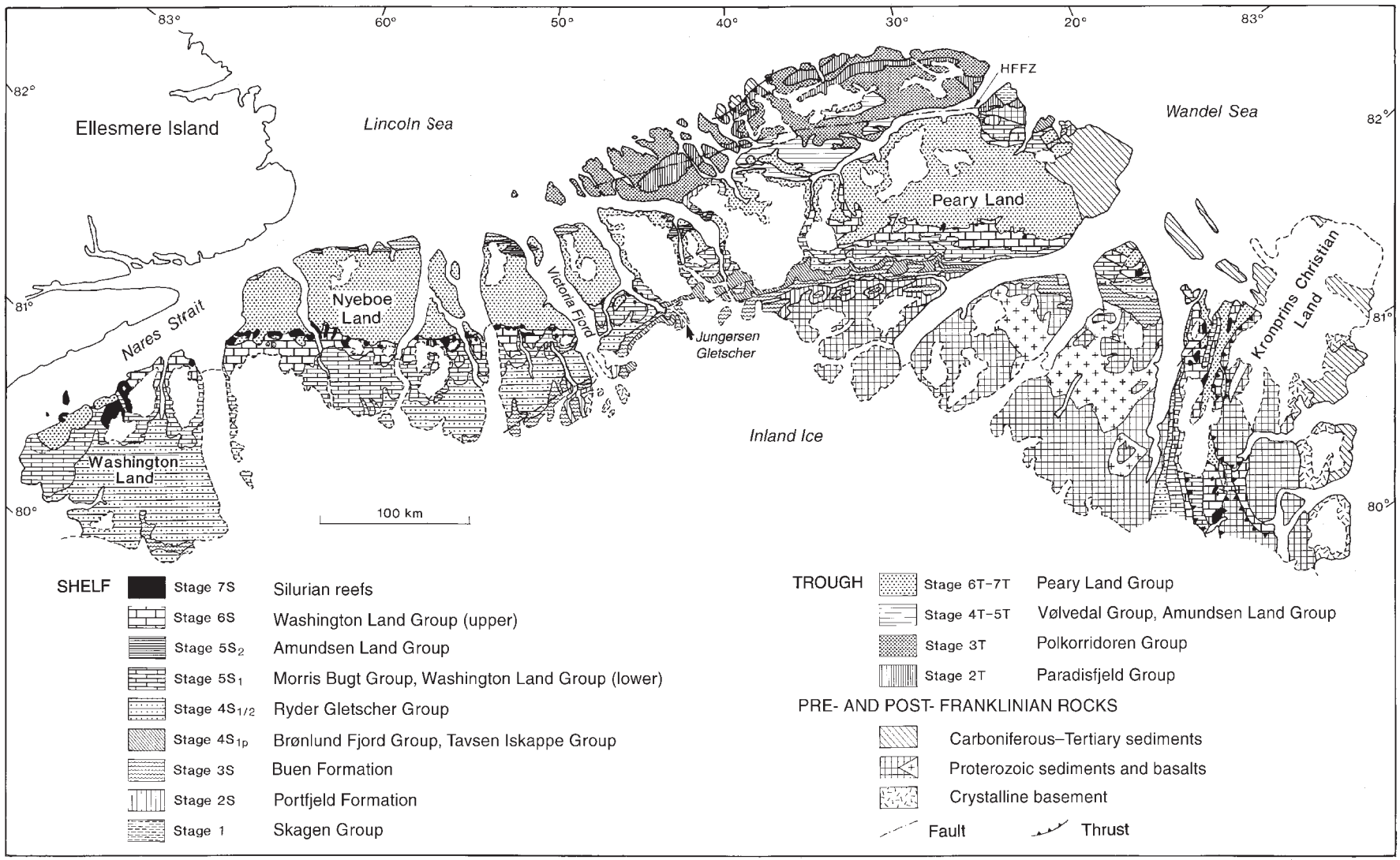

Fig. 3. Geological map of North Greenland. The map shows the major stratigraphic units of the Franklinian Basin corresponding to the basin evolutionary stages recognized by Higgins *et al.* (1991a). **HFFZ**: Harder Fjord fault zone. Slightly modified from Ineson & Peel (1997, fig. 2).

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												
Loganellia cf. *L. tuvaensis*	x	x	x	x	x	x	x	x	x	x	x	?
Loganellia almgreeni sp. nov.												x
Paralogania foliala sp. nov.				x								
Praetrilogania grabion gen. et sp. nov.	x	x		x	x							x
Order Thelodontida Kiær 1932												
Family Nikoliviidae Karatajute-Talimaa 1978												
Nikolivia sp.		x		x	x							?
Canonia cf. *C. grossi*												x
Family Incertae sedis												
Thulolepis striaspina 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												
Nostolepis halli sp. nov.	x	x	x	x	x							
Climatiida indet.	x	x	x	x								
Order Ischnacanthida Berg 1940												
Family Ischnacanthidae Woodward 1891												
Gomphonchus cf. *G. sandelensis*	x	x	x	x	x							x
Poracanthodes cf. *P. punctatus*	x	x	x	x	x					x		x
Poracanthodes cf. *P. porosus*	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
Incertae 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 detection, 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). *Canonia 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 *Canonia* cf. *C. grossi*. *Canonia 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 *Canonia* 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 *Canonia* cf. *C. grossi* may be potential indicators of a Devonian age in future biostratigraphic schemes. *Praetrilogania grabion* gen. et sp. nov. is present in both assemblages and its distribution would therefore extend across the Silurian–Devonian boundary. Loganiids such as *Paralogania 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 *Canonia 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. and *Praetrilogania grabion* gen. et sp. nov. *Canonia* cf. *C. grossi* from Monument suggests an Early Devonian age and the fauna is complemented by the new taxa *Loganellia almgreeni* sp. nov., *Praetrilogania 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.

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 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-

ing body morphology, was revised by Märss & Ritchie (1998).

Diagnosis. Scales vary from small to large (0.1–2.0 mm); head scales round or oval with serrated crown edges; median part of crown surface is smooth and flat; shallow pulp cavity placed centrally on the base; transitional scales oval or rhomboidal, oblong, with crown of 'oak leaf' type; pulp canal usually not developed; trunk scales rhomboidal, wedge-shaped and oblong; crown consists of rhomboidal median part with flat surface or longitudinal groove; ridged lateral part which is shorter and narrower; trunk scales with posteriorly extending pulp canal or concentration of wider dentine canals; base of mature trunk scales is usually high. (Modified from Karatajute-Talimaa 1997.)

Species content. *Loganellia scotica* (Traquair 1898); *L. asiatica* (Karatajute-Talimaa 1978); *L. cuneata* (Gross 1947); *L. einari* Märss 1996; *L. grossi* Fredholm 1990; *L. incompta* (Karatajute-Talimaa 1990); *L. sibirica* (Karatajute-Talimaa 1978); *L. tuvaensis* (Karatajute-Talimaa 1978); *L. aldridgei* sp. nov. Turner in press; *L. avonia* sp. nov. Turner in press.

Range. Early Silurian (early Llandovery) – earliest Devonian.

Remarks. Since the earlier proposed genera names *Logania* (Gross 1967a) and *Loganella* (Turner & Peel 1986) are preoccupied *Loganellia* Turner 1991 is used as a replacement name.

Loganellia cf. *L. tuvaensis* (Karatajute-Talimaa 1978)

Figs 5–7

1978 *Logania tuvaensis* sp. nov. Karatajute-Talimaa, pp. 79–78, plate 18, figs 1–6; plate 19, figs 1–13; pict. 18, figs 1–3; pict. 19, fig. 7.
1986 *Loganella* cf. *L. tuvaensis* – Turner & Peel, p. 82, fig. 3D, E.
1990 *Logania tuvaensis* – Karatajute-Talimaa, plate 10.

Holotype. *Logania tuvaensis*, LitNIGRI, scale No. T-395 (Karatajute-Talimaa 1978, plate 18, fig. 1a–c). Upper Silurian, Pridoli, river Elegest sample 236, Pichi-shui Beds, Tuva region, south of Siberia in Russia.

Figured material. Head and rostral scales; MGUH VP 3394–3397 from GGU sample 82738, MGUH VP 3398–3400 from GGU sample 298937, MGUH VP 3433 from GGU sample 82736. Transitional scales; MGUH VP 3401, 3402 from GGU sample 82738, MGUH VP 3403–3410, 3431, 3432, 3434 from GGU sample 298937. Trunk scales; MGUH VP 3411–3413, 3415 from GGU sample 82738, MGUH VP 3414, 3416–3424 from GGU sample 298937, MGUH VP 3435, 3436 from GGU sample 82736. Posterior trunk scales; MGUH VP 3425 from GGU sample 82738, MGUH VP 3426–3430 from GGU sample 298937.

Other material. Several thousand scales are available from GGU samples 82734, 298938, 298950, 298953, 298954, 298960 and 298963 and about five questionable scales from GGU sample 319264.

Locality and age. The Halls Grav locality and Monument, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Diagnosis. Loganiid scales, medium size, up to 1.2 mm long, with rhomboidal or sagittate crown; flat horizontal median crown area with smooth margins; vertical lateral part with one short lateral ridge inclining from base towards a posterior apex; base convex and displaced anteriorly with diffuse posterior pulp aperture, alternatively evenly convex with central pulp aperture; dentine tissue with irregular branching dentine tubules and narrow dentine canals; pulp canal not developed; posteriorly concentrated wider dentine canals extend towards crown apex; basal layer thick with tubules of Sharpey's fibres. (Translated and modified from Karatajute-Talimaa 1978.)

Scale morphology. The scales are medium sized, varying in length between 0.4–1.2 mm, and the majority of those examined represent a mature stage of development. They are mainly well preserved, white, yellow to dark brown in colour and seem not to be waterworn. Some samples, however, contain heavily etched specimens probably due to weathering of the rock.

The rare head or rostral scales (Fig. 5A, C, D; Fig. 6.1–7) are rounded or slightly elongated and have a smooth flat or slightly convex crown with up to 14 almost vertical ribs and notches on the crenulated margins. Scales which are more elongated are less symmetrical with deeper notches ascending from the anterior crown margin toward the centre of the crown. Some of these scales have a crown that resembles an

oak leaf (Fig. 5D). The neck is weakly developed at the connection of the sharp junction between the crown and base of the rostral scales. The swollen base is usually as large and deep as the crown. In mature scales the centrally situated pulp openings are often relatively wide and deep, if compared with the trunk scales.

There are two types of transitional scales. The first type represented by some asymmetric scales has leaf-shaped or navicular crowns similar to rostral scales but with notches concentrated on the anterior part at the crown margin. Secondly, there are symmetrical scales, sometimes with a pair of notches on the anterior crown margin. Transitional scales of the first type (Fig. 5B; Fig. 6.8–11) could be included together with the group of head scales, but they are relatively larger. The oval base is often slightly larger than the crown which is oval to elongated and sometimes very asymmetrical. Deep notches are directed towards the centre of the flat or slightly convex crown and are situated along the anterior and central margin. When a pulp opening or depression is visible on the deep base it has a central position and is quite often elongated. Transitional scales of the second type (Fig. 5E, F; Fig. 6.12–15) are much more abundant than the first type. They are relatively large, oval or elongated with a flat and smooth crown forming a rhomboidal, sagittate or oval platform. The extension of the crown margins is longer in the posterior part forming a low angled posterior point. In the middle of the anterior part of the crown the smooth left and right margins bend horizontally towards the centre of the crown, forming an edge-cutting notch or vertical groove, sometimes flanked by a vertical lateral ridge. In some scales only the notch is visible, not the ridge, and vice versa. Anteriorly, where the crown becomes narrower, the upper crown surface bends down towards the neck. The narrowing sometimes results in a sharp anterior point or apex before the bent down portion. The lateral sides of the crown, likewise lateral areas, are almost vertical and bend slightly inwards, forming a sharp junction towards the base. A high neck is therefore represented just above this junction.

In some scales a tiny lateral wing runs on each side from the centre of the neck towards the posterior point of the crown. This feature is typical for most trunk scales, suggesting that these scales are located more posteriorly. Some of the smaller forms may come from the area of the dorsal fin (Fig. 6.18, 19). Scale forms between transitional scales of type one and type two are also present. The large oval and convex base is broader but shorter than the crown and is thicker in its central part, or rarely in its anterior part. The deep anterior part of the base is also a character more common in trunk scales. The small pulp opening is located posteriorly when the base is deepest anteriorly or located centrally when the base is deepest in the central part. Dentine canals are sometimes recognisable as small holes or depressions on the surface of the base (Fig. 5K).

The crown of trunk scales (Fig. 5G–K; Fig. 6.16, 17, 20–26) is wide in the central part and smoothly rhomboidal with a flat upper surface. The extension of the margins is undisturbed and often straight, giving the crown an angular feature. Postero-laterally the margins are longer and more stretched than antero-laterally, and they meet at a lower angle, forming a sharply pointed, but still rounded, posterior apex. Anteriorly the margins often bend down towards the base, where they meet with a less sharp angle than at the posterior apex. The lateral sides of the crown are vertical and slightly concave, forming a high neck. Typical for this type of scale is the lateral ridge running on each side from the posterior apex towards the central part of the scale and the neck base junction. These ridges are tiny and rarely reach as far back as to the lateral corner of the rhomboidal crown. The base is wider than the crown and anteriorly displaced. Anteriorly the base is much deeper than posteriorly and in some scales a weak and poorly developed anterior basal process is developed. In mature scales, a tiny pulp aperture is

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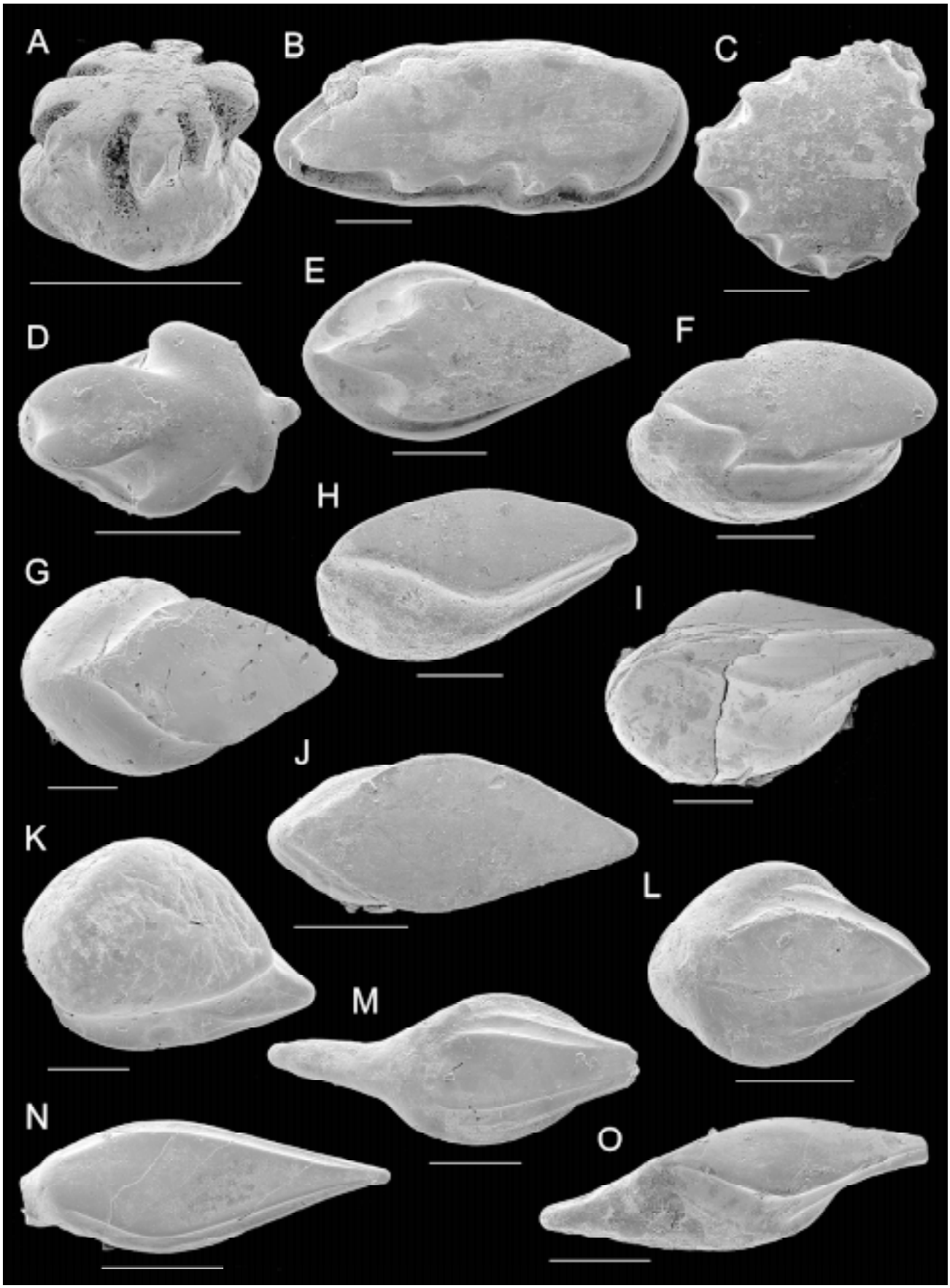
Fig. 5. *Loganellia* cf. *L. tuvaensis* (Karatajute-Talimaa 1978). SEM photomicrographs. Scale bars equal 0.2 mm.
A: Head or rostral scale in oblique crown view, MGUH VP 3394. **B**: Transitional scale in crown view, MGUH VP 3403. **C**: Head or rostral scale in crown view, MGUH VP 3395. **D**: Head or rostral scale in crown view, MGUH VP 3396. **E**: Transitional scale in crown view, MGUH VP 3401. **F**: Transitional scale in oblique crown view, MGUH VP 3402. **G**: Trunk scale in crown view, MGUH VP 3414. **H**: Trunk scale in oblique crown view, MGUH VP 3411. **I**: Trunk scale in oblique crown view, MGUH VP 3412. **J**: Trunk scale in crown view, MGUH VP 3413. **K**: Trunk scale in basal view, MGUH VP 3415. **L**: Posterior trunk scale in crown view, MGUH VP 3424. **M**: Posterior trunk scale in crown view, MGUH VP 3426. **N**: Posterior trunk scale in crown view, MGUH VP 3425. **O**: Posterior trunk scale oblique crown view, MGUH VP 3427.
MGUH VP 3394–3396, 3401, 3402, 3411–3413, 3415, 3425 from GGU sample 82738, Halls Grav; MGUH VP 3403, 3414, 3424, 3426, 3427 from GGU sample 298937, Halls Grav.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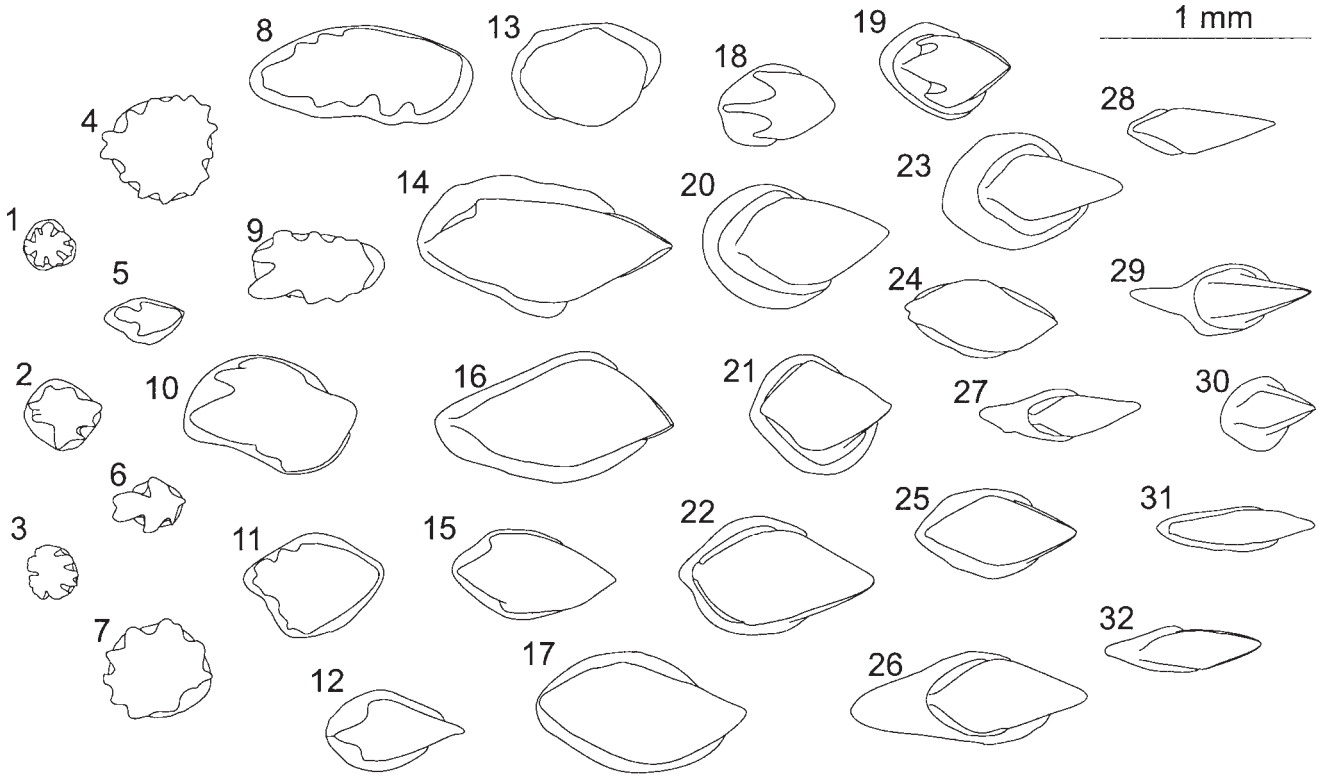

Fig. 6. *Loganellia* cf. *L. tuvaensis* (Karatajute-Talimaa 1978). The main morphological scale varieties in crown view.
1: Head or rostral scale, MGUH VP 3394. **2**: Head or rostral scale, MGUH VP 3398. **3**: Head or rostral scale, MGUH VP 3397. **4**: Head or rostral scale, MGUH VP 3395. **5**: Head or rostral scale, MGUH VP 3399. **6**: Head or rostral scale, MGUH VP 3396. **7**: Head or rostral scale, MGUH VP 3400. **8**: Transitional scale, MGUH VP 3403. **9**: Transitional scale, MGUH VP 3404. **10**: Transitional scale, MGUH VP 3405. **11**: Transitional scale, MGUH VP 3406. **12**: Transitional scale, MGUH VP 3407. **13**: Transitional scale, MGUH VP 3408. **14**: Transitional scale, MGUH VP 3409. **15**: Transitional scale, MGUH VP 3410. **16**: Trunk scale, MGUH VP 3416. **17**: Trunk scale, MGUH VP 3417. **18**: Transitional scale, MGUH VP 3431. **19**: Transitional scale, MGUH VP 3432. **20**: Trunk scale, MGUH VP 3414. **21**: Trunk scale, MGUH VP 3418. **22**: Trunk scale, MGUH VP 3419. **23**: Trunk scale, MGUH VP 3420. **24**: Trunk scale, MGUH VP 3421. **25**: Trunk scale, MGUH VP 3422. **26**: Trunk scale, MGUH VP 3423. **27**: Posterior trunk scale, MGUH VP 3427. **28**: Posterior trunk scale, MGUH VP 3428. **29**: Posterior trunk scale, MGUH VP 3426. **30**: Posterior trunk scale, MGUH VP 3424. **31**: Posterior trunk scale, MGUH VP 3429. **32**: Posterior trunk scale, MGUH VP 3430.
MGUH VP 3394–3397 from GGU sample 82738, Halls Grav; MGUH VP 3398–3400, 3403–3410, 3414, 3416–3424, 3426–3432 from GGU sample 298937, Halls Grav.

situated posteriorly, when not completely overgrown. Younger scales, which are very rare, have a larger opening in the centre. During scale-growth the basal layer grows posteriorly and in the end, if visible at all, a tiny hole is left posteriorly (Fig. 5K). In the area where the former main cavity was, it is possible to trace small dentine canal openings on the basal surface.

Smaller and more elongated scales with a strongly pointed posterior apex indicate a position on the most posterior part of the body (Fig. 5L–O; Fig. 6.27–32). Some of them are specialized by having lower and less vertical lateral parts of the crown (Fig. 5L, M; Fig. 6.29, 30). These scales have a crown with a flat or slightly concave median region, flanked by wide single or double-ridged lateral areas. Scales of both types have quite often an anterior basal process. When compared with other scales of *L.* cf. *L. tuvaensis,* this type of scale has a more extreme morphology, which may indicate a fin edge squamation. The first and more general type of posteriorly placed scales is thereby probably situated more anteriorly on the fin or posteriorly on the tail.

Scale histology. Histological structure seen among the set of scales is less variable than their morphology. Crowns of head scales (Fig. 7A) are penetrated by several branching dentine tubules, which tend to be more abundant in the median part. Towards the base, ap-

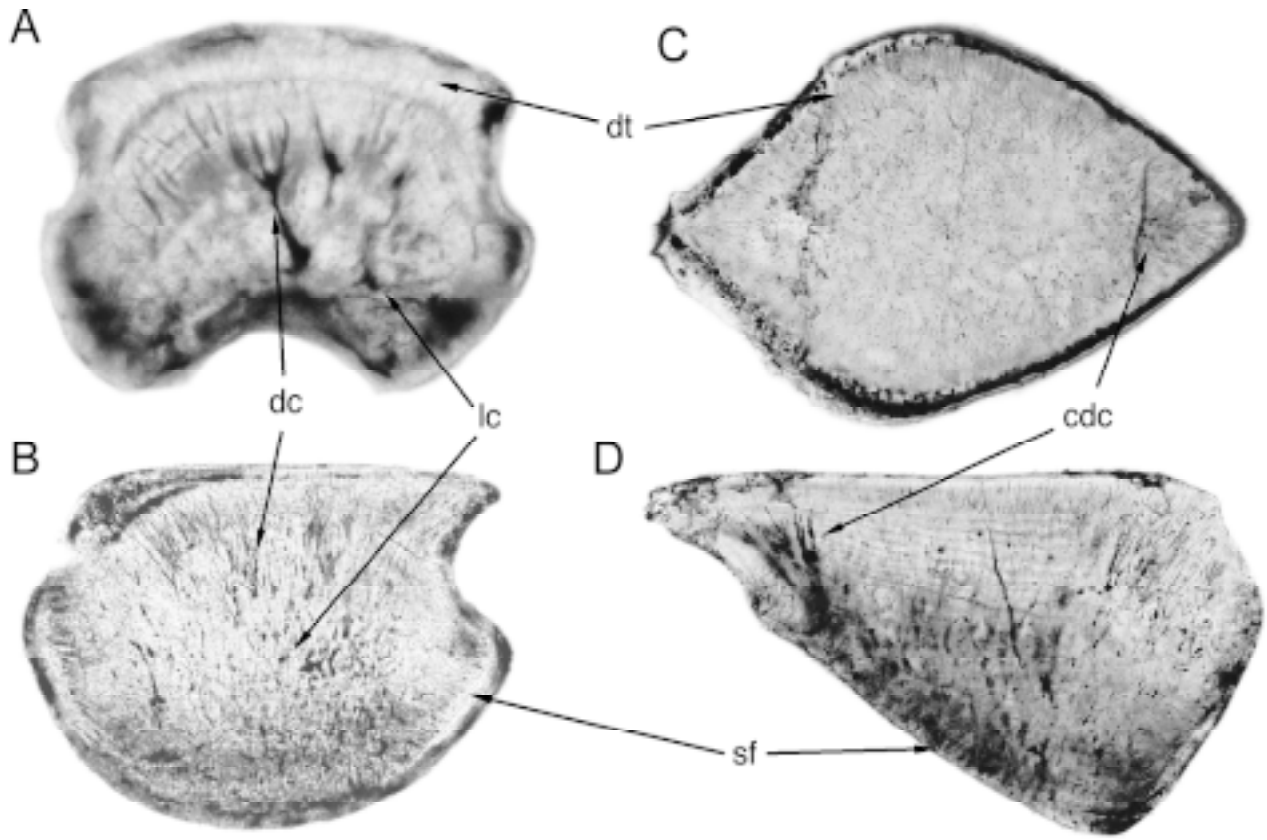

Fig. 7. *Loganellia* cf. *L. tuvaensis* (Karatajute-Talimaa 1978). Histology of the scales.
A: Head or rostral scale in vertical longitudinal section, MGUH VP 3433, × 203. **B**: Transitional scale in vertical longitudinal section, MGUH VP 3434, × 111. **C**: Trunk scale in horizontal crown section, MGUH VP 3435, × 83. **D**: Trunk scale in vertical longitudinal section, MGUH VP 3436, × 94.
MGUH VP 3433, 3435, 3436 from GGU sample 82736, Halls Grav; MGUH VP 3434 from GGU sample 298937, Halls Grav.
cdc: concentration of dentine canals; **dc**: dentine canals; **dt**: dentine tubules; **lc**: odontoblast joining lacunae; **sf**: tubules for Sharpey's fibres.

proximately at neck level, the tubules converge to wide straight dentine canals and lacunae. A pulp canal is not visible, but a shallow central pulp cavity is preserved until the head scales reach full maturity by full development of basal tissue. In mature scales, the dense basal tissue with well developed tubules for Sharpey's fibres forms a quite high convex base.

A high base is also characteristic for the mature transitional scales (Fig. 7B), which usually have a uniform basal thickness. A central depression is sometimes visible at the base where canals and lacunae converge. The branching dentine tubules are straight and regular in the uppermost part of the crown. Towards the central part of the scale they are thicker and more scarce and irregular, and when joining they often form lacuna-like cavities.

Trunk scales of *L.* cf. *L. tuvaensis* have a concentration of thicker tubules, canals and lacuna-like cavities in the posterior part of the crown (Fig. 7C, D). They extend from a small depression or aperture in the base, caused by the junction of canals, towards the posterior part of the crown. This concentration is equivalent to the typical short pulp canal usually found in other loganiid scales. The basal tissue is thicker in the anterior part, which also reflects the height of the anteriorly displaced base. Where the basal tissue is thicker, there is also a higher amount of irregularly oriented tubules of Sharpey's fibres.

Scale dimensions. Length 0.4–1.2 mm; width 0.2–0.7 mm.

Remarks. Karatajute-Talimaa (1978) originally described *Loganellia tuvaensis* as a quite homogeneous set of scales, collected in sections by the river Elegest in the Tuva region, south of Siberia, Russia. In comparison with original material and a complementary morpho-

logical set (Karatajute-Talimaa 1990), the material from North Greenland clearly is morphologically much more diverse with forms not described earlier, as detected by Turner & Peel (1986). It is also clearly morphologically different from the related taxon, *L. incompta* (Karatajute-Talimaa 1990), by having less expressed lateral wings. The largest differences between the original material and the scales under discussion are found among the transitional scales, and especially in the presence of smaller scales from the most posterior part of the body. The present material also shows lower inclination of the crown, as well as smaller and shorter lateral ridges. The difference may reflect the enormous amount of material available from the Chester Bjerg Formation, giving new information about scale forms, but the differences are not sufficient to establish a new species.

Occurrence. *Loganellia tuvaensis*, Pridoli, Tuva, south of Siberia in Russia; *Loganellia* cf. *L. tuvaensis*, Pridoli–Lochkovian, Halls Grav, Hall Land, North Greenland.

Loganellia almgreeni sp. nov.

Figs 8–10

Derivation of name. For Svend Erik Bendix-Almgreen, Geological Museum, Copenhagen, Denmark, for his studies of Greenland vertebrates.

Holotype. Trunk scale; MGUH VP 3449 from GGU sample 319264 (Fig. 8G; Fig. 9.8).

Figured material. Head scales; MGUH VP 3437. Transitional scales; MGUH VP 3440–3448, 3459. Trunk scales; MGUH VP 3449–3458. Scales from the leading edge of the fin or around the eye; MGUH VP 3438, 3439. All from GGU sample 319264.

Other material. About 100 scales, moderately well preserved, from GGU sample 319264.

Locality and age. The top of Monument, Hall Land, North Greenland, Chester Bjerg Formation, Early Devonian (Lochkovian).

Diagnosis. Small loganiid scales with a high convex anteriorly displaced base; smoothly rhomboidal or oval flat crown with a pair of anterior notches or furrows running posteriorly towards a single crown apex; rhomboidal or sagittate median crown area; central or slightly posterior pulp aperture; branching and slightly irregular dentine tubules converging towards a narrow pulp cavity and canal.

Scale morphology. The scales of *Loganellia almgreeni* sp. nov. are small and do not exceed 0.5 mm in length. They are well preserved, although the apex sometimes is broken, and are variably pale brown in colour.

Head scales are round or irregular, with marginal notches or deep furrows that together with intermediate ridges are oriented towards the centre or slightly posterior of the convex crown (Fig. 8A; Fig. 9.1). The base is relatively deep and about the same width as the crown. Centrally situated on the base is a small pulp depression or aperture. The neck is weakly developed with the shape of a shallow furrow.

Another type of scale is here interpreted to come from the leading edge of a fin, alternatively to be situated close to or around the eye (Fig. 8F, I; Fig. 9.2, 3). This scale type is smoothly rhomboidal or saggitate with a clear posteriorly pointing apex. The whole crown has a higher inclination from the flat or concave base, which has very little basal tissue. Since most of the other scales of the same species are mature, it is possible that the lack of well developed basal tissue is characteristic for this type of scale. The narrow median part of the crown, which is furrowed along half its length, is flanked by deep wide furrows and narrow marginal ridges. With a steeper angle the furrows bend

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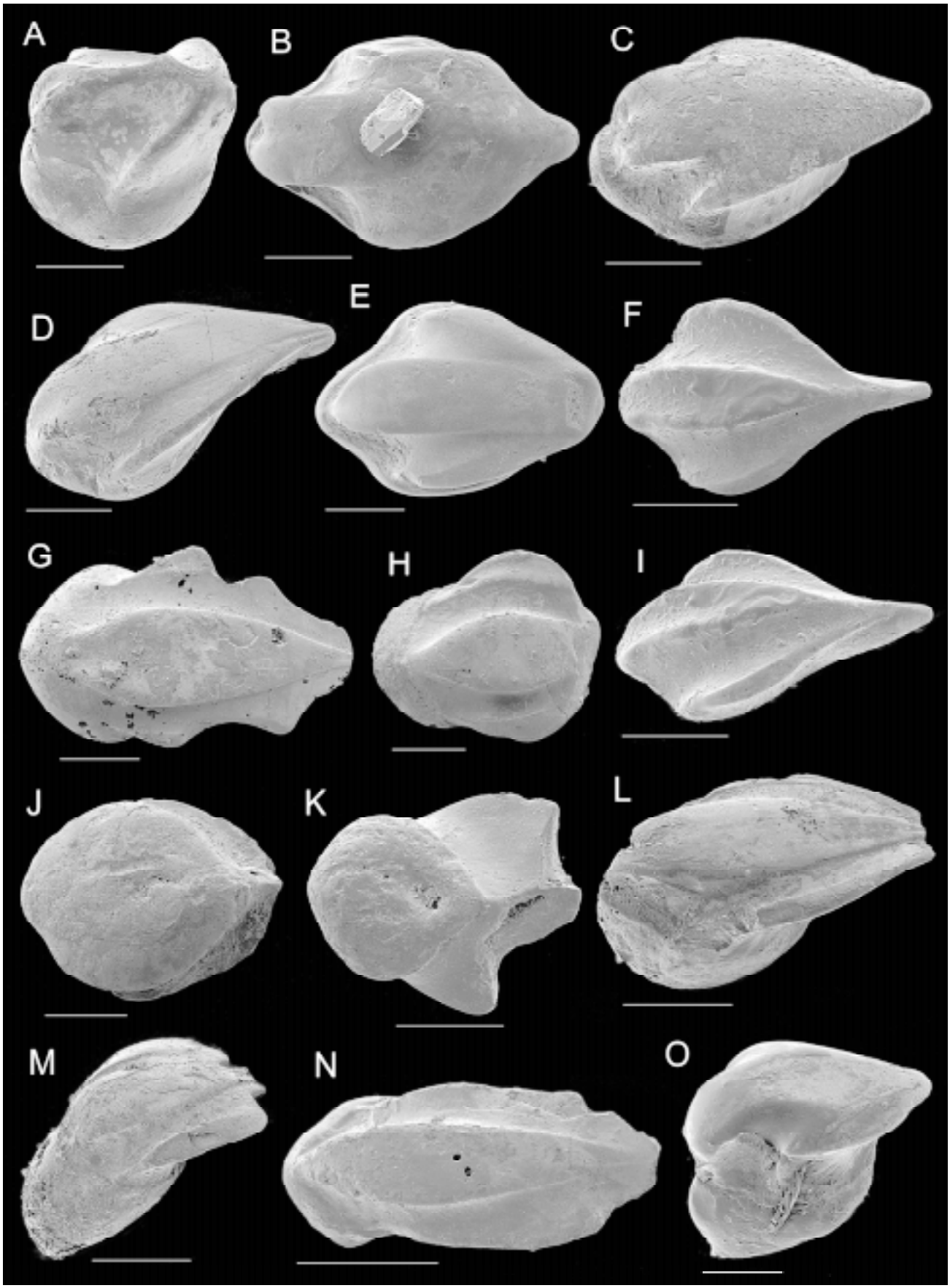
Fig. 8. *Loganellia almgreeni* sp. nov. SEM photomicrographs. Scale bars equal 0.1 mm.
A: Head scale in oblique crown view, MGUH VP 3437. **B**: Transitional scale in crown view, MGUH VP 3440. **C**: Transitional scale in oblique crown view, MGUH VP 3441. **D**: Transitional scale in oblique crown view, MGUH VP 3442. **E**: Transitional scale in crown view, MGUH VP 3443. **F**: Scale from the leading edge of a fin or around the eye in crown view, MGUH VP 3439. **G**: Trunk scale in crown view, holotype, MGUH VP 3449. **H**: Trunk scale in crown view, MGUH VP 3450. **I**: Scale from the leading edge of a fin or around the eye in oblique crown view, MGUH VP 3439. **J**: Transitional scale in basal view, MGUH VP 3444. **K**: Trunk scale in basal view, MGUH VP 3451. **L**: Trunk scale in oblique crown view, MGUH VP 3452. **M**: Trunk scale in oblique crown view, MGUH VP 3453. **N**: Trunk scale in crown view, MGUH VP 3454. **O**: Transitional scale in oblique crown view, MGUH VP 3445.
All specimens from GGU sample 319264, Monument.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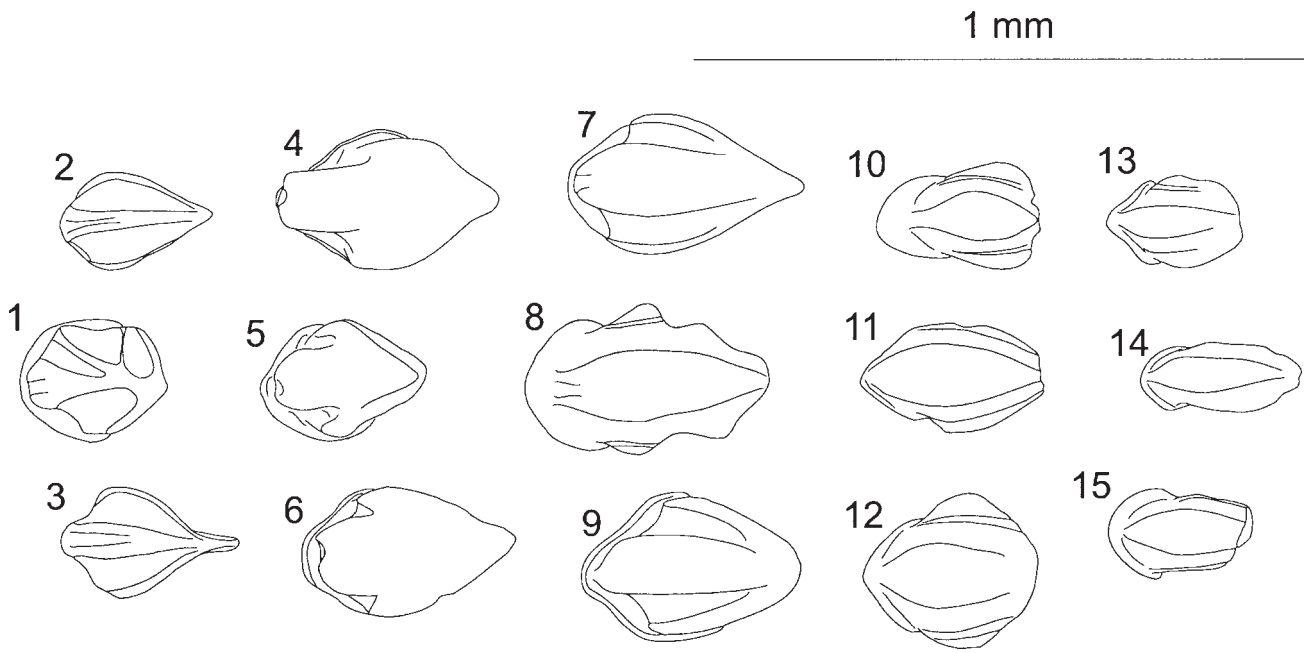


Fig. 9. *Loganellia almgreeni* sp. nov. The main morphological scale varieties in crown view.
1: Head scale, MGUH VP 3437. **2**: Scale from the leading edge of a fin or around the eye, MGUH VP 3438. **3**: Scale from the leading edge of a fin or around the eye, MGUH VP 3439. **4**: Transitional scale, MGUH VP 3440. **5**: Transitional scale, MGUH VP 3459. **6**: Transitional scale, MGUH VP 3441. **7**: Transitional scale, MGUH VP 3442. **8**: Trunk scale, holotype, MGUH VP 3449. **9**: Transitional scale, MGUH VP 3443. **10**: Trunk scale, MGUH VP 3453. **11**: Trunk scale, MGUH VP 3452. **12**: Trunk scale, MGUH VP 3450. **13**: Trunk scale, MGUH VP 3455. **14**: Trunk scale, MGUH VP 3454. **15**: Trunk scale, MGUH VP 3456.
All specimens from GGU sample 319264, Monument.

towards the basal region. This type of scale lacks a distinct neck and on the lower side of the crown a crest runs from the base towards the apex.

Transitional scales are oval or elongated, with a smooth flat or slightly convex crown forming a rhomboidal or sagittate outline (Fig. 8B–E, J, O; Fig. 9.4–7, 9). Crown margins converge posteriorly, forming a low angled point. In the middle of the anterior part of the crown the smooth margins bend horizontally towards the centre of the crown, forming a notch or short steep angled furrow. Anteriorly, where the crown margins meet in a smooth curve, the margin is disturbed by a median notch. A shallow neck is developed just above the junction between the often very high base and the vertical sides of the crown. From the posterior part of the round or oval base, on the lower side of the crown, a clear crest runs towards the apex. Pulp apertures or depressions are indistinct in mature scales, but are visible in younger scales and situated centrally or slightly posterior.

The difference between transitional and trunk scales is not large. Instead of small antero-lateral notches in the margins, larger furrows develop and run further back on the otherwise flat or slightly convex crown. The anterior median part of the crown with its small notch, also bends down towards the high base. In the more elongated trunk scales the crown cutting furrows are even more pronounced (Fig. 8G, H, K–M; Fig. 9.8, 10–13, 15). They run all the way from the anteriorly displaced base to the posterior apex. The median part of the crown is smooth, flat or slightly concave and bends down anteriorly towards the base. Here a short, shallow, antero-median furrow or notch is visible. Ridges are visible parallel to these running towards the apex, either along the margin or just in the central region of the lateral part of the crown. The smaller base is still high and convex with a tiny pulp aperture displaced posteriorly. An even sharper ridge runs on the lower side of the crown, from the clear neck and associated base to the posterior apex.

Smaller and more elongated scales with a general morphology very similar to the other trunk scales may come from the most posterior part of the tail or from the fins (Fig. 8N; Fig. 9.14).

Scale histology. *L. almgreeni* sp. nov. possesses a katoporid histology with regularly branching or anastomosing dentine tubules (Fig. 10). Towards the cen-

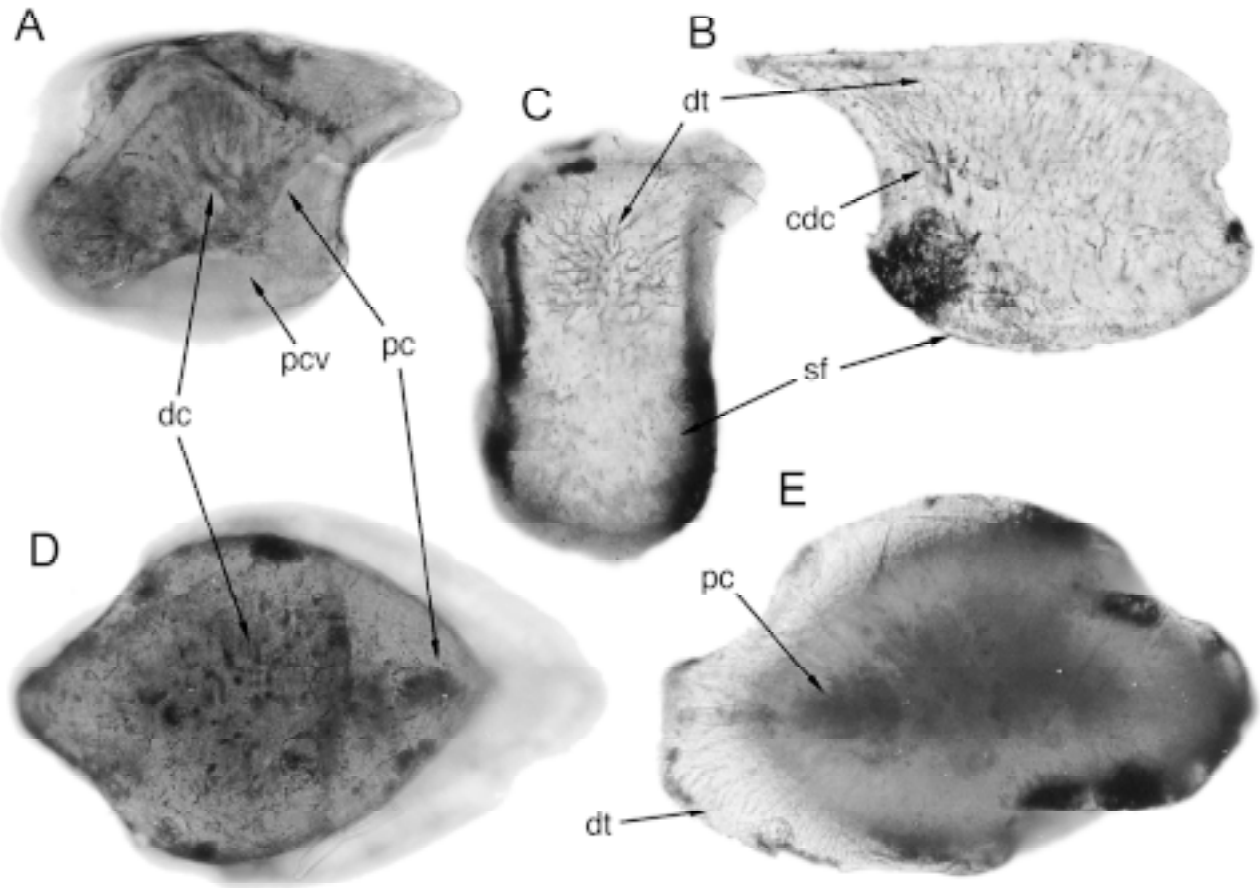


Fig. 10. *Loganellia almgreeni* sp. nov. Histology of the scales.
A: Trunk scale in lateral view, immersed in aniseed oil, MGUH VP 3457, × 199. **B**: Transitional scale in vertical longitudinal section, MGUH VP 3446, × 210. **C**: Trunk scale in vertical transversal section, MGUH VP 3458, × 206. **D**: Transitional scale in basal view, immersed in aniseed oil, MGUH VP 3447, × 176. **E**: Transitional scale in crown view, immersed in aniseed oil, MGUH VP 3448, × 164. All specimens from GGU sample 319264, Monument.
cdc: concentration of dentine canals; **dc**: dentine canals; **dt**: dentine tubules; **pc**: pulp canal; **pcv**: pulp cavity; **sf**: tubules for Sharpey's fibres.

tre of the trunk scale, the rather straight tubules attain greater thickness and pass into a relatively deep (for loganiids) and narrow pulp cavity, and short wide pulp canal (Fig. 10A). In more mature scales, when the pulp cavity is not present, the converging tubules just end in the compact base (Fig. 10B), alternatively penetrate and open onto the basal surface (Fig. 10D). Scales of *L. almgreeni* sp. nov. do not always show a clear pulp canal, but may instead show a concentration of tubules which converge towards the central pulp cavity or the compact base (Fig. 10B). Tubules of Sharpey's fibres are only found in the most distal part of the thick base and have a tendency to be oriented perpendicular to each other.

Scale dimensions. Length 0.2–0.4 mm; width 0.1–0.3 mm.

Remarks. Loganellia almgreeni sp. nov. is similar to *L. tuvaensis* (Karatajute-Talimaa 1978), *L. incompta* (Karatajute-Talimaa 1990), *L. cuneata* (Gross 1947), *L. asiatica* (Karatajute-Talimaa 1978) and *L. grossi* (Fredholm 1990) since they all have only one pair of lateral ridges or wings. In *L. almgreeni* sp. nov., however, these lateral ridges or wings are much wider and more elevated, forming more clear lateral areas. Other species within the same genus have two or more lateral ridges which also are much less pronounced than the single pair of wings present in *L. almgreeni* sp. nov. Some scales of *L. almgreeni* sp. nov. could on the other hand be confused with *Boreania minima* Karatajute-Talimaa 1985 in terms of gross morphology and histology (Fig. 8O; Fig. 10A). The similarity to the complementary set, however, as well as the higher

number of branching dentine tubules and greater irregularity of dentine tubules, support a position within the genus *Loganellia*. Some trunk scales of *L. almgreeni* sp. nov. are characterized by a central or slightly posterior pulp cavity or aperture, which is unusual for loganiid scales of other scales types than head and transitional ones.

Occurrence. Lochkovian, Monument, Hall Land, North Greenland.

Genus *Paralogania* Karatajute-Talimaa 1997

Type species. *Logania kummerowi* Gross 1967a; Upper Silurian? erratic boulder (Bey. 6), lowlands of northern Germany.

Diagnosis. Scales vary from small to large (0.3–2.0 mm); small head scales round or oval with a flat smooth crown, serrated on edges; transitional scales oval rhomboidal and very diverse in shape of crown; median crown area wedge- or spine-shaped; spiny postero-lateral part of crown; rhomboidal trunk scales with smooth and flat median crown area; postero-lateral wall of crown having either two pairs of longitudinal ridges and one underlying row of spines, one pair of longitudinal ridges and one pair of rows of thornlets or smooth postero-lateral walls; between three and eight lateral spines and one or two posteriorly median spines situated symmetrical near median line; distinct pulp cavity and canal; wide dentine canals diverging from pulp canal to lateral spines. (Modified from Karatajute-Talimaa 1997.)

Species content. *Paralogania kummerowi* (Gross 1967a); *P. borealis* (Karatajute-Talimaa 1978); *P. ludlowiensis* (Gross 1967a); *P. martinssoni* (Gross 1967a).

Range. Early Silurian (Wenlock) – Late Silurian (Pridoli).

Paralogania foliala sp. nov.

Figs 11, 12

Derivation of name. A combination of the Latin words *folium*, for leaf and *ala*, for wing, referring to the leafy appearance of the large lateral wings.

Holotype. Transitional scale; MGUH VP 3462 from GGU sample 82738 (Fig. 11B).

Figured material. Head scales; MGUH VP 3460. Transitional scales; MGUH VP 3461–3463. Trunk scales; MGUH VP 3464–3467. All from GGU sample 82738.

Other material. About 25 scales from GGU sample 82738.

Locality and age. The Halls Grav locality, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian (Pridoli).

Diagnosis. Small loganiid scales with large anteriorly displaced base and posteriorly positioned pulp aperture; large flat crown with triangular, elongated or rhomboidal median area, disturbed anteriorly by one short, deep, median furrow; large lateral wings forming at least three posteriorly pointing spines at same level as a median posteriorly pointing spine; dentine tubules irregular, independent and with homogeneous thickness.

Scale morphology. The morphological set of *Paralogania foliala* sp. nov. includes very small head, transitional and trunk scales which do not exceed 0.4 mm in length.

The most extreme form, probably a head or rostral scale, is round with a large round base, slightly displaced anteriorly (Fig. 11A, D). In the centre of the base, or slightly posterior, a small pulp aperture or depression is visible. The round, heavily ornamented crown is characterized by a flat narrow median part which has one deep median furrow and two short shallow furrows at the anterior margin. The lateral margins of the median area converge centrally, but they run parallel towards the posterior end before they meet. Between the median and the wide lateral crown areas two furrows are developed. These postero-lateral areas or wings are triangular and flat with three apices or spines spreading and pointing postero-laterally. They are on a slightly lower level than the median part and, on account of their delicate nature, are always broken. One median spine is developed on the posterior end of the crown. It lies just below the apex of the median part at the same lower level as the lateral wing. All furrows bend down anteriorly towards the narrow and quite high neck.

Transitional scales are less ornamented and differ from the rostral ones (Fig. 11B, C) in that the median part of the crown is larger and triangular or sector-shaped, still with a deep median anterior furrow. The two flanking furrows, seen in head scales, are less pro-

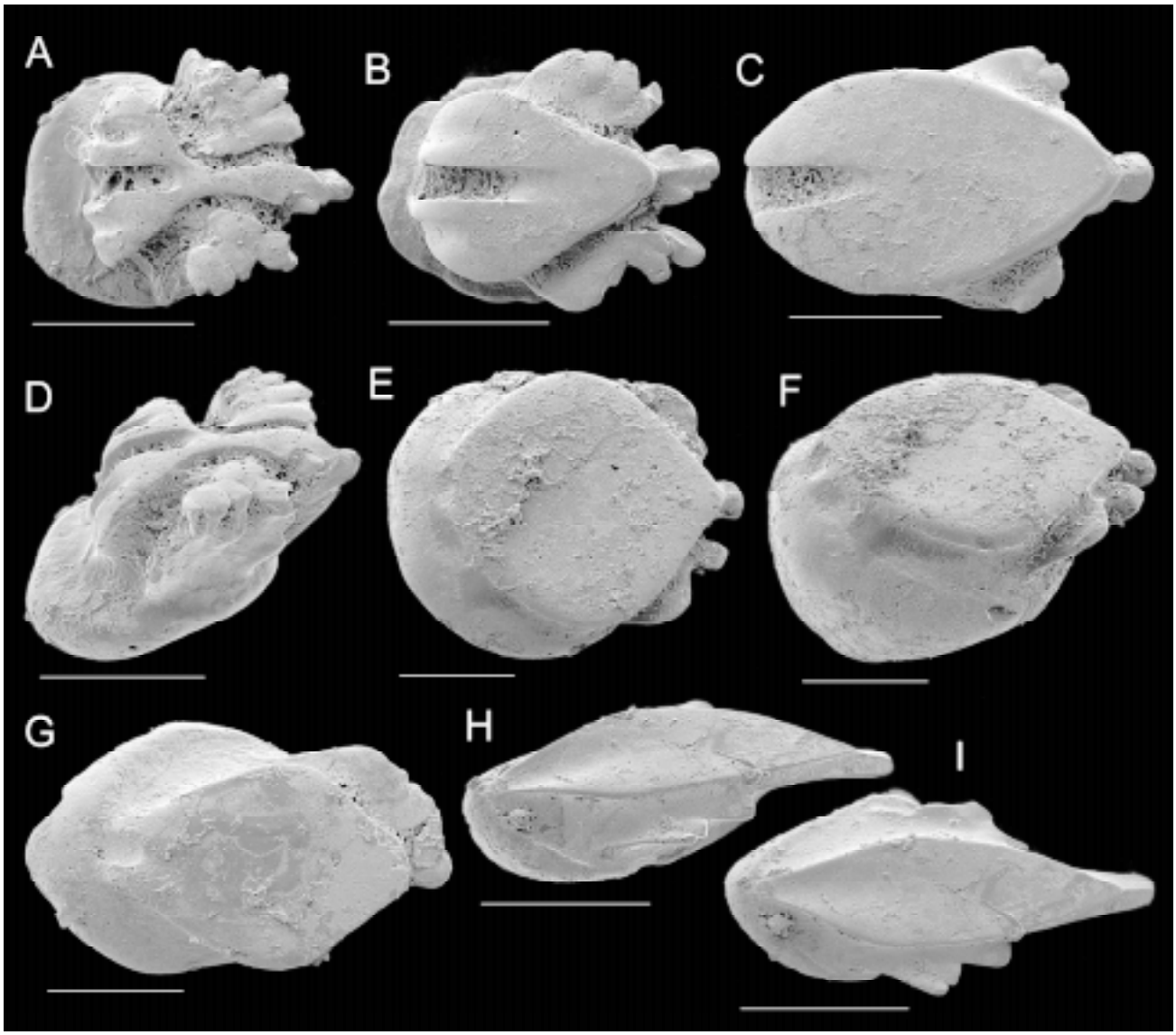


Fig. 11. *Paralogania foliala* sp. nov. SEM photomicrographs. Scale bars equal 0.1 mm.
A: Head scale in crown view, MGUH VP 3460. **B**: Transitional scale in crown view, holotype, MGUH VP 3462. **C**: Transitional scale in crown view, MGUH VP 3463. **D**: Head scale in oblique crown view, MGUH VP 3460. **E**: Trunk scale in crown view, MGUH VP 3464. **F**: Trunk scale in oblique crown view, MGUH VP 3464. **G**: Trunk scale in crown view, MGUH VP 3465. **H**: Trunk scale in oblique crown view, MGUH VP 3466. **I**: Trunk scale in crown view, MGUH VP 3466.
All specimens from GGU sample 82738, Halls Grav.

nounced. In the holotype (Fig. 11B) the median posterior spine preserves a leafy shape. The two lateral wings with spines are still wide.

The general trend, giving a less ornamented crown, continues on the larger more elongated trunk scales, in which the median section is large and round, oval or rhomboidal (Fig. 11E–G). One clear anterior furrow may be present, but it is usually just visible as a small notch. Close to the junction a clear neck is developed between the anteriorly displaced base, with its posterior pulp aperture, and the crown. The lateral wings are usually proportionally smaller.

Scales from the most posterior part or from the fins are small and elongated (Fig. 11H, I). The elongated lenticular median part of the crown is anteriorly slightly concave and bends down towards the oval base, which also is anteriorly displaced with a posterior pulp aperture. The postero-lateral wings are smaller in these scales. On the lower surface of the posterior median spine a sharp ridge or crest is developed.

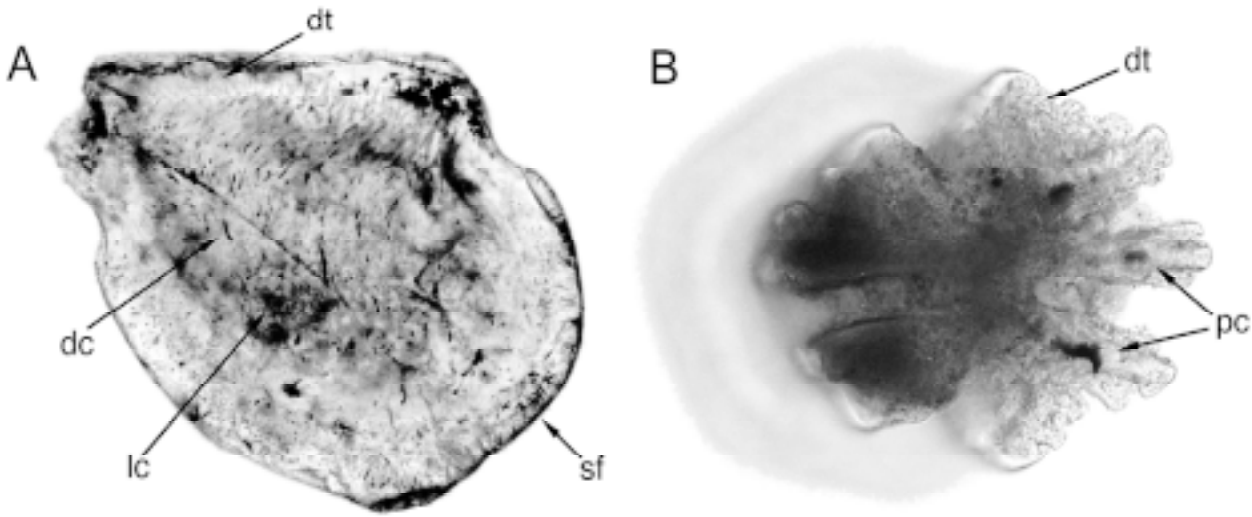


Fig. 12. *Paralogania foliala* sp. nov. Histology of the scales.
A: Trunk scale in vertical longitudinal section, MGUH VP 3467, × 219. **B**: Head scale in crown view, immersed in aniseed oil, MGUH VP 3462, × 362.
Both specimens from GGU sample 82738, Halls Grav.
dc: dentine canals; **dt**: dentine tubules; **lc**: odontoblast joining lacunae; **pc**: pulp canal; **sf**: tubules for Sharpey's fibres.

Scale histology. The dentine tissue in the crown is penetrated by irregular dentine canals and tubules (Fig. 12A). The wider tubules seem to be independent and homogeneous in thickness, seldom converging to greater thickness (it is uncertain from the few available sections if this is a feature of preservation). Several lacuna-like cavities are visible in the very irregular dentine tissue. Some tubules, however, open towards an indistinct short posterior pulp canal, which after branching can be traced into the lateral region (Fig. 12B). The basal tissue with irregular tubules of Sharpey's fibres is quite thin.

Scale dimensions. Length 0.2–0.3 mm; width 0.1–0.3 mm.

Remarks. *Paralogania foliala* sp. nov. is similar to *P. kummerowi* (Gross 1967a), *P. martinssoni* (Gross 1967a) and *P. borealis* (Karatajute-Talimaa 1978), all having one pair of lines or ridges with spines. In *P. foliala* sp. nov. these structures are much more well pronounced, forming a wide spiny wing instead of a weak line of spines. *P. ludlowiensis* (Gross 1967a) differs by usually having one fine ridge above the line of spines. The deep and short anterior crown notch, visible in some scales of *P. foliala* sp. nov. is not found in any of the other *Paralogania* species. The base of *P. foliala* differs from other species of *Paralogania* in not showing the wide anterior basal concavity.

Although it is not generally recommended to designate a transitional scale as a holotype in scale taxonomy, MGUH VP 3462 is selected since it shows the common morphological characters of the whole set of scales, such as the crown sculpture and the lateral wings with spines.

The scales of *Paralogania foliala* sp. nov. follow the same general morphological trends in the crown ornamentation as *Thulolepis striaspina* gen. et sp. nov. with respect to the sector-shaped median area and large spined lateral wings. In detail, however, they are clearly different. The lateral crown part of *Thulolepis striaspina* gen. et sp. nov. is more deeply furrowed with striated spines pointing posteriorly, while in *P. foliala* sp. nov. the lateral part is more developed as a spiny wing with a flat spreading leaf-like outline. Histological structures and base morphology of *P. foliala* sp. nov. show a close relationship with known loganiids, and especially with other species of *Paralogania* (Karatajute-Talimaa 1997). The lateral wing-like structures in *P. foliala* sp. nov. are much more pronounced and specialized than in other loganiids, but there is no further justification to establish a new genus. Histologically it shows *Paralogania* affinity, by having narrow pulp canals extending into the postero-lateral spines.

The small size and similar gross morphology promotes discussion of the squamation pattern and the relationship between *P. foliala* sp. nov. and *T. striaspina* gen. et sp. nov. The morphology may reflect a specific position on the trunk of the living animal which is

already represented among the other scale sets from the Chester Bjerg Formation. In effect this would mean that *P. foliala* sp. nov. is a specific type of scale from one of the other loganiids, while *T. striaspina* sp. nov. comes from the same position on a related thelodontid such as *Nikolivia* or *Canonia*. This idea is rejected on account of the wide variety of different forms within each morphological set for both mentioned taxa, but it can only be truly answered by new finds of articulated material.

Occurrence. Lochkovian, Halls Grav, Hall Land, North Greenland.

Genus *Praetrilogania* gen. nov.

Derivation of name. From the Latin word *praeter*, meaning 'beyond' or 'more than', referring to the extension of the loganiid group, and the former generic name *Logania*.

Type species. Praetrilogania grabion gen. et sp. nov.

Diagnosis. Small loganiid scales with heavily ridged and furrowed crown, wider posteriorly; oval crown, often inflated, with 3–5 posteriorly pointing apices or spines; narrow median part of crown furrowed along almost the whole length; anteriorly displaced base, smaller than crown; irregular dentine tubules converge repeatedly towards canal thickness and large joining lacunae, 1–5 pulp canals extend toward 1–5 apices.

Range. Late Silurian – Early Devonian (Pridoli–Lochkovian).

Remarks. *Praetrilogania* has a histological structure which is typical for scales placed within the family Katoporidae. Like *Goniporus* and *Katoporodus* it has irregular dentine tubules that often converge to almost canal thickness and up to five pulp canals. *P. grabion* gen. et sp. nov., however, differs notably by not having canal or tubule openings on the mature base and especially by its inflated crown.

Praetrilogania grabion gen. et sp. nov.

Figs 13–16

1978 *Thelodus trilobatus* – Bendix-Almgreen, fig. 443A.

1986 *Thelodus trilobatus* – Turner & Peel, p. 82, fig. 2E.

1986 *Turinia* sp. – Turner & Peel, p. 83, fig. 4.

Derivation of name. From *grabion*, the Latin word for torch, in reference to the torch-like appearance of some of the specialized head scales.

Holotype. Trunk scale; MGUH VP 3478 from GGU sample 82738 (Fig. 13K, L; Fig. 15.15).

Paratypes. Head scales; MGUH VP 3469, 3471, 3472, 3492, 3493 (Fig. 13B, C, I; Fig. 14I; Fig. 15.3, 4, 7; Fig. 16A, B). Trunk scales; MGUH VP 3473, 3475–3477, 3480, 3481, 3485 (Fig. 13D, F–H, J; Fig. 14D, E; Fig. 15.5, 8, 12, 14; Fig. 16C, D). Scales from tail or fins. MGUH VP 3486–3488, 3490 (Fig. 14A–C, H; Fig. 15.16–18, 21). All from GGU sample 82738.

Figured material. Head scales; MGUH VP 3468 from GGU sample 319264, MGUH VP 3469–3472, 3492, 3493 from GGU sample 82738. Trunk scales; MGUH VP 3473–3478, 3480, 3481, 3485 from GGU sample 82738, MGUH VP 3479, 3482–3484 from GGU sample 319264; Scales from tail or fins. MGUH VP 3486–3488, 3490 from GGU sample 82738, MGUH VP 3489, 3491, 3494 from GGU sample 319264.

Other material. About 300 well-preserved specimens have been studied from GGU samples 82734, 82736, 82738, 298937 and 319264.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Diagnosis. As for the genus.

Scale morphology. *Praetrilogania grabion* gen. et sp. nov. is represented by a morphological set of scales with many varieties (Figs 13–16). The scales are relatively small and do not exceed 1 mm in length. Depending on which sample the scales come from, the colour varies from dark brown to white. They are usually well preserved and only the delicate posterior edge of the crown is repeatedly broken. Scales of all varieties seem most often to be mature, since the base is inflated and the pulp aperture usually is small.

The head scales of *P. grabion* gen. et sp. nov. are morphologically quite variable. The simplest type has

a low round base and a high inflated round crown (Fig. 13A; Fig. 15.1, 2). In crown view, the scale is almost radially symmetrical and is heavily notched by furrows and ridges. Eight ridges run laterally from a narrow neck towards a meeting point in the central part of the upper crown surface. A distinct, but low, neck is formed near the base, which is low and round with a central pulp cavity. The inflated crown gives the entire scale a balloon-shaped appearance. Some scales are more bilaterally symmetrical, with the base slightly displaced anteriorly and with a small anterior basal process (Fig. 13B; Fig. 15.3). The meeting point for the lateral ridges is more posterior on the upper crown surface. This type may represent a more posterior location or specialized head scales, e.g. around the eye.

Another similar but round and inflated scale type is slender with up to ten lateral ridges (Fig. 13I; Fig. 14I; Fig. 15.7). The majority of the ridges meet in a central upper crown point or apex, but some of them, instead of meeting centrally, tend to form three smooth extensions or spines on each crown. The base is low with a slightly posterior wide pulp cavity and has a long slender basal process. Morphologically, this scale type looks like a burning torch and has motivated the specific name. This kind of ornamentation may indicate a position on the dorsal side of the head.

Less ornamented similar scales without the spines and with a slightly flattened crown, show a smoother morphology that suggests a ventral head squamation (Fig. 13C; Fig. 15.4). This scale type also has a more robust anterior process and more swollen base.

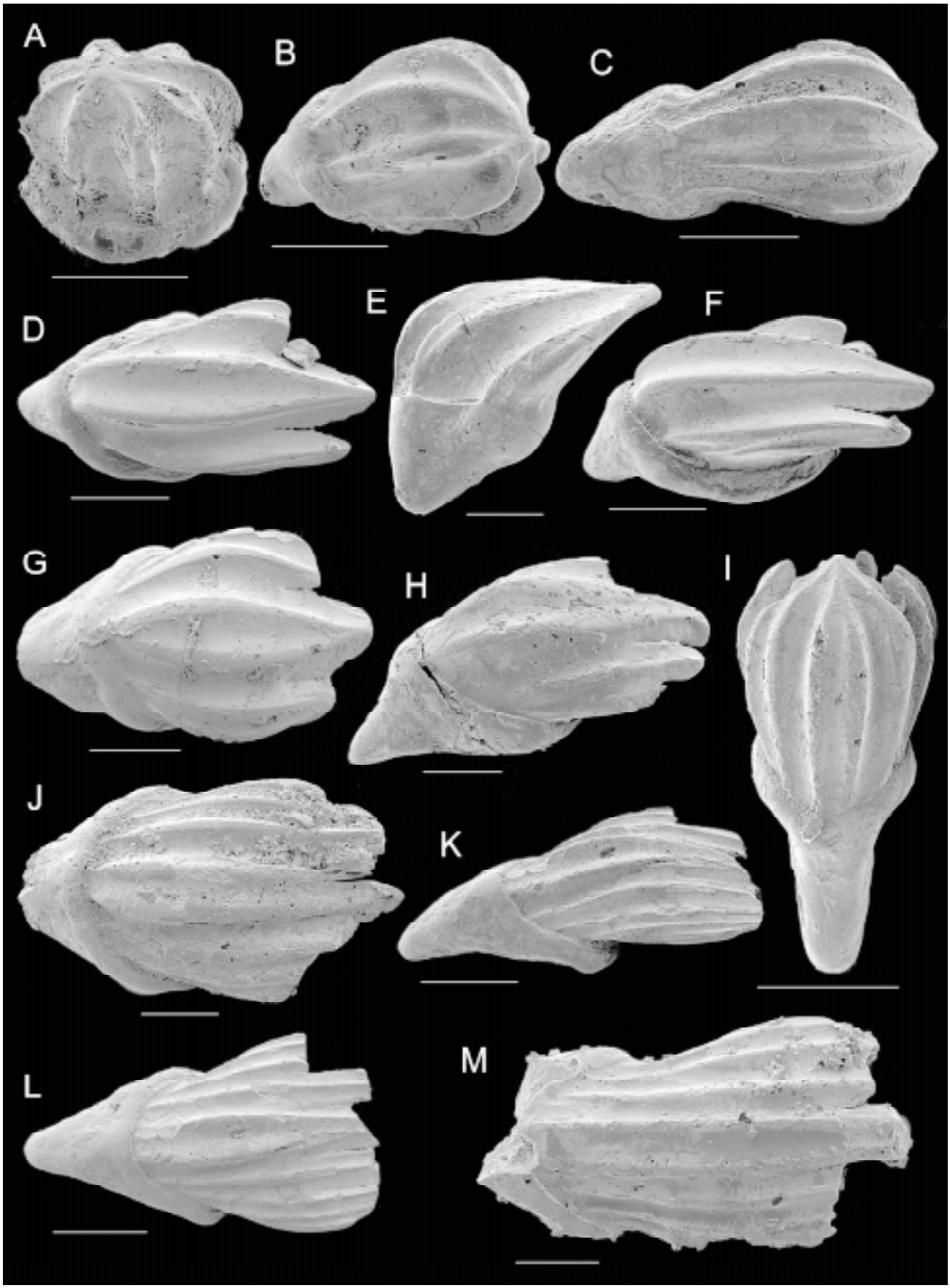
A general morphological trend with anteriorly displaced base and pulp aperture continues backward on the body (Fig. 13D–H; Fig. 15.5, 6, 8–10, 12). With these changes follows a flattening of the crown, which is oval or elongated and divided into three distinct parts; the median (wide central ridge) and the paired lateral ones. The crown is wider posteriorly and each part of the crown ends posteriorly as separated apices. They are almost always broken, however, which makes the true form of the apices uncertain. From the sharp narrow neck the distinct lenticular median part of the crown runs backwards converging on the median apex. The median part, which has a wide shallow furrow along almost its full length, is usually widest centrally. Characteristic for the lateral crown area is one or usually two ridges that run parallel towards the lateral apices. Between each ridge deep and wide intermediate furrows are developed, bent down anteriorly towards the base. The furrow closest to the median part is always wider than the outer ones. Smooth rounded ridges run from the base towards each apex on the lower side of the crown.

More specialized trunk scales of *P. grabion* gen. et sp. nov. differ mainly from previous scales by the presence of an extra lateral ridge on each side of the median crown area, followed by an increased number of apices to the total of five (Fig. 13J–M; Fig. 15.13–15). An extra pair of ridges may also occur on the lower side.

Scales from the tail are more elongated with a smoother upper side of the crown (Fig. 14A–C; Fig. 15.16–19). The crown is still wider posteriorly and ends as a smooth rounded margin and not in 3–5 apices. The median part of the crown is wider more anteriorly and the furrow is less deep. On each lateral part of the crown wide shallow furrows run parallel with one to two lateral ridges. The lower side of the crown is convex and smooth, sometimes with a sharp median crest. Displaced posteriorly is the very small pulp aperture and the convex base has sometimes developed a basal process.

Possible fin scales are small with a crown also divided into three parts (Fig. 14G, H; Fig. 15.20, 21). The lenticular median part is furrowed and converges towards a sharp posterior apex. The flanking lateral parts are characterized by a wide and anteriorly steeply down-bending furrow between the median part and a smooth margin or marginal ridge, which when present seems to follow the margin all the way towards the posterior apex. A median crest often occurs on the smooth lower crown surface. The pulp aperture is posteriorly displaced while the basal process, when present, points anteriorly.

Fig. 13. *Praetrilogania grabion* gen. et sp. nov. SEM photomicrographs. Scale bars equal 0.1 mm.
A: Head scale in oblique crown view, MGUH VP 3468. **B**: Head scale in lateral view, MGUH VP 3469. **C**: Head scale in crown view, MGUH VP 3471. **D**: Trunk scale in crown view, MGUH VP 3473. **E**: Trunk scale in antero-lateral view, MGUH VP 3474. **F**: Trunk scale in oblique crown view, MGUH VP 3473. **G**: Trunk scale in crown view, MGUH VP 3475. **H**: Trunk scale in oblique crown view, MGUH VP 3476. **I**: Head scale in crown view, MGUH VP 3472. **J**: Trunk scale in crown view, MGUH VP 3477. **K**: Trunk scale in oblique crown view, holotype, MGUH VP 3478. **L**: Trunk scale in crown view, holotype, MGUH VP 3478. **M**: Trunk scale in crown view, MGUH VP 3479.
MGUH VP 3468, 3479 from GGU sample 319264, Monument; MGUH VP 3469, 3471–3478 from GGU sample 82738, Halls Grav.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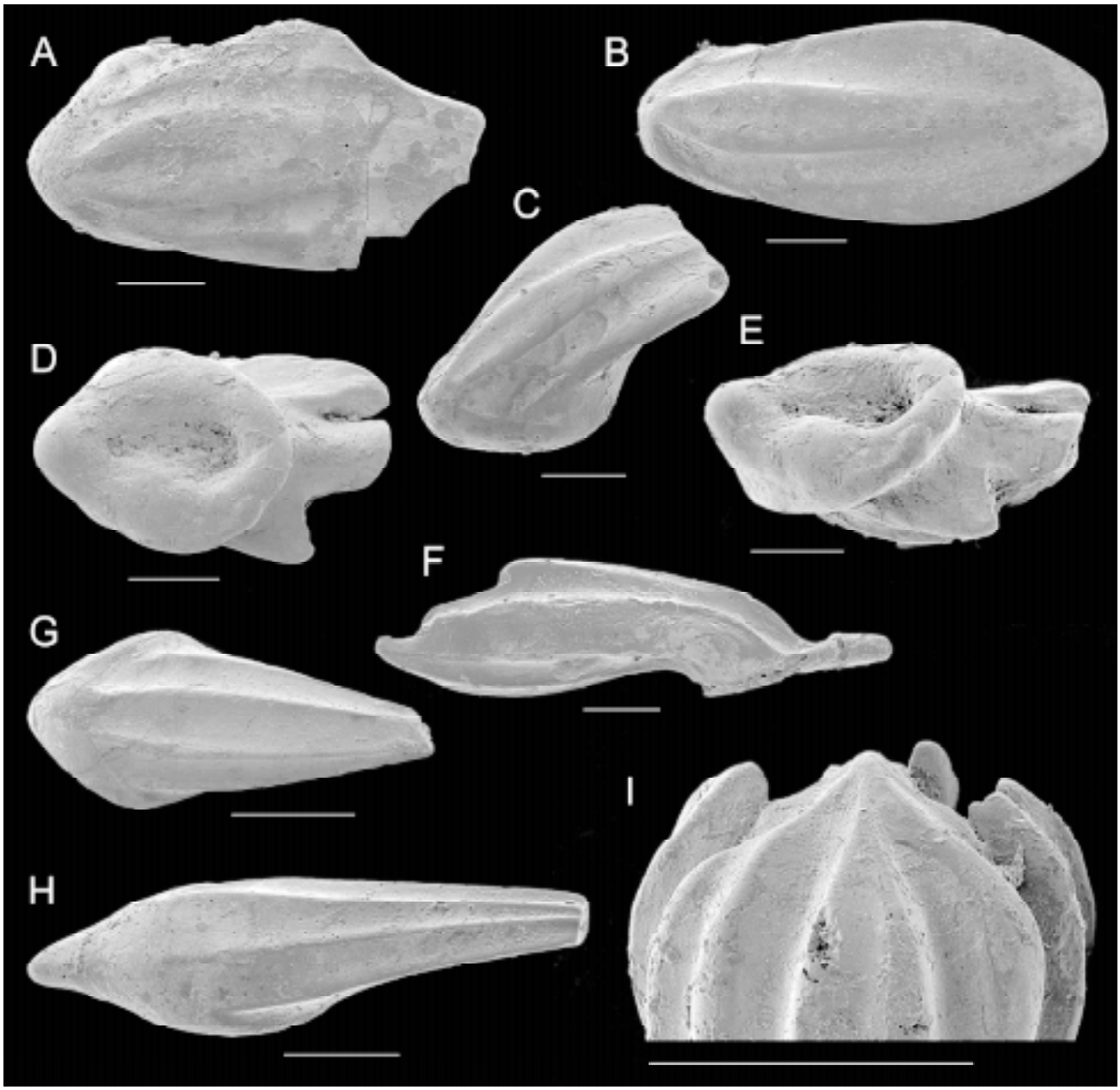


Fig. 14. *Praetrilogania grabion* gen. et sp. nov. SEM photomicrographs. Scale bars equal 0.1 mm.
A: Scale from fin or tail in crown view, MGUH VP 3486. **B**: Scale from fin or tail in crown view, MGUH VP 3487. **C**: Scale from fin or tail in oblique crown view, MGUH VP 3488. **D**: Trunk scale in basal view, MGUH VP 3485. **E**: Trunk scale in oblique basal view, MGUH VP 3485. **F**: Scale from a fin edge? in lateral view, MGUH VP 3494. **G**: Scale from fin or tail in crown view, MGUH VP 3489. **H**: Scale from fin or tail in oblique crown view, MGUH VP 3490. **I**: Head scale in crown view, close up on posterior crown edge, MGUH VP 3472.
MGUH VP 3472, 3485–3488, 3490 from GGU sample 82738, Halls Grav; MGUH VP 3489, 3494 from GGU sample 319264, Monument.

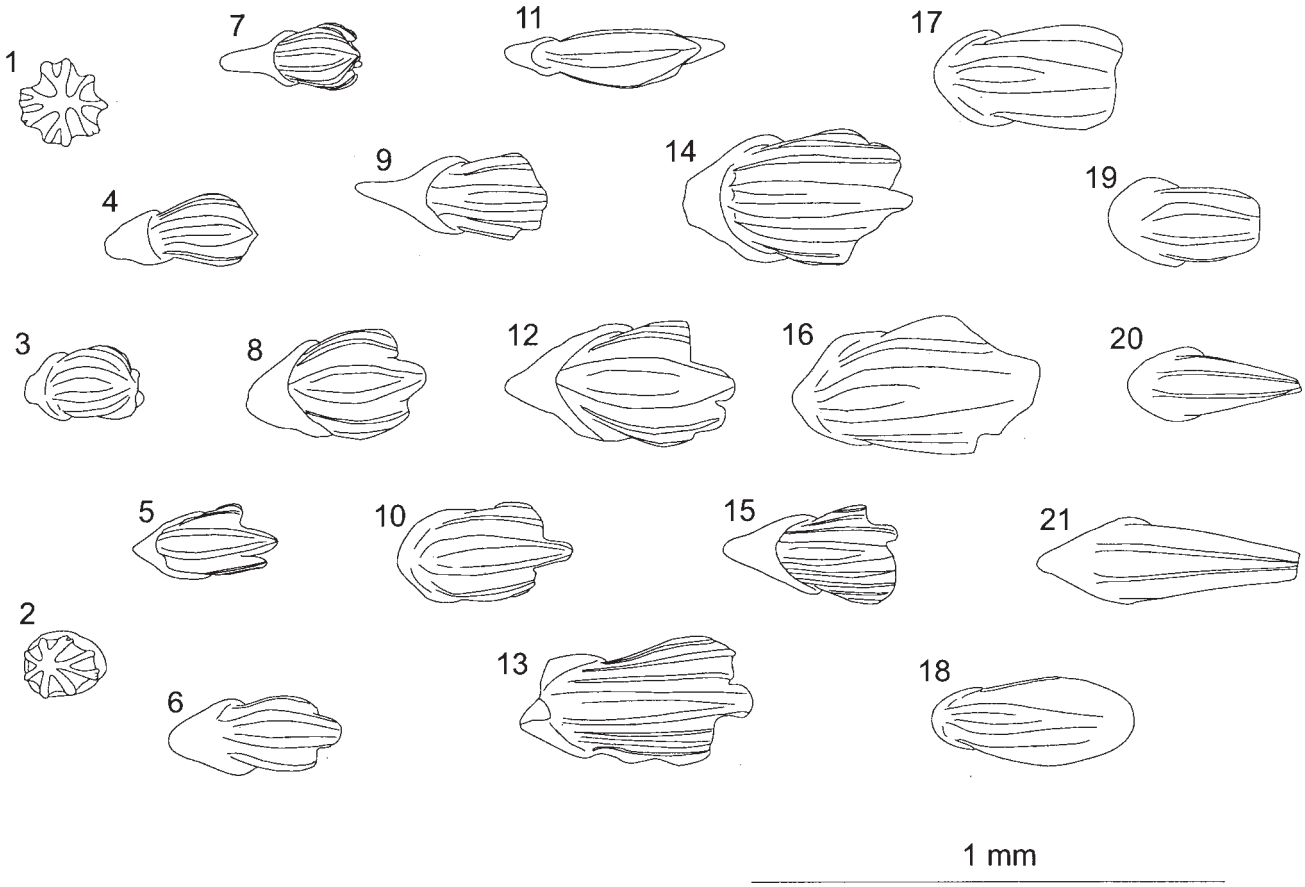


Fig. 15. *Praetrilogania grabion* gen. et sp. nov. The main morphological scale varieties in crown view.
1: Head scale, MGUH VP 3470. **2**: Head scale, MGUH VP 3468. **3**: Head scale, MGUH VP 3469. **4**: Head scale, MGUH VP 3471. **5**: Trunk scale, MGUH VP 3473. **6**: Trunk scale, MGUH VP 3482. **7**: Head scale, MGUH VP 3472. **8**: Trunk scale, MGUH VP 3475. **9**: Trunk scale, MGUH VP 3484. **10**: Trunk scale, MGUH VP 3483. **11**: Scale from a fin edge?, MGUH VP 3494. **12**: Trunk scale, MGUH VP 3476. **13**: Trunk scale, MGUH VP 3479. **14**: Trunk scale, MGUH VP 3477. **15**: Trunk scale, holotype, MGUH VP 3478. **16**: Scale from a fin or tail, MGUH VP 3486. **17**: Scale from a fin or tail, MGUH VP 3488. **18**: Scale from a fin or tail, MGUH VP 3487. **19**: Scale from a fin or tail, MGUH VP 3491. **20**: Scale from a fin or tail, MGUH VP 3489. **21**: Scale from a fin or tail, MGUH VP 3490. MGUH VP 3468, 3479, 3482–3484, 3489, 3491, 3494 from GGU sample 319264, Monument; MGUH VP 3469–3473, 3475–3478, 3486–3488, 3490 from GGU sample 82738, Halls Grav.

There is one abnormal and unusual scale which might be from a fin edge (Fig. 14F; Fig. 15.11). It is long and very slender, with an extremely small base. From the base a proportionally enormous crown points backwards like an elongated balloon which thickens posteriorly. A very high central dorsal ridge runs from the narrow sharp neck to a point 3/4 of the length posterior from the base. Two smooth lateral ridges on each side extend to the posterior end where two thin ventral ridges extend to a posterior apex. Attached to the base is a large, probably broken or worn, anteriorly pointing basal process.

Scale histology. Histologically the scales are of typical katoporid type (Fig. 16). The dentine tissue is characterized by frequently branching dentine tubules or canals. Distally, in the outermost layer, dentine tubules are straight and parallel. In the next growth layer they start to converge and join to thicker tubules. This continues proximally towards the basal tissue, where the tubules have reached almost canal thickness. Most known scales are mature and have a very dense basal tissue with many irregularly oriented Sharpey's fibres. Only the larger posterior pulp canal is capable of penetrating the posterior part of the basal tissue. Some dentine tubules in the posterior part of the scale pass directly into the pulp canal which branches towards each posteriorly pointing apex. The other canals and tubules end towards the basal tissue, where they join and form larger lacunae-like cavities. In younger scales it is possible to see how finer tubules and canals pass into the shallow pulp cavity. Also in younger scales,

but less frequently, smaller lacunae are visible which are formed at the junction of branching dentine tubules and canals. Scales with a displaced base have a concentration of tubules of Sharpey's fibres in this anterior swelling.

A pulp canal is not developed in most head scales and therefore dentine tubules pass directly into a central pulp cavity. The outer layer, representing the initial cap, is usually distinct while growth lines of other layers are more difficult to detect.

Scale dimensions. Length 0.2–0.5 mm; width 0.1–0.3 mm (the total length given is less than the true, since the scales are almost always broken posteriorly).

Remarks. Trunk scales of *Praetrilogania grabion* gen. et sp. nov. are morphologically similar to those on the articulated thelodont *Shielia taiti* (Märss & Ritchie 1998). Also scales from the tail and the fins have their equivalents in both types. *Shielia taiti*, however, lacks the round inflated scales from the head region seen in *Praetrilogania grabion* gen. et sp. nov. The affinity of these scales can only be supported by comparison to the head scales of e.g. *Turinia* Traquair 1896 (Karatajute-Talimaa 1978; Turner 1986; Turner & Young 1992; Turner *et al*. 1981; Märss & Ritchie 1998). Head scales of *P. grabion* gen. et sp. nov. are in gross morphology quite similar to *Turinia*, as suggested by Turner & Peel (1986), but cannot be placed within this histologically completely different group. Included in this set are also the trunk scales earlier described by Turner & Peel (1986) as *Thelodus trilobatus*.

The most posterior trunk scales of *L. almgreeni* sp. nov. are also similar to some scales of *P. grabion* gen. et sp. nov. They differ, however, notably by lacking clear long furrows in the median part of the crown. Scales of *P. grabion* gen. et sp. nov. are generally wider in the posterior part of the crown while scales of *L. almgreeni* sp. nov. are wider closer to the centre. The base is also higher in *L. almgreeni* sp. nov. When both taxa occur together, it can be difficult to separate some of the most posterior trunk scale types. The notion that *P. grabion* gen. et sp. nov. is a separate taxon is also supported by its presence in several samples from the Halls Grav locality which do not contain scales of *L. almgreeni* sp.nov.

Occurrence. Pridoli–Lochkovian, Hall Land, North Greenland.

Order Thelodontida Kiær 1932
Family Nikoliviidae Karatajute-Talimaa 1978

Genus *Nikolivia* Karatajute-Talimaa 1978

Type species. *Thelodus oervigi* Karatajute-Talimaa 1968; Early Devonian (Lochkovian, D1), Ivanev horizon, sections Dobrovljany, Bedrikovtzy (upper part), Zaleschiki (lower part), Pechora (lower part), Ivane-Zolotoe (lower part), Podolia, Ukraine.

Diagnosis. Large and medium sized scales; trunk scales large with flat leaf-like, elongated, oval or wedge-liked crown, covered with longitudinal ridges; crowns often with slightly raised median area; longitudinal ridges developed on lateral areas of different width; anterior border rounded with slightly anteriorly displaced median part; posteriorly wedge-like and monolithic or split into three apices; central apex much longer than lateral; postero-lateral borders of crown smooth or slightly notched; lower crown surface smooth, flat and convex; crown of head scales high and short with thorn-like lifted end; crown of transitional scales relatively short and wide; neck on all scales low and recognisable as compact furrow; base relatively small, two to four times smaller than crown, low, round and oval, anteriorly located; pulp cavity large, wide and low with long posteriorly extending pulp canal; crown with branched, straight or slightly curved dentine tubules opening into pulp cavity and canal; proximal part of dentine tubules slightly enlarged. (Translated and modified from Karatajute-Talimaa 1978.)

Species content. *Nikolivia oervigi* (Karatajute-Talimaa 1968); *N. balabayi* Karatajute-Talimaa 1978; *N. elongata* Karatajute-Talimaa 1978; *N. gutta* Karatajute-Talimaa 1978; *N. milesi* Turner 1982.

Range. Early Devonian (Lochkovian–Pragian).

***Nikolivia* sp.**
Fig. 17E–L; Fig. 18B, C

Figured material. MGUH VP 3495 from GGU sample 298937, MGUH VP 3496–3501 from GGU sample 82738.

Other material. About 25 scales from GGU samples 82736, 82738, 298937 and a questionable occurrence from GGU sample 319264.

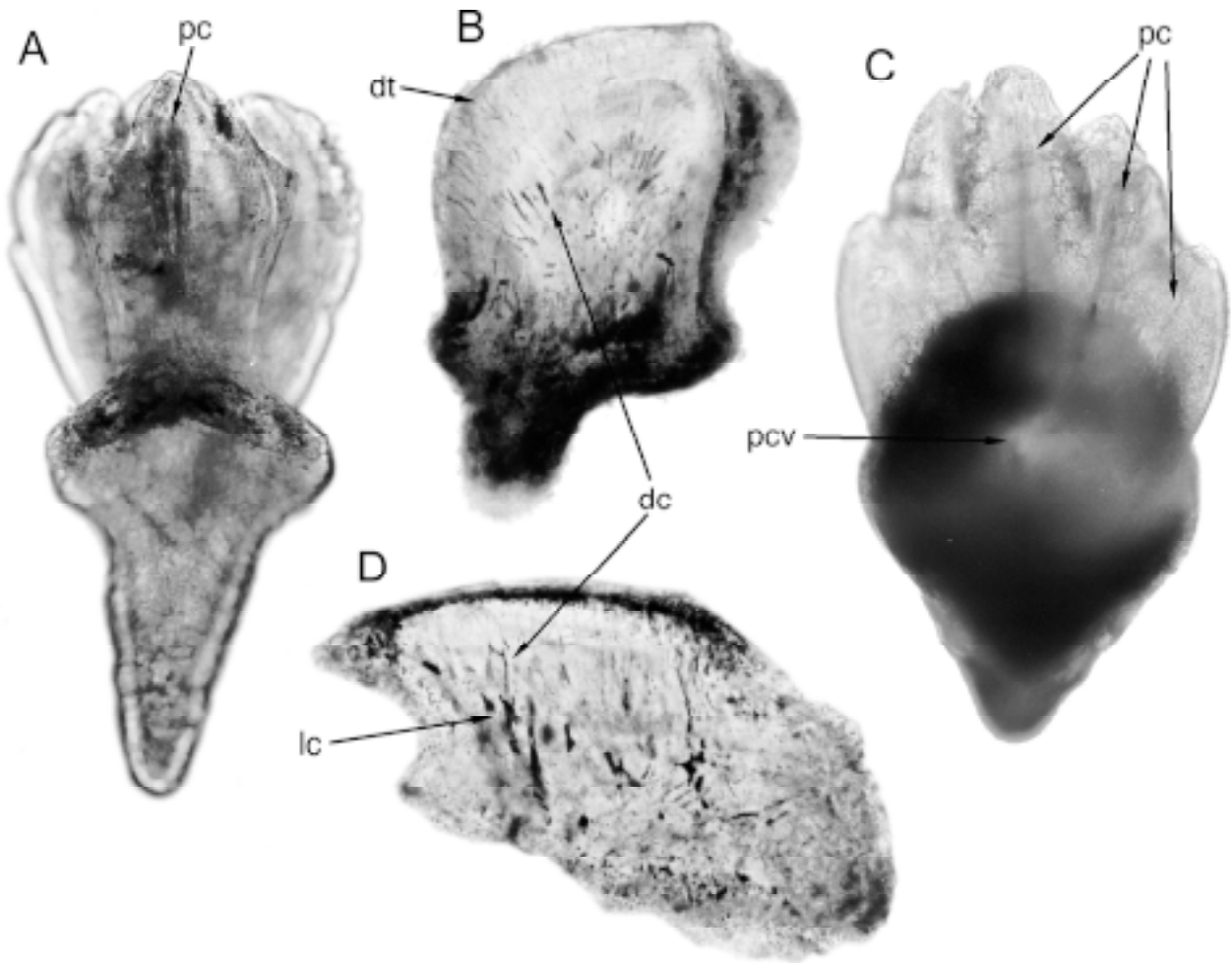


Fig. 16. *Praetrilogania grabion* gen. et sp. nov. Histology of the scales.
A: Head scale in crown view, immersed in aniseed oil, MGUH VP 3492, × 304. **B**: Head scale in vertical longitudinal section, MGUH VP 3493, × 184. **C**: Trunk scale in basal view, immersed in aniseed oil, MGUH VP 3480, × 175. **D**: Trunk scale in vertical longitudinal section, MGUH VP 3481, × 199.
All specimens from GGU sample 82738, Halls Grav.
dc: dentine canals; **dt**: dentine tubules; **lc**: odontoblast joining lacunae; **pc**: pulp canal; **pcv**: pulp cavity.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Scale morphology. This morphological set of nikoliviid scales is variable and may not reflect a single taxon. The low number of scales found also makes it difficult to define a consistent set and the nomenclature is therefore best left open.

A few rounded scales, presumably from the head region, have been found (Fig. 17G). They have a short crown that rises with a quite steep angle towards a posterior apex. The median area of the crown is smooth, narrow and wedge-shaped, and bends down anteriorly towards the base. The median crown area is usually flanked on the lateral sides by two pairs of lateral crown ridges or wings that run towards a weakly developed or non-existent neck. The upper one, closest to the median part, is more pronounced and wing-like. A wide open pulp cavity is visible on the typical round base.

The next scale type is less thorn-like with lower inclination of the crown (Fig. 17E, F). The median crown area is wider in the rounded anterior part and joins the base; there is no neck at this point. A larger lateral wing or ridge runs from mid-length of the base towards the posteriorly pointing apex. The apex forms the meeting point of the margins of the median part and the less pronounced lateral ridges.

One type of trunk scale is larger and more elongated, but similar to the previous one (Fig. 17H, I). The oval median crown region is proportionally very large and wide, with a flat and smooth upper surface, anteriorly meeting the base without an intervening neck. From the posterior pointing apex one pair of lateral ridges or wings runs towards the oval base, which is large and quite swollen.

A fourth scale type is shorter and more robust, with a wide slightly convex median crown area (Fig. 17J). The anterior part of the median area, which curves slightly towards the base, is slightly notched or furrowed. Laterally only one pair of wide ridges or wings is developed. This scale type, which has an oval base and low inclination of the crown, can be regarded as a typical trunk scale.

Scales from a more posterior position are elongated with a narrow concave or furrowed median crown area (Fig. 17K, L). Their size is variable and reflects their position, such that smaller scales of this type had a more posterior location. The whole crown is covered by longitudinal ridges that converge towards a posteriorly pointing apex, that includes the margin of the median crown part, as well as two or three pairs of lateral ridges. No distinct neck is developed between the crown and the elongated base, which has a wide open, or slit-shaped, aperture.

Scale histology. When immersed in aniseed oil, these scales show a typical nikoliviid histology (Fig. 18B, C). The studied young scales show a large wide pulp cavity and a pulp canal which extends posteriorly towards the crown apex. Branched, straight or slightly curved dentine tubules or canals open into the main cavity or canal. The tubules are slightly enlarged proximally towards the pulp cavity and canal.

Scale dimensions. Length 0.3–0.8 mm; width 0.2–0.5 mm.

Remarks. Problems concerning the validity of different species of *Nikolivia* were discussed by Turner (1982) in connection with her description of an articulated thelodont bearing scales that resemble different described species.

Scales of *Nikolivia* sp. from North Greenland are variable and types within this set may belong to several different species. The scale type here referred to as the most posterior one is quite similar to the holotype of *N. elongata* (Karatajute-Talimaa 1978). The other types, on the other hand, find no exact equivalent among the original set. Some of the larger scales with a large, flat, median region are also comparable to *Nikolivia gutta* Karatajute-Talimaa 1978, but have slightly larger and different lateral wings. *N. gutta* and *N. elongata* have been found together at several different localities (Karatajute-Talimaa 1978; Turner 1982) but in the absence of evidence to the contrary, the available Greenland material is all placed in *Nikolivia* sp.

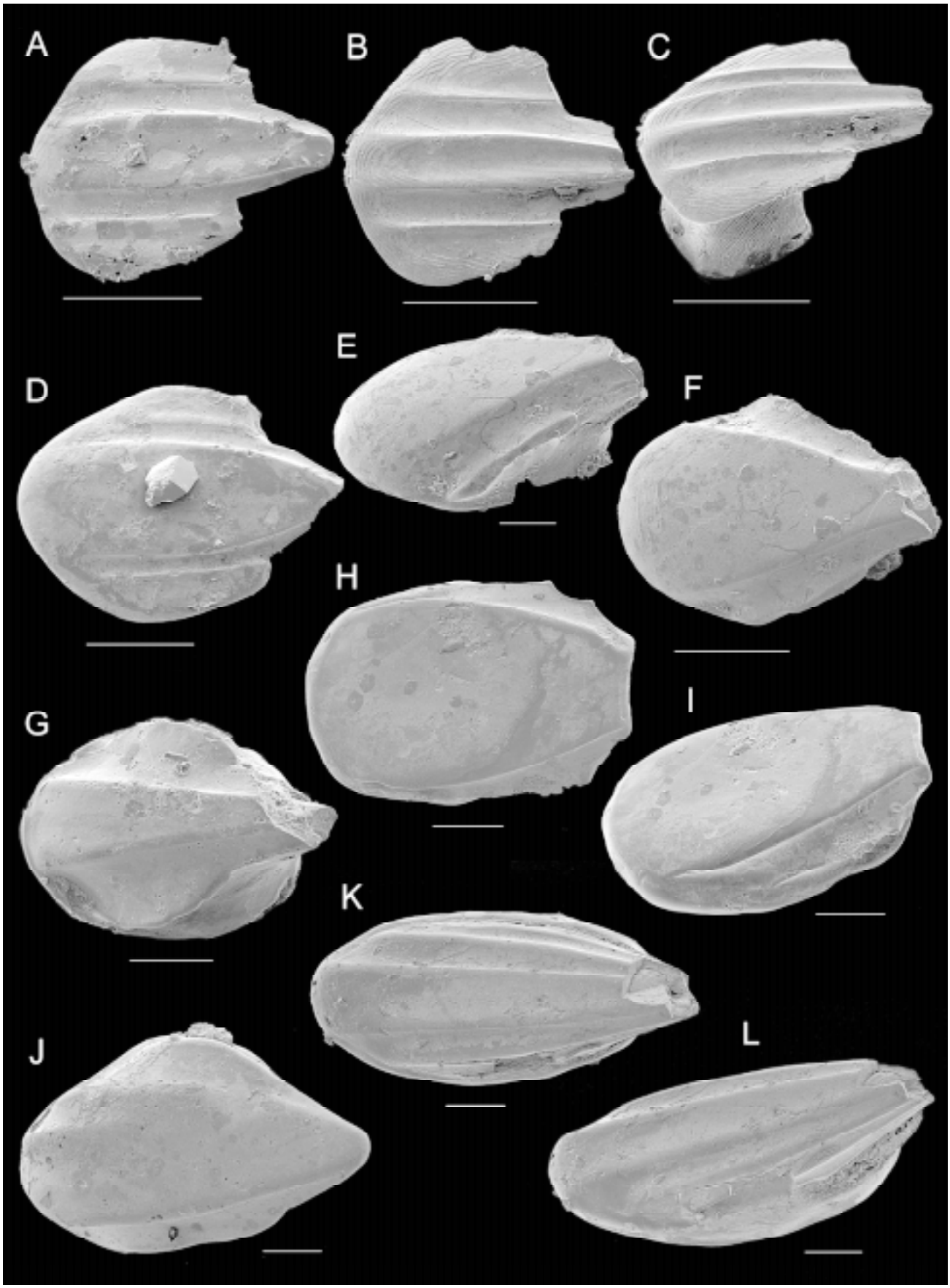
Occurrence. Pridoli-Lochkovian, Hall Land, North Greenland.

Genus *Canonia* Vieth 1980

Type species. *Canonia grossi* Vieth 1980; Early Devonian (Lochkovian–Pragian), Member A, Red Canyon River Formation, Ellesmere Island; Drake Bay Formation, Prince of Wales Island; Member C, Stallworthy Formation, Axel Heiberg Island; all from Arctic Canada.

Diagnosis. Small, symmetrical, thelodontid scales with a small round to oval base and narrow neck; flat crown, round to oval, with three posteriorly pointing apices; wide median crown area flanked by horizontal lateral area with 0–2 longitudinal ridges or furrows, alternatively flat crown with 4–8 longitudinal ridges; anastomosing almost straight branching dentine tubules all radiate from pulp cavity; locally, mainly proximally, dentine tubules converge and join to canal thickness;

Fig. 17. *Canonia* cf. *C. grossi* and *Nikolivia* sp. SEM photomicrographs. Scale bars equal 0.1 mm.
A–**D**. *Canonia* cf. *C. grossi*. **A**: In crown view, MGUH VP 3502. **B**: In crown view, MGUH 3503. **C**: In oblique crown view, MGUH VP 3503. **D**: In crown view, MGUH VP 3504.
E–**L**. *Nikolivia* sp. **E**: Transitional scale in oblique crown view, MGUH VP 3495. **F**: Transitional scale in crown view, MGUH VP 3495. **G**: Head scale in crown view, MGUH VP 3496. **H**: Trunk scale in crown view, MGUH VP 3497. **I**: Trunk scale in oblique crown view, MGUH VP 3497. **J**: Trunk scale in crown view, MGUH VP 3498. **K**: Trunk scale in crown view, MGUH VP 3499. **L**: Trunk scale in oblique crown view, MGUH VP 3499.
MGUH VP 3495 from GGU sample 298937, Halls Grav; MGUH VP 3496–3499 from GGU sample 82738, Halls Grav; MGUH VP 3502–3504 from GGU sample 319264, Monument.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posteriorly, long dentine tubules or canals extend from pulp cavity towards crown. (Translated and modified from Vieth 1980.)

Range. Early Devonian (Lochkovian–Pragian).

Remarks. The original description of *Canonia* was based on a uniform group of disarticulated thelodont scales. This monospecific genus is defined by the small base and narrow neck together with the anastomosing almost straight dentine tubules, which all radiate from the pulp cavity. Following histological examination, Vieth (1980) considered *Canonia* to be of *Thelodus*-type, following Gross' (1967a) classification. Following Turner (1991), *Canonia* should be included with *Thelodus*, *Turinia*, *Apalolepis*, *Nikolivia* and others in the thelodontid histological group. *Canonia* was originally placed closest to *Nikolivia* within the family Nikoliviidae, due to the round base, overlying crown with parallel ridges and relatively straight dentine tubules or canals (Vieth 1980). Such a connection, however, is difficult to discern if one considers their diagnostic features. A small round base, narrow neck and a flat posteriorly overlying crown are characters commonly observed in *Apalolepis*. This genus, placed within another family, Apalolepidae, differs notably by having a much more delicate crown morphology. Also the histology differs in *Canonia* by having anastomosing dentine tubules and canals and by not having more than one pulp canal and curved dentine tubules. These diagnostic histological features, however, are not supported by *Canonia* scales from Severnaya Zemlya Archipelago (V. Karatajute-Talimaa, personal communication 1999). The taxonomical treatment of *Canonia* has been further complicated by new finds of articulated jawless vertebrates with thelodont scales from the Silurian and Devonian of northern Canada (Caldwell & Wilson 1995; Wilson & Caldwell 1998). Based on this new order of 'fork-tailed' agnathans, the Furcacaudiformes, Wilson & Caldwell (1998) suggest that *Canonia grossi* and other nikoliviids are found in several different genera, classified by body morphology, and thereby are not diagnostic of any particular species or genus of furcacaudiforms. They also suggest that scale-based species with furcacaudid affinity should be treated with form taxonomy, parallel to the taxonomy based on articulated specimens. It should, however, be noted that the morphological varieties of scales of furcacaudids so far is weakly characterized and many questions about the relationship between these two types of taxonomy still remain.

***Canonia* cf. *C. grossi* Vieth 1980**
Fig. 17A–D; Fig. 18A

1980 *Canonia grossi* n. gen., n. sp. Vieth, pp. 28–32, fig. 18A–H; plate 3, fig. 1–8.
1988 *Canonia* sp. – Turner & Murphy, p. 959, figs 1.22, 23, 29–34.
1993 Unnamed specimens Wilson & Caldwell, fig. 1f, g.

Holotype. *Canonia grossi*, GSC 202, juvenile scale (Vieth 1980, plate 3, fig. 1a–c), Member A, Red Canyon River Formation, Ellesmere Island, Canada.

Figured material. MGUH VP 3502–3505 from GGU sample 319264.

Other material. About 15 scales from GGU sample 319264.

Locality and age. The top of Monument, Hall Land, North Greenland, Chester Bjerg Formation, Early Devonian (Lochkovian).

Diagnosis. As for the genus.

Scale morphology. The present scales of *Canonia* cf. *C. grossi* are very small and fragile, with an average size of about 0.2 mm. Nevertheless, they are well preserved and only broken at the most delicate posterior part of the crowns. Most scales seem not to be etched or water-worn and they are pale brown in colour. Two general scale types have been found of this uniform species each with a small round base, a narrow neck and a round to oval crown with three posteriorly pointing apices. The first type has a flat crown with a wide, smooth longitudinal median part which is on a slightly higher level than the horizontal lateral parts of the crown (Fig. 17D). Starting anteriorly, the margins of the median area converge to a posteriorly pointing median apex. The lateral areas, which are relatively small in the first scale type, have one pair of longitudinal ridges continuing to two lateral apices, but they are almost always broken. The second, slightly smaller, scale type differs by having a narrower median area with one wide and shallow longitudinal furrow (Fig. 17A–C). The longitudinal ridges are slightly higher on the proportionally larger lateral areas before ending posteriorly at the apices. Both scale types have a small fragile base with a wide open central pulp cavity and

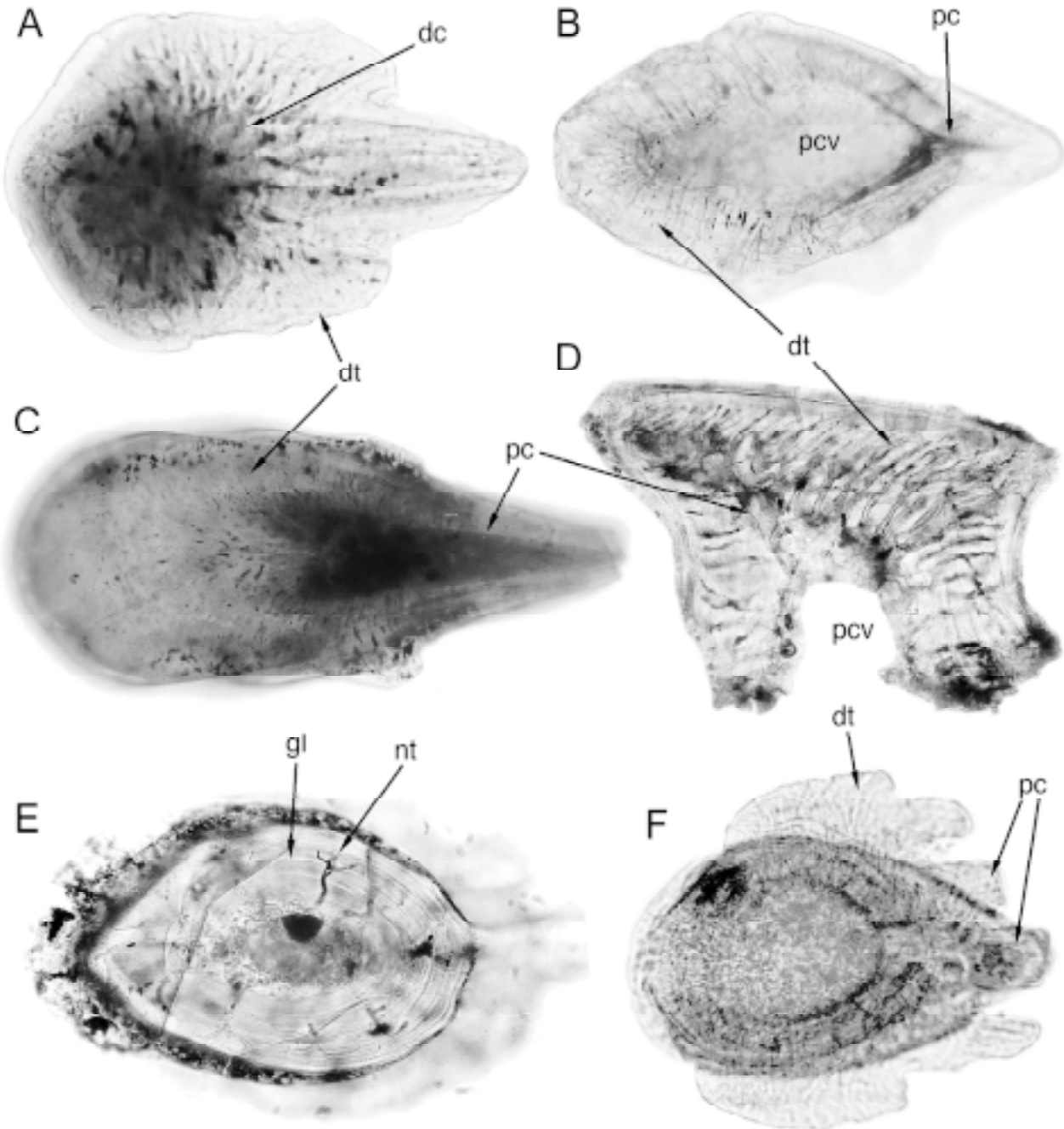


Fig. 18. *Canonia* cf. *C. grossi*, *Nikolivia* sp. and *Thulolepis striaspina* gen. et sp. nov. Histology of the scales.
A: *Canonia* cf. *C. grossi*. in crown view, immersed in aniseed oil, MGUH VP 3505, × 451.
B, **C**. *Nikolivia* sp. immersed in aniseed oil. **B**: Trunk scale in basal view, MGUH VP 3500, × 108. **C**: Trunk scale in crown view, MGUH VP 3501, × 157.
D–**F**. *Thulolepis striaspina* gen. et sp. nov. **D**: Transitional scale in vertical longitudinal section, MGUH VP 3517, × 394. **E**: Head scale in horizontal section, MGUH VP 3506, × 376. **F**: Transitional scale in crown view, immersed in aniseed oil, MGUH VP 3518, × 219. MGUH VP 3500, 3501 from GGU sample 82738, Halls Grav; MGUH VP 3505, 3506, 3517, 3518 from GGU sample 319264, Monument.
dc: dentine canals; **dt**: dentine tubules; **gl**: growth lines; **nt**: neck tubules; **pc**: pulp canal; **pcv**: pulp cavity; **sf**: tubules for Sharpey's fibres.

high narrow neck. These presumed juvenile scales are therefore probably of similar age.

Scale histology. The scales from Greenland are similar to the type material from the Canadian Arctic; they are of thelodontid type with dentine tubules all radiating from a central or anterior pulp cavity (Fig. 18A). Many dentine tubules repeatedly converge on the pulp cavity, forming a typical tree-like branching pattern. When the tubules open into the pulp cavity they have almost reached canal thickness. In the posterior part, longer but still branching dentine tubules extend from the pulp cavity towards the crown. Growth lines and tubules of Sharpey's fibres are present but difficult to see in the few specimens available.

Scale dimensions. Length 0.2–0.3 mm; width 0.1–0.2 mm.

Remarks. The general features of the material from Greenland are similar to the type material from Canada (Vieth 1980). The first type described above (Fig. 17D), with a wide and smooth median area, does not have any exact equivalent in Vieth's material, but can in general be compared to one of her most common forms, with a smooth flat central platform and only one pair of lateral crown ridges (Vieth 1980, plate 3, fig. 1). The other type described herein is similar to the second most common type described by Vieth (1980, plate 3, figs 2, 4, 6). This form, which is characterized by a narrower slightly concave median ridge, is also figured by Wilson & Caldwell (1993, fig. 1f, g) from Canada, as well as by Turner & Murphy (1988, fig. 1.22, 23, 29–34) from USA. Types with more than one pair of lateral ridges are not represented in the poor set of *Canonia* cf. *C. grossi* from the Chester Bjerg Formation (Vieth 1980, plate 3, figs 3, 5, 7, 8). Scales of *C. grossi* type are also found in residues from Severnaya Zemlya, the Timan-Pechora Region, Podolia and Spitsbergen (Talimaa in press, V. Karatajute-Talimaa, personal communication 1999). They all lie within the morphological ranges present in the type material and are all of Lochkovian age.

Occurrence. *Canonia* cf. *C. grossi*, Lochkovian, Monument, Hall Land, North Greenland; *Canonia grossi* Lochkovian–Pragian, eastern Arctic Canada; Lochkovian, Severnaya Zemlya, Russia; Lochkovian, Timan-Pechora Region, north-eastern part of European Russia; Lochkovian, Podolia, Ukraine; Lochkovian, Nevada, USA.

Family Incertae sedis

Genus *Thulolepis* gen. nov.

Derivation of name. A combination of the name Thule, referring to the original Eskimo settlement Thule in North-West Greenland (*thule* is also Latin form of the Greek word used of an island or point of land in the extreme north), and the Greek word *lepis*, for scale.

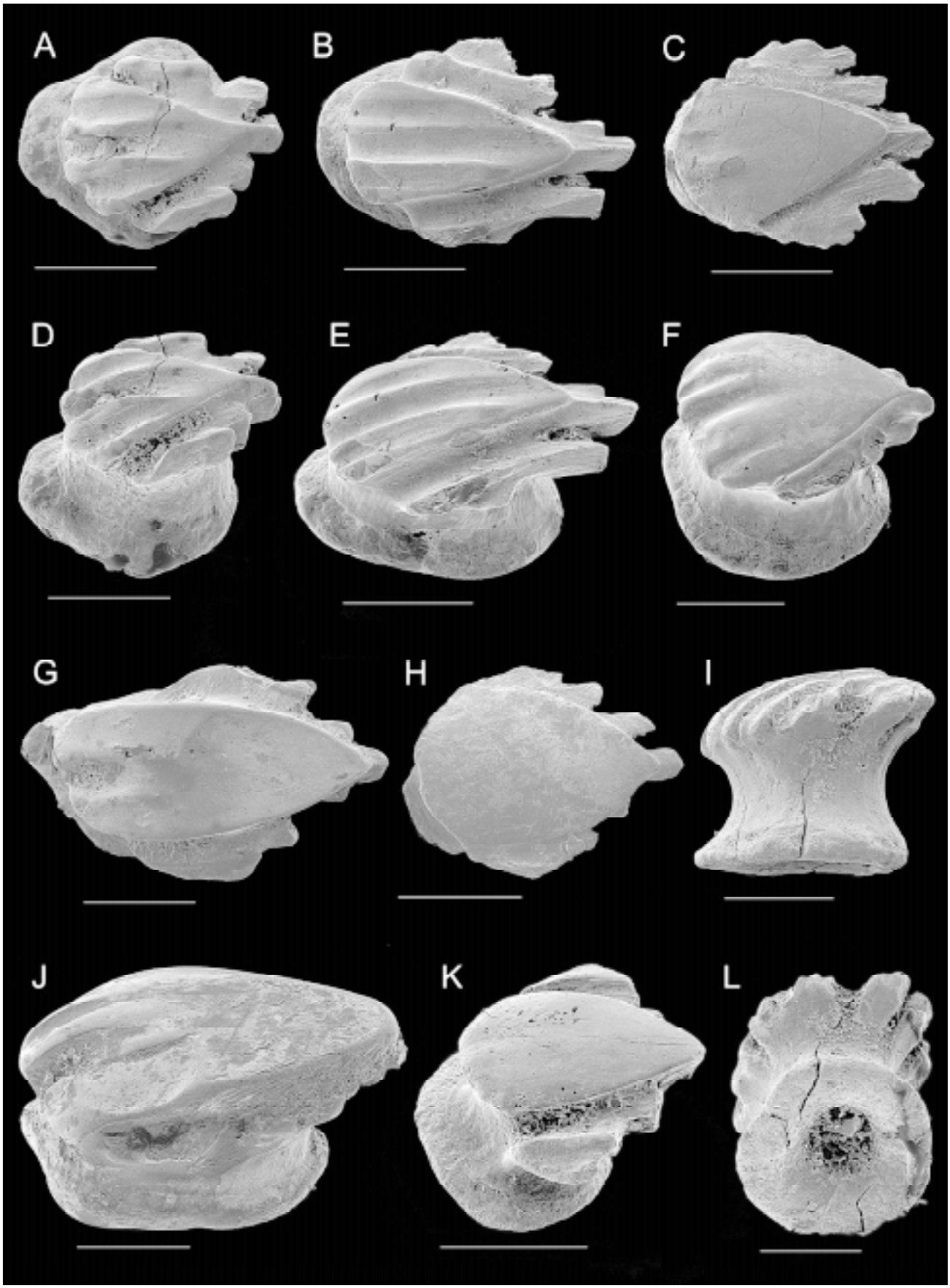
Type species. *Thulolepis striaspina* gen. et sp. nov.

Diagnosis. Very small thelodontid scales, length about 0.2 mm, with ornamented or smooth sub-triangular shaped median crown area, furrowed anteriorly; ridged and furrowed dorso-lateral crown area, forming five posteriorly pointing spines or apices with small longitudinal micro-ridges; base round to oval, often smaller than crown; neck smooth high and narrow; straight or curved dentine tubules pass directly into pulp cavity; tubules converge and join to greater thickness towards pulp cavity; distinct dentine tubules in neck; 1–5 narrow pulp canals extend from pulp cavity towards spines.

Range. Early Devonian (Lochkovian).

Remarks. This genus is established for a thelodontid scale with wide, slightly curved, dentine tubules, branched narrow pulp canals and distinctive morphological characters, such as a high neck and a heavily ornamented crown. *Apalolepis* Karatajute-Talimaa 1967 (Obruchev & Karatajute-Talimaa 1967) also has bran-

Fig. 19. *Thulolepis striaspina* gen. et sp. nov. SEM photomicrographs. Scale bars equal 0.1 mm.
A: Head scale in crown view, MGUH VP 3507. **B**: Transitional scale in crown view, holotype, MGUH VP 3510. **C**: Transitional scale in crown view, MGUH VP 3512. **D**: Head scale in oblique crown view, MGUH VP 3507. **E**: Transitional scale in oblique crown view, holotype, MGUH VP 3510. **F**: Transitional scale in oblique crown view, MGUH VP 3513. **G**: Trunk scale in crown view, MGUH VP 3515. **H**: Transitional scale in crown view, MGUH VP 3514. **I**: Head scale in lateral view, MGUH VP 3511. **J**: Trunk scale in oblique crown view, MGUH VP 3516. **K**: Transitional scale? in oblique crown view, MGUH VP 3519. **L**: Head scale in basal view, MGUH VP 3511.
All specimens from GGU sample 319264, Monument.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ched pulp canals and curved tubules of a slightly different kind in the crown, but *Thulolepis* gen. nov. differs in terms of its higher more robust crown, larger base and posteriorly pointing spines. In crown morphology *Thulolepis* gen. nov. resembles most closely genera such as *Turinia* Traquair 1898 or *Nikolivia* Karatajute-Talimaa 1978, but the base and the neck are similar to scales of *Thelodus* Agassiz 1839. In some species of *Thelodus* it is possible to find curved dentine tubules but characters such as branched pulp canals and heavily ornamented crown are not diagnostic for *Thelodus*.

While *Thulolepis* gen. nov. shares characters with several different genera it shows no clear affinity regarding family level assignment.

***Thulolepis striaspina* gen. et sp. nov.**
Fig. 18D–F; Fig. 19; Fig. 20; Fig. 21A

Derivation of name. From Latin *stria* and *spina*, referring to the striated crown spines.

Holotype. Transitional scale; MGUH VP 3510 from GGU sample 319264 (Fig. 19B, E; Fig. 21.4).

Figured material. Head scales; MGUH VP 3506–3509, 3511. Trunk scales; MGUH VP 3515, 3516. Transitional and specialized scales; MGUH VP 3510, 3512–3514, 3517–3519. All from GGU sample 319264.

Other material. 75 head and transitional scales from GGU sample 319264.

Locality and age. The top of Monument, Hall Land, North Greenland, Chester Bjerg Formation, Early Devonian (Lochkovian).

Diagnosis. As for the genus.

Scale morphology. *Thulolepis striaspina* gen. et sp. nov. is represented by probable head and trunk scales and intermediate morphologies, some of which may represent transitional scales. The scales are quite well preserved, although some are broken, and vary in colour from pale brown to dark brown or black. They are not etched or water-worn and their histological characters are well preserved. All scales are very small and only the presumed trunk scales exceed 0.3 mm in length. The more rounded head and transitional scales have a diameter about 0.2 mm.

The typical head scale is rounded with a heavily ornamented crown, a distinct and relatively high neck, and a round base which is almost as large as, or wider than, the crown (Fig. 19A, D, I, L; Fig. 20.1–3). A round wide open pulp cavity is visible at the central part of the base. The convex crown is almost round with downturned anterior ridges and furrows. These deep furrows are almost as wide as the intermediate ridges they are placed between and the number of furrows varies between one and five in different scale forms. The median furrow is mostly deeper than the flanking ones and its length varies greatly from scale to scale. One pair of deep lateral furrows, which also turns down towards the neck at the antero-lateral part, divides the median crown areas and the wide lateral crown area. These lateral regions should be regarded as a second, more posterior and slightly lower level of the crown. Posteriorly these two different crown levels intergrade to an apex and spine extension, flanked on the same lateral level by two pairs of spines. Posteriorly, on the lower side of the crown, narrow ridges run from each spine towards the base.

On the larger and more elongated trunk scales, the crowns are larger and much smoother, having only one deep short anterior furrow (Fig. 19G, J; Fig. 20.8, 9). The lateral areas of the crowns are proportionally smaller but show traces of a third pair of posteriorly pointing spines. The triangular median crown area is elongated and converges to an apex just above the posterior spine, which lies on the same level as the spiny lateral areas. Similar to the typical head scales, the trunk scales of *Thulolepis striaspina* gen. et sp. nov. have a wide, open, pulp cavity and a high narrow neck. The basal part of the trunk scales, however, follows the general trend shown in the crown by having a more elongated base and pulp opening when compared with the head scales.

Various scales lying between the morphological extremes represented by the head and the trunk scales can be regarded as transitional scales and other specializations (Fig. 19B, C, E, F, H, K; Fig. 20.5–7, 10). The main variable character is the anterior furrows of the crowns which can be less pronounced than in the typical head scale. The number and length of furrows also varies, and in some scales, the furrows are completely absent (Fig. 19H, K; Fig. 20.6, 10).

Several thin parallel ridges are visible along the surface of several of the posteriorly pointing spines, almost all of which are broken (Fig. 21A). Almost all scales have a thin base and wide open pulp cavity (Fig. 19I, L) and are of similar, relatively young, age.

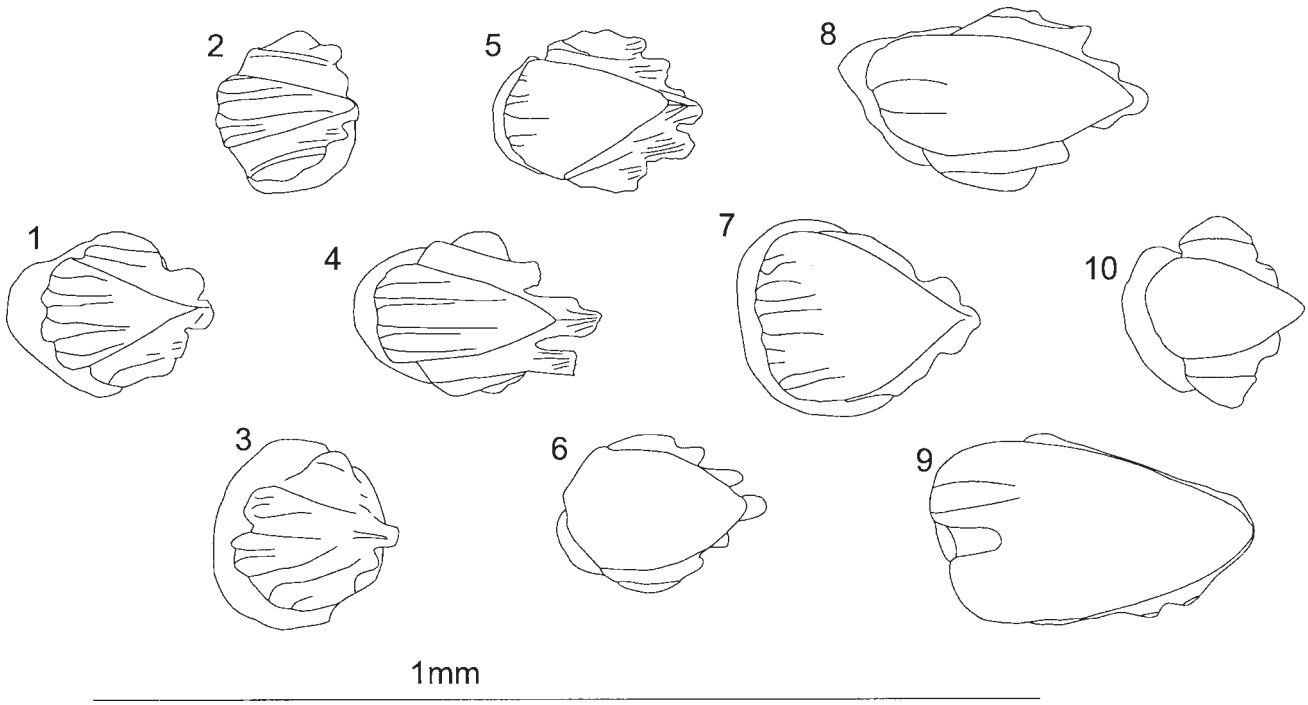


Fig. 20. *Thulolepis striaspina* gen. et sp. nov. The main morphological scale varieties in crown view.
1: Head scale, MGUH VP 3507. **2**: Head scale, MGUH VP 3508. **3**: Head scale, MGUH VP 3509. **4**: Transitional scale, holotype, MGUH VP 3510. **5**: Transitional scale, MGUH VP 3512. **6**: Transitional scale, MGUH VP 3514. **7**: Transitional scale, MGUH VP 3513. **8**: Trunk scale, MGUH VP 3515. **9**: Trunk scale, MGUH VP 3516. **10**: Transitional scale, MGUH VP 3519.
All specimens from GGU sample 319264, Monument.

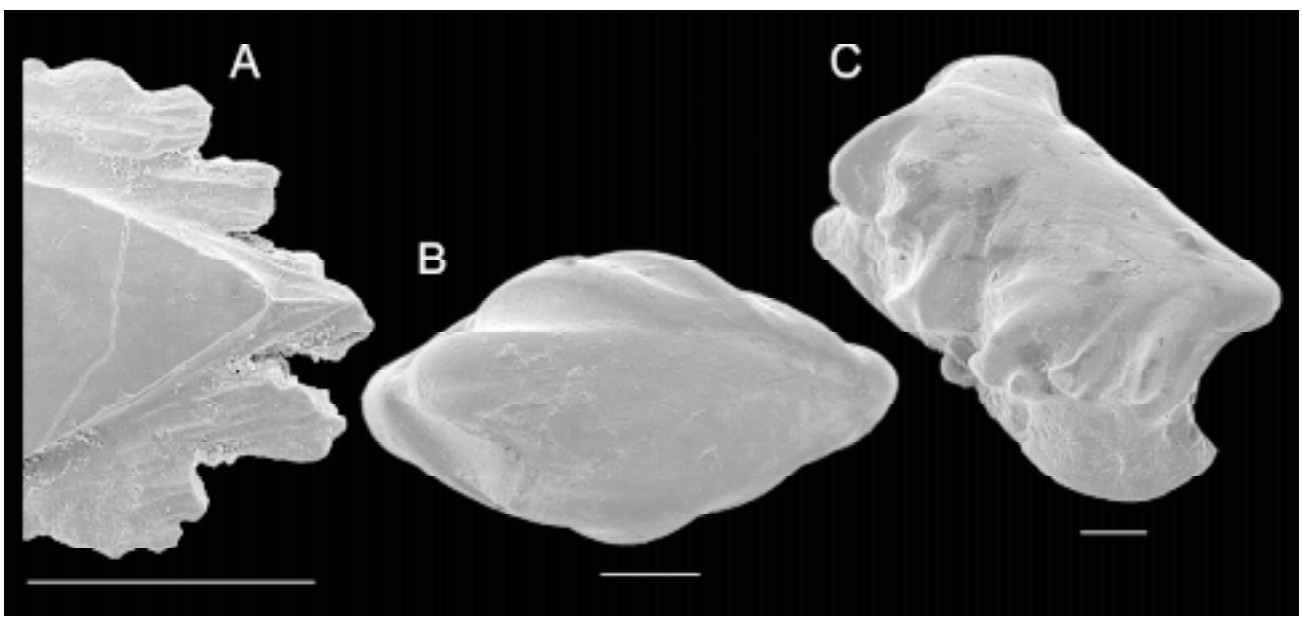


Fig. 21. Thelodont scales. SEM photomicrographs. Scale bars equal 0.1 mm.
A: *Thulolepis striaspina* gen. et sp. nov. Transitional scale in crown view, close up of posterior crown edge, MGUH VP 3512.
B, **C**. Thelodontida indet. **B**: Scale in crown view, MGUH VP 3520. **C**: Two scales grown together in oblique crown view, MGUH VP 3521.
MGUH VP 3512, 3520 from GGU sample 319264, Monument; MGUH VP 3521 from GGU sample 82737, Halls Grav.

Scale histology. The scales of *Thulolepis striaspina* gen. et sp. nov. have a typical thelodontid histology with straight or slightly curved dentine tubules passing directly into a central or slightly anterior pulp cavity (Fig. 18D–F). Some of the dentine tubules also radiate from each of the pulp canals which extend from the pulp cavity towards the postero-lateral crown spines. The converging tubules join and increase in thickness one or two times before they open into the pulp cavity. The outer layer of the crown, representing the initial cap, is proportionally thick with quite dense structure. In the neck area, towards the base, a few thicker longitudinal tubules are visible. The abundant growth lines are most clearly visible in central parts of the scales. The basal tissue is distinct with only a weak indication of tubules of Sharpey's fibres.

Scale dimensions. Length 0.1–0.4 mm; width 0.2–0.3 mm; height 0.1–0.2 mm.

Remarks. The small sample of scales of *Thulolepis striaspina* gen. et sp. nov. does not give a true picture of the proportion of scale types. Very few of the larger, presumed trunk, scales are found and there is not enough information to interpret the true squamation. The crown ornamentation of head and transitional scales is equivalent to *Thelodus admirabilis*, described by Märss (1982). *Thulolepis striaspina* gen. et sp. nov. differs notably by having a lateral wing or area on a slightly lower level and branched pulp canal.

Occurrence. Lochkovian, Monument, Hall Land, North Greenland.

Thelodontida indet.
Fig. 21B, C

Figured material. MGUH VP 3520 from GGU sample 319264 and MGUH VP 3521 from GGU sample 82737.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonion (Pridoli–Lochkovian).

Remarks. These problematic scales show typical thelodontid characters, including a high distinct neck, robust base and a central pulp cavity. The rhomboidal or oval crown is flat and smooth, often with up to three pairs of smooth and wide lateral ridges and furrows running posteriorly with a steep angle from the neck. Scales of this type have been found growing together in pairs (Fig. 21C). They have a turiniid appearance but more material is required before their affinity can be assessed.

Occurrence. Pridoli–Lochkovian, Hall Land, North Greenland.

Heterostraci

Cyathaspidiformes indet.
Fig. 22A–F

1976 *Poraspis* sp.; Bendix-Almgreen, Fig. 443F.

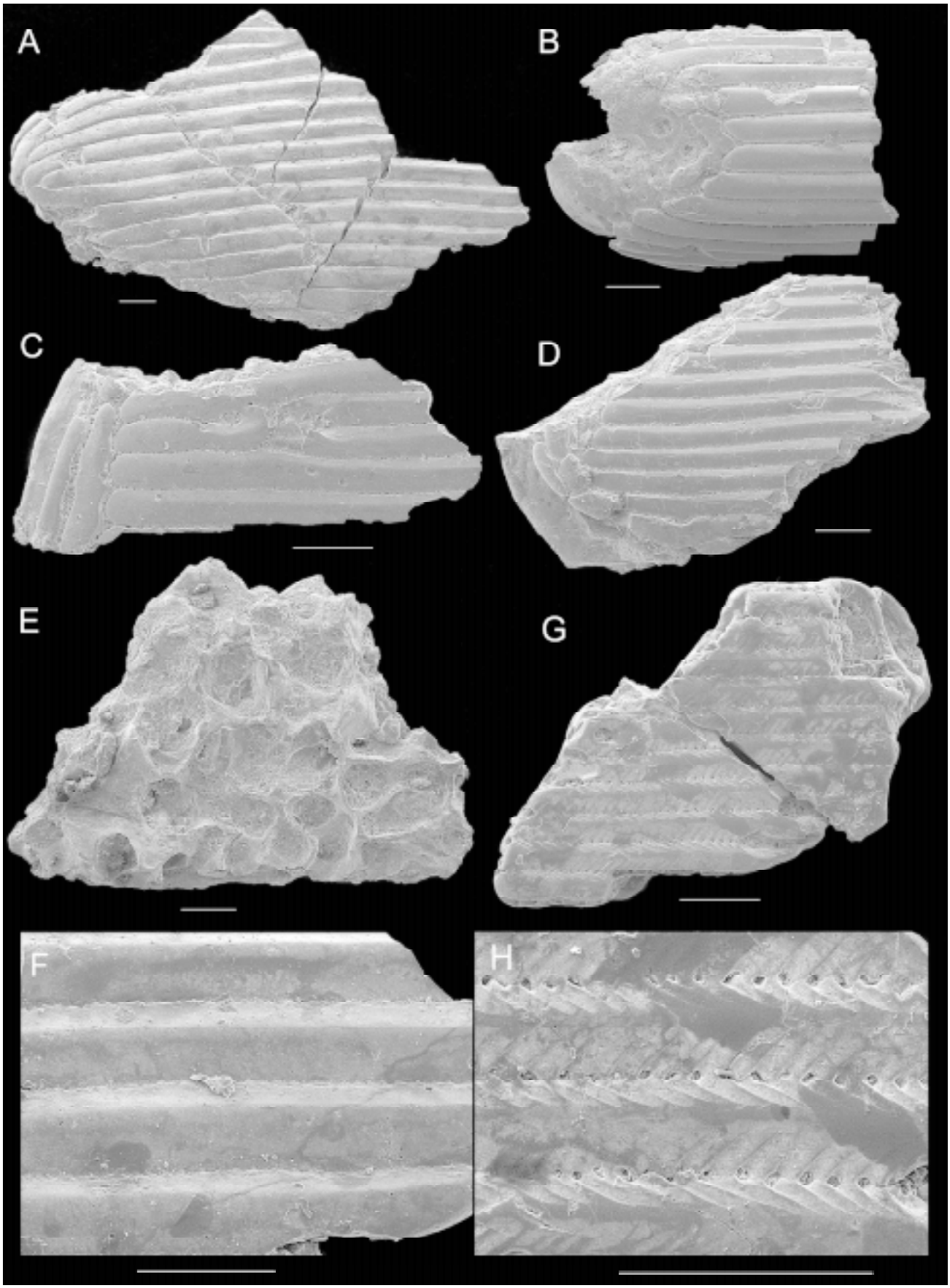
Figured material. MGUH VP 3522 from GGU sample 82737, MGUH VP 3523, 3524 from GGU sample 82738, MGUH VP 3525, 3526 from GGU sample 298937.

Other material. About 20 fragments of variable size and preservation from GGU samples 82736, 82737, 82738, 298937.

Locality and age. The Halls Grav locality, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian (Pridoli).

Description. Fragments of Cyathaspidiformes indet. are

Fig. 22. Indeterminate Cyathaspidiformes and Pteraspidiformes. SEM photomicrographs. Scale bars equal 0.2 mm.
A–**F**. Cyathaspidiformes indet. **A**: Fragment of antero-lateral part of head shield or branchial plate in upper view, MGUH VP 3522. **B**: Median dorsal trunk scale in upper view, MGUH VP 3523. **C**: Fragment of anterior part of head shield in upper view, MGUH VP 3524. **D**: Ventro-lateral? trunk scale in upper view, MGUH VP 3525. **E**: Fragment in visceral view, MGUH VP 3526. **F**: Fragment of antero-lateral part of head shield or branchial plate, close up of tubercles in upper view, MGUH VP 3522.
G, **H**. Pteraspidiformes indet. **G**: Fragment in upper view, MGUH VP 3527. **H**: Fragment in upper view, close up of tubercles, MGUH VP 3527.
MGUH VP 3522 from GGU sample 82737, Halls Grav; MGUH VP 3523, 3524 from GGU sample 82738, Halls Grav; MGUH VP 3525, 3526 from GGU sample 298937, Halls Grav; MGUH VP 3527 from GGU sample 319264, Monument.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relatively common and make up most of the larger fragments found in the processed samples. Several larger specimens from different broken parts of the main shield are found together with a few almost complete trunk scales. They show typical cyathaspidiform ornamentation with fine, about 7–10 per mm, tightly packed longitudinally arranged dentine ridges with a smooth upper surface and lateral margins (Fig. 22F). The dentine ridges are flat, round or even triangular in cross section, which may reflect from which part of the body they are derived or simple variation. In basal view, when the basal layer is broken, it is possible to see the cancellous layer with aspidine around large honeycomb-shaped cavities (Fig. 22E).

One specimen, MGUH VP 3522, is a fragment of the antero-lateral part of the ventral or dorsal shield, or the anterior of a branchial plate (Fig. 22A). The elongated dentine ridges bend inwards and meet anteriorly. They are tightly packed and are almost triangular in cross section, which gives the appearance of a median crest.

MGUH VP 3524 (Fig. 22C) is a small fragmental specimen from the rostral part of a dorsal shield or the anterior part of a ventral shield. It shows one group of fine longitudinal dentine ridges with two pores of the lateral line system disturbing their arrangement. The dentine ridges are smooth with flat, rounded or almost triangular cross section. Perpendicular at their anterior end are three transverse broken ridges with smooth, flat or slightly convex upper surfaces.

Trunk scales are found as median and ventro-lateral scales. One poorly preserved median dorsal scale is symmetrical and strongly curved, almost semicircular in cross section (Fig. 22B). It is about 1 mm long, but the posterior part is broken. On the outside, the scale is ornamented by fine, about 9 per mm, parallel longitudinal dentine ridges. They have a flat or rounded upper surface. Anteriorly, and closest to the midline, the ridges end earlier than the more lateral ones, forming a poorly preserved, anterior, triangular area free of longitudinal ridges. Smaller tubercles fill up at least the posterior part of this area. The most anterior part of the scale is rounded and free from dentine ornamentation. In basal view, the dorsal median scale is strongly concave.

One flat trunk scale of a probable ventro-lateral scale is broken, but indicates a rhomboidal outline. Anteriorly a narrow overlapping brim of basal tissue is free of dentine ornamentation (Fig. 22D). The main part of the scale has longitudinally arranged dentine ridges which are tightly packed and strongly parallel. Few, small, short or almost round transverse ridges or tubercles run between the overlapping brim and the longitudinal ridges, which are slightly rounded in cross section.

Remarks. These fragments show typical cyathaspidiform characters and can be compared with the exoskeleton of *Poraspis* Kiær 1930 and other poraspidids (Denison 1964; Blieck 1982), as also noted by Bendix-Almgreen (1976). The variation in ridge cross section, round, flat and V-shaped, may reflect both positional and taxonomical differences.

Occurrence. Pridoli, Halls Grav, Hall Land, North Greenland.

Pteraspidiformes indet.
Fig. 22G, H

Figured material. MGUH VP 3527 from GGU sample 319264.

Other material. One poorly preserved fragment from GGU sample 319264.

Locality and age. The top of Monument, Hall Land, North Greenland, Chester Bjerg Formation, Early Devonian (Lochkovian).

Description. Pteraspidiformes indet. is known from very few fragments found in the residues of the Chester Bjerg Formation, showing finely serrated ridge margins. They are best represented by a single specimen having a superficial layer of tightly packed, long, narrow dentine ridges and a thick layer of basal and middle tissue. The ridges are narrow, about 0.1 mm in width, but their total length is unknown since no fragments with complete ridges are found (Fig. 22F, H). They are longer, however, than 1 mm and probably extend along a large part of the not preserved full length of the head shields. The upper surface is flat and smooth except for some marginal ornamentation. Many small notches frequently disturb the lateral margins and bend dorso-posteriorly towards the median part. They are flanked by tiny processes or lobes which have short narrow ribs running parallel with anteriorly facing notches. Each tubercle is parallel with the next, forming pore-like holes where the notches, respectively the lobes, meet.

The rarity of material prohibited preparation of thin

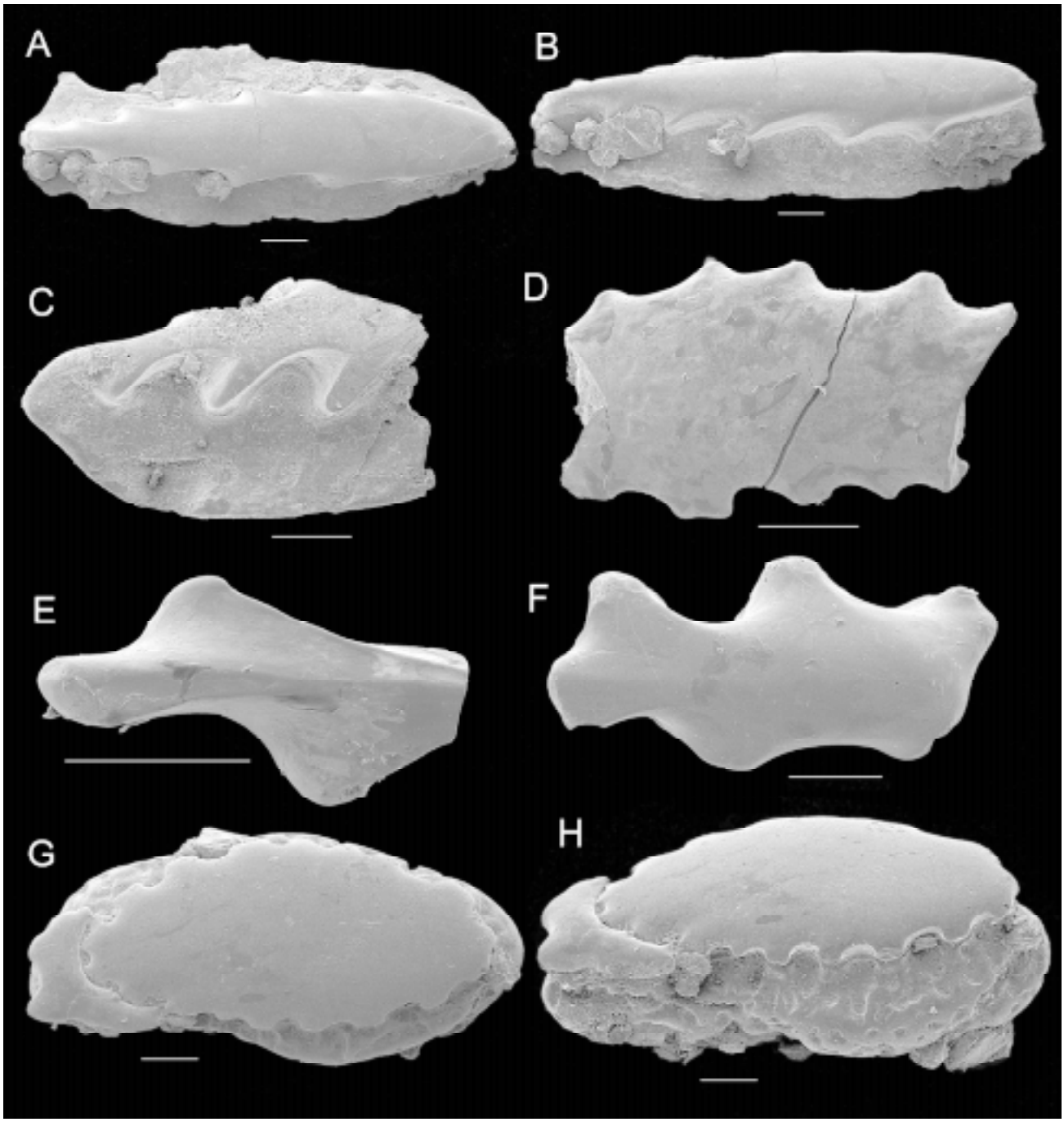

Fig. 23. Heterostraci indet. SEM photomicrographs. Scale bars equal 0.2 mm.

A–**C**. Heterostraci indet., type A. **A**: Fragment in upper view, MGUH VP 3528. **B**: Fragment in oblique upper view, MGUH VP 3528. **C**: Fragment in oblique upper view, MGUH VP 3529.

D: Heterostraci indet., type C. Tubercle in upper view, MGUH VP 3532.

E, **F**. Heterostraci indet., type B. **E**: Tubercle in upper view, MGUH VP 3530. **F**: Tubercle in upper view, MGUH VP 3531.

G, **H**. Heterostraci indet., type D. **G**: Fragment in upper view, MGUH VP 3533. **H**: Fragment in oblique upper view, MGUH VP 3533. MGUH VP 3528 from GGU sample 82738, Halls Grav; MGUH VP 3529, 3533 from GGU sample 82736, Halls Grav; MGUH VP 3530–3532 from GGU sample 319264, Monument.

sections, but available material shows a cancellar middle layer with large cavities.

Remarks. There are few detailed studies of pteraspidiform tubercles and the only figured form similar to the material under discussion is *Protopteraspis* Leriche 1924 (Blieck 1982).

Occurrence. Lochkovian, Monument, Hall Land, North Greenland.

Heterostraci indet., type A
Fig. 23A–C

Figured material. MGUH VP 3528 from GGU sample 82738, MGUH VP 3529 from GGU sample 82736.

Other material. A few fragments in bits and pieces from GGU samples 82736, 82737, 82738.

Locality and age. The Halls Grav locality, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian (Pridoli).

Description. This rare type is best known from MGUH VP 3528 which may represent a scale-like unit with a basal plate and a large elongated ridge (Fig. 23A, B). The basal plate is oval, more than 2 mm long and almost 1 mm maximum width. It has slightly uneven basal margins and edges, and no pores are visible, neither on the upper nor lower surface of the basal plate. The dentine ridges are almost as long as the base, having an elongated almost lacrymiform shape with its widest part posteriorly. The ridge is serrated with notches and intermediate rib-like barbs or processes. They all face anteriorly with a low angle, bending dorso-posteriorly towards the smooth, slightly convex median surface. Some units are much smaller, not exceeding 1 mm in length (Fig. 23C). Their ridges are usually narrower, higher and have more deeply serrated margins. The basal plate seems to be quite dense, but thin sections were not prepared.

Remarks. The main type of elongated, slightly lacrymiform, serrated ridges is similar to those described by Dineley & Loeffler (1976) within the family Traquairaspidae, part of the group of tessellated taxa which also includes *Weigeltaspis* Brotzen, 1933 and the Psammosteidae; all have serrated dentine ridges with anterior directed lateral processes (Tarlo 1964, 1965; Dineley & Loeffler 1976). The ridges differ, however, by having less pronounced lateral projections and notably by the indication of being part of a scale-like unit, represented by an oval basal plate. Such scale-like units and serrated margins are typical for *Lepidaspis* Dineley & Loeffler 1976 known from the Lower Devonian of the Canadian Arctic (Dineley & Loeffler 1976) and Spitsbergen (Blieck 1982). However, *Lepidaspis* differs by having deeper notches and most importantly, by having pore openings on the upper surfaces of the basal plate. Moreover, the shape of the ridges of *Lepidaspis* is usually not lacrymiform. The second, smaller, type is morphologically more similar to *Lepidaspis* but its rarity and poor preservation preclude further taxonomic treatment.

Occurrence. Pridoli, Halls Grav, Hall Land, North Greenland.

Heterostraci indet., type B
Fig. 23E, F

Figured material. MGUH VP 3530, 3531 from GGU sample 319264.

Other material. A few badly preserved specimens from the same collection.

Locality and age. The top of Monument, Hall Land, North Greenland, Chester Bjerg Formation, Early Devonian (Lochkovian).

Description. These fragments of large elongated oak leaf-like dentine ridges are never longer than 1 mm. Although the dentine is well preserved, complete ridges of full length have not been found. They usually lack all traces of the basal tissue, but when present this shows a complicated spongy tissue in the middle layer. The ridge is dark and very shiny with a high, very convex upper surface. They are slightly wider posteriorly and have smooth rounded indentations or notches in the lateral margins which bend smoothly up towards an imaginary midline on the convex upper surface. They, as well as the intermediate processes, are all oriented to face with a low angle to the anterior. This angle is larger for the notches in the posterior part and decreases towards the anterior. At the narrower end the last indentation, flanked by one pair of semiparallel processes, faces anteriorly.

A few very small and badly preserved ridges with

similar morphology are also found. They may represent different stage of development or may be interstitial ridges.

Remarks. The tubercles and the spongy middle parts of Heterostraci indet. type B resemble fragments described and referred to as *Traquairaspis* sp. indet. by Gross (1961). The U-shaped indentations of Heterostraci indet., type B are oriented, however, to face more to the anterior than those of *Traquairaspis* sp. indet. Such orientation is also more common among *Weigeltaspis*, *Lepidaspis*, *Tesseraspis* Wills 1935 and other traquairaspids different from Gross' (1961) *Traquairaspis* sp. indet. All these taxa can easily be confused with each other in fragmentary condition. Gross (1961) did not report any interstitial ridges like those found in traquairaspids from the Canadian Arctic by Dineley & Loeffler (1976). The presence of interstitial ridges in Heterostraci indet., type B is only speculative and based on the presence of a few smaller fragments of similar type.

Occurrence. Lochkovian, Monument, Hall Land, North Greenland.

Heterostraci indet., type C
Fig. 23D

Figured material. MGUH VP 3532 from GGU sample 319264.

Other material. A few badly preserved specimens from GGU samples 82736, 82738 and 319264.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Description. This rare type of low and wide ridge has a smooth flat or weakly convex upper surface. This type is only found as small isolated broken pieces which do not exceed 1 mm in length. These ridges are almost 0.5 mm wide and the lateral margins are serrated, with shallow U-shaped indentations of variable width between small sharp lateral processes which, in the central regions, have no clear orientation. The processes are sometimes weakly bi-lobed. Basal tissue is not preserved, but some fragments indicate a spongy middle layer.

Remarks. In size and state of preservation this type resembles Heterostraci indet., type B. In type C, however, the ridges are much lower, flatter and with less well oriented lateral processes and notches. Traquairaspids from the Canadian Arctic show considerable variability of tubercles within the same taxon (Dineley & Loeffler 1976), suggesting a close relation between Heterostraci indet., types B and C. Also *Strosipherus* may have ridges of this type (Märss 1986a).

Occurrence. Pridoli–Lochkovian, Hall Land, North Greenland.

Heterostraci indet., type D
Fig. 23G, H

Figured material. MGUH VP 3533 from GGU sample 82736.

Other material. About ten fragments of variable size and preservation from GGU samples 82736 and 82738.

Locality and age. The Halls Grav locality, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian (Pridoli).

Description. This type is best represented by specimen MGUH VP 3533, which has a large oval main ridge with serrated margins and small irregular ridges draping the anterior margin. The characteristic main ridge is about 1.5 mm long and 1 mm wide and it has a smooth, flat or slightly convex upper surface. Along the lateral margins are notches, with shallow indentations separated by lateral processes, the latter with slightly radial orientation. The preserved basal tissue is quite thick, approximately 70% of the thickness of the whole fragment, and it exposes a spongy middle layer. Anteriorly, a much smaller irregular ridge has a smooth flat upper surface. Its posterior margin follows the anterior outline of the main ridge and has a smoothly irregular or notched anterior margin.

Remarks. This type of oval and irregular interstitial ridges resembles those found on the central areas of the ventral shield of ?*Traquairaspis* cf. *T. postulata* and related taxa from the Late Silurian of the North West Territories, Canada (Dineley & Loeffler 1976). The flat upper surface is also similar to Heterostraci indet., type C, a comparison supported by some variability among both types.

Occurrence. Priodi, Halls Grav, Hall Land, North Greenland.

Heterostraci indet., type E
Fig. 24

1976 *Oniscolepis*? sp. – Bendix-Almgreen, fig. 443 B–E.

Figured material. MGUH VP 3534, 3539, 3540 from GGU sample 319264, MGUH VP 3535–3537 from GGU sample 82738, MGUH VP 3538 from GGU sample 82736.

Other material. About 100 fragments of variable size and preservation from GGU samples 82734, 82736, 82737, 82738, 298937, 298953 and 319264.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Description. The most common type of heterostracan fragment in the fauna of the Chester Bjerg Formation is included here. No complete head shields have been found, but ridges and several almost complete trunk scales indicate a pteraspidiform or related form. Although the characteristic ridges sometimes are notably different they are kept within the same taxa by their similar general morphology and because they sometimes are attached to the same basal plate. Another important character, common for all forms within this type, is the basal tissue which is composed of spongy aspidine.

One small, isolated ridge has very little of the spongy basal tissue preserved. It has a flat upper surface and deep sub-circular marginal notches, and apparent alignment of the intervening processes (Fig. 24A). The intervening processes are angular, irregular and sometimes weakly bi-lobed. This type of ridge is usually curved, suggesting an anterior position where it drapes the anterior end of more longitudinal ridges.

A larger ridge type with a smooth upper surface also has a slightly curved outline and less pronounced notches. This type of ridge is probably from the marginal part of the main shields; it is less curved than the previous one and sometimes flanks longer and more ornamented ridges (Fig. 24D, H). Similar shorter, but irregular, ridges with a smooth upper surface and marginal notches, clearly drape the anterior part of the longitudinal ridges, indicating that smoother intermediate forms are found in the marginal and anterior parts of the head shield (Fig. 24C, D). These ridges are commonly more curved and irregular than the longitudinal ridges and serve to fill up the space between the straight and more ornamented ridges.

Ridges with more pronounced ornamentation may reach about 1 mm in length and are characterized by having a median crest or rib running longitudinally along the whole length (Fig. 24B–G). The lateral notches bend up towards the upper surface with a more hydrodynamic and posterior orientation. An intervening smooth process or lobe is developed between each notch and a narrow rib extends dorsoposteriorly from the process towards the median part of the tubercle. The anterior end of the ridge is rounded and flanked by a pair of posteriorly pointing notches. Together with the more pointed posterior end this contrives to give the ridge an oak-leaf appearance.

The more sculptured types of ridges with a median crest and oriented lateral serration, vary both in size and the expression of ornamentation. One of these types, which is often flanked by the more elongated smooth ridges (Fig. 24B, D), is slender and relatively smoother while another with the same proportions has a quite sharp median crest and deeper lateral notches (Fig. 24F). The variation among the intervening processes and their ribs, usually follows the expression and the orientation of the notches. Sometimes the small ribs of the lateral lobes almost meet and merge with the upper median crest.

Larger fragments representing trunk scales have proportionally wider ridges with well pronounced sculpture, emphasizing the oak-leaf appearance (Fig. 24E, G). In these, the notches and intervening processes

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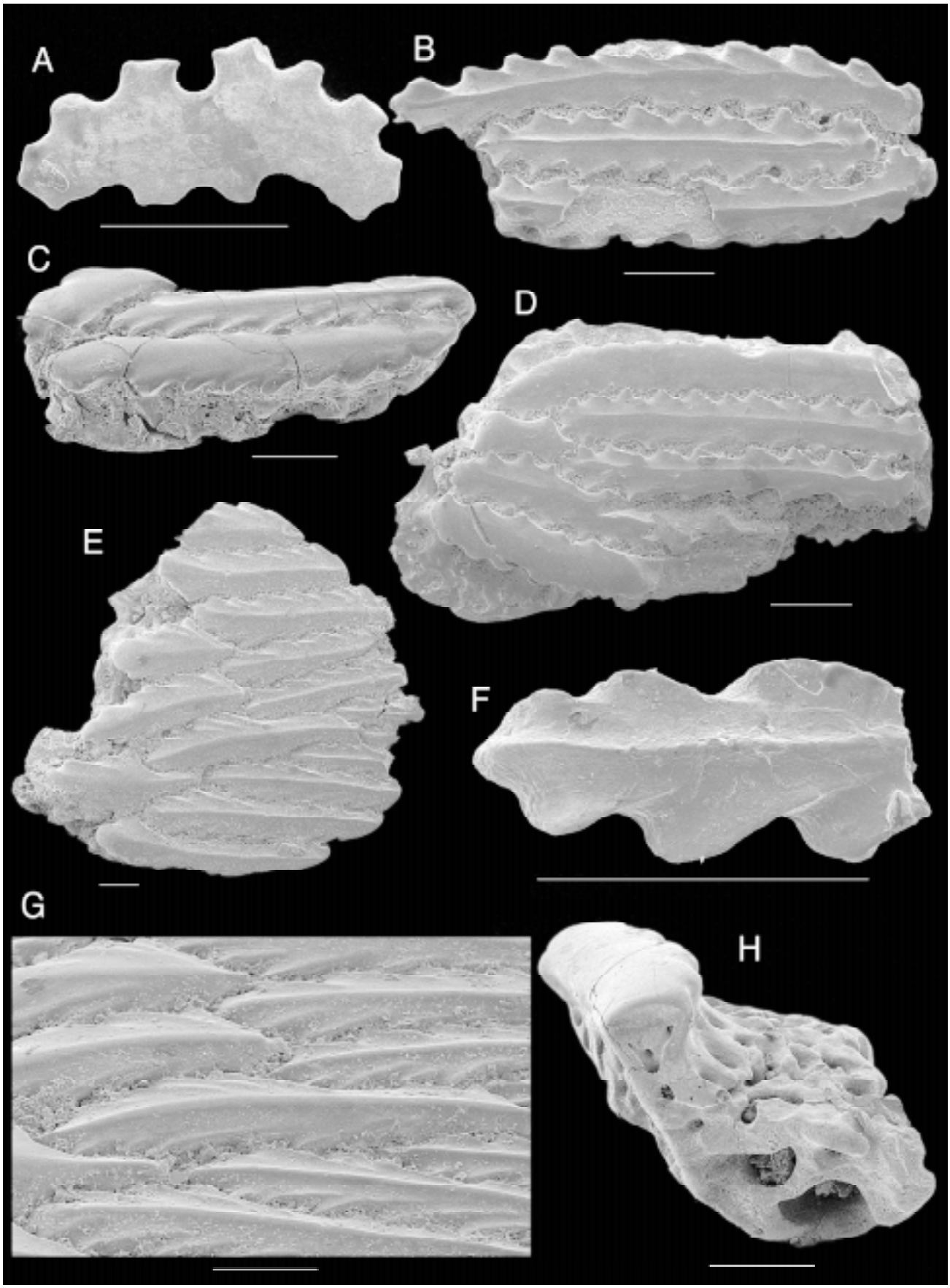
Fig. 24. Heterostraci indet., type E. SEM photomicrographs. Scale bars equal 0.2 mm.
A: Tubercle in upper view, MGUH VP 3534. **B**: Fragment in upper view, MGUH VP 3535. **C**: Fragment in oblique upper view, MGUH VP 3536. **D**: Fragment in upper view, MGUH VP 3537. **E**: Trunk scale in upper view, MGUH VP 3538. **F**: Tubercle in upper view, MGUH VP 3539. **G**: Trunk scale in oblique crown view, close up of tubercles, MGUH VP 3538. **H**: Fragment seen from the broken edge, MGUH VP 3540.
MGUH VP 3534, 3539, 3540 from GGU sample 319264, Monument; MGUH VP 3535–3537 from GGU sample 82738, Halls Grav; MGUH VP 3538 from GGU sample 82736, Halls Grav.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with ribs extend quite far posteriorly towards the upper surface and its rounded median crest.

Remarks. Bendix-Almgreen (1976, fig. 443B–E) figured as *Oniscolepis*? sp. specimens of this type from samples at the Halls Grav locality; they are similar to *Oniscolepis* sp. indet. of Gross (1961). Fragments of this type from the Baltic region were originally described by Pander (1856) as several different species, but they have been grouped into two genera, *Oniscolepis* and *Strosipherus* (Rohon 1893; Gross 1947, 1961; Tarlo 1965; Märss 1986a). Although the variation within these forms is quite large, they have been regarded as synonyms. The European and the North Greenland forms have similar leaf-like ridges and a spongy middle layer of the basal tissue. However, they are not identical since the ridge ornamentation is more pronounced in the North Greenland forms. Variation in this type of ridge from the Chester Bjerg Formation may reflect both positional and taxonomical differences, but this cannot be verified on the basis of available material. The first type of ridge found within Heterostraci indet., type E is similar to the much larger secondary ridges of *Lepidaspis serrata* from the North West Territories, Canada, described by Dineley & Loeffler (1976), but the difference in size and the other types of tubercle clearly exclude this group from *Lepidaspis*.

Also *Miltaspis* Blieck 1981 and *Corvaspis* Woodward 1934 sometimes show similarities with the material under discussion (Blieck 1982).

Occurrence. Pridoli–Lochkovian, Hall Land, North Greenland.

Anaspida

Anaspida indet.

Figs 25, 26

Figured material. MGUH VP 3541–3543 from GGU sample 319264, MGUH VP 3544 from GGU sample 82736, MGUH VP 3545, 3546 from GGU sample 82738.

Other material. About 50 fragments of variable preservation and size from GGU samples 82734, 82736, 82738, 298937 and 319264.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Description. Anaspid fragments are represented within the Chester Bjerg Formation by fragments of small elongate trunk scales with similar sculpture (Fig. 25). Most scales are broken, with a maximum preserved size of about 1.5 mm in width and 1 mm in length (Fig. 25B). They are characterized in crown view by coarse elongated tubercles, some of which are almost drop-shaped and clearly separated from each other. Some specimens also have small round tubercles between the larger elongated ones (Fig. 25B). The sculptured area covers more than half of the posterior scale part, and lies on a higher level than the smooth anterior. The slightly concave anterior region bends up towards the posterior sculptured part. This anterior region is overlapped by the posterior part of the previous scale when the scales are articulated. Circular pores occur on the upper surface between the tubercles. The whole scale is almost rectangular with one end slightly narrower having an extension or process for attachment when articulated. In basal view, the scales are characterized by one large smooth longitudinal median rib which is almost square in cross section (Fig. 25E). The rib widens and becomes lower before merging with the main visceral surface at the end opposite to the attachment process. At the other end the rib becomes narrower, forming the main part of the process for attachment.

A second scale type has a smoother transition from the anterior overlapping area to the posterior sculptured part. A wide and low longitudinal median rib is developed in the junction between these two areas (Fig. 25A). This type lacks the pores on the upper surface seen in the first type, but the sculpture is otherwise almost identical.

A fragment of a scale or most likely a plate, differs from the previous one by having tubercles that are almost grown together, forming long irregularly shaped ridges (Fig. 25C). It also has a flatter and smoother visceral side.

Due to the poor preservation and the lack of material, only remnants of tubules of Sharpey's fibres and radial fibres in the basal central rib have been observed (Fig. 26).

Remarks. Articulated material of anaspids from Scotland and Norway rarely shows the microscopic ornamentation of the scales and the plates (Kiær 1924; Stetson 1928). This ornamentation could be a good basis for scale taxonomy, but detailed studies of anaspid exoskeletal elements and their sculpture have previously only been made by Gross (1938, 1958, 1968), Märss (1986a) and Fredholm (1988, 1990). The forms

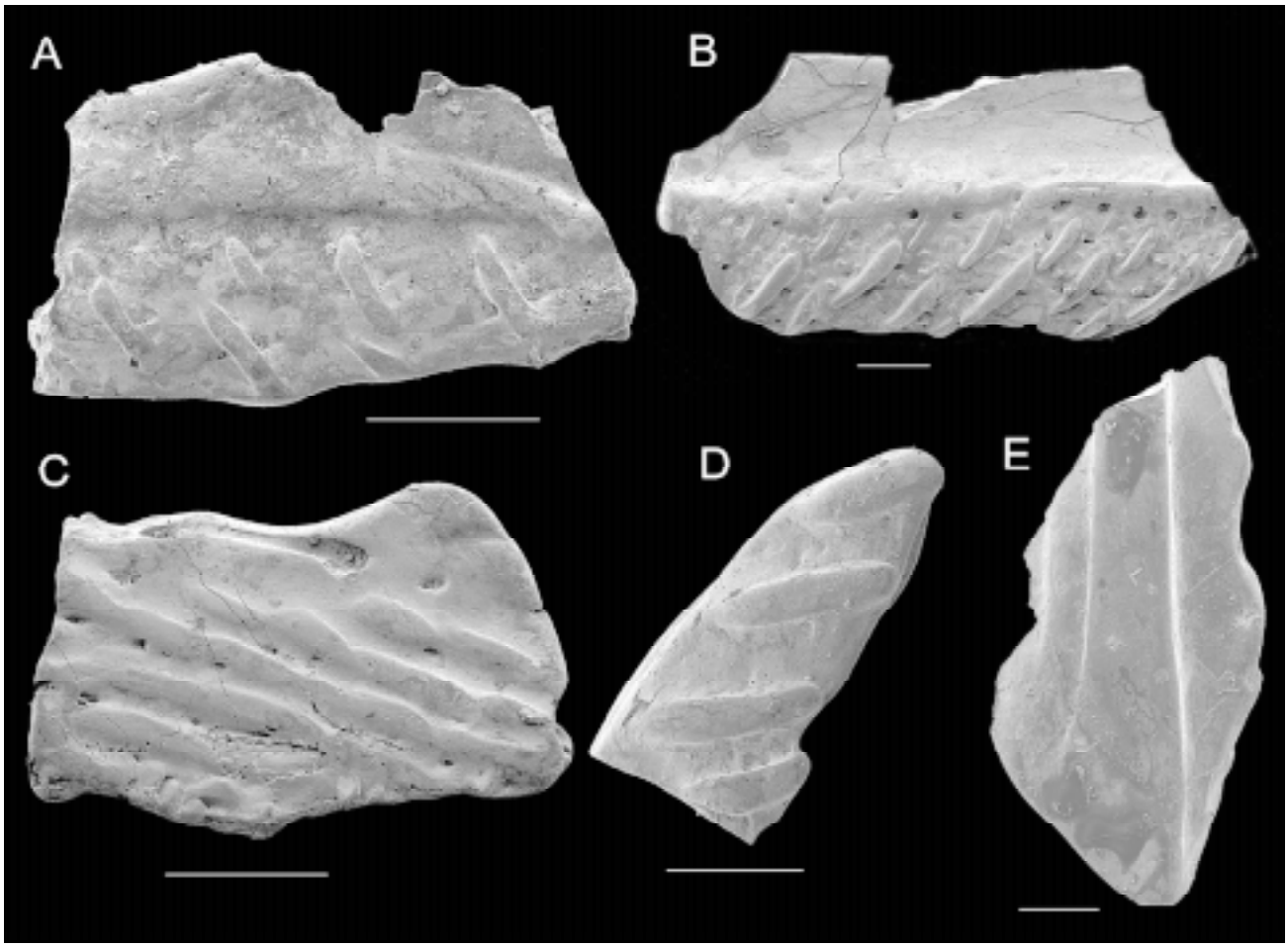


Fig. 25. Anaspida indet. SEM photomicrographs. Scale bars equal 0.2 mm.
A: Scale fragment in upper view, MGUH VP 3544. **B**: Scale fragment in upper view, MGUH VP 3541. **C**: Plate fragment in upper view, MGUH VP 3542. **D**: Scale fragment in upper view, MGUH VP 3545. **E**: Scale fragment in visceral view, MGUH VP 3543. MGUH VP 3541–3543 from GGU sample 319264, Monument; MGUH VP 3544 from GGU sample 82736, Halls Grav; MGUH VP 3545 from GGU sample 82738, Halls Grav.

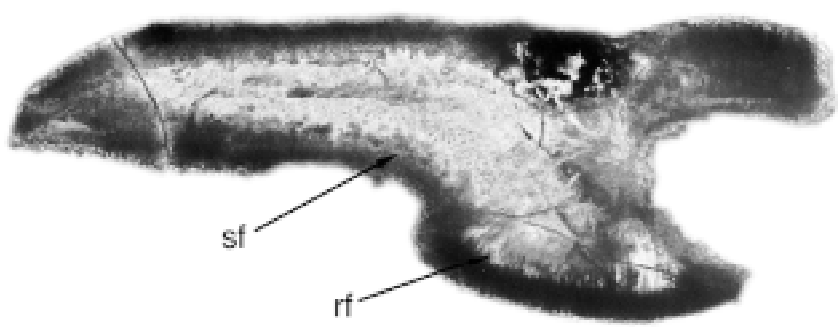


Fig. 26. Anaspida indet. Vertical antero-posterior thin section, MGUH VP 3546 from GGU sample 82738, Halls Grav, × 221.
rf: tubules for radial fibres; **sf**: tubules for Sharpey's fibres.

recovered from the Chester Bjerg Formation bear little resemblance to these Baltic forms.

Occurrence. Pridoli–Lochkovian, Hall Land, North Greenland.

Osteostraci

Osteostraci indet.

Fig. 27A, B, D–J

Figured material. MGUH VP 3548 from GGU sample 319264, MGUH VP 3549 from GGU sample 82736, MGUH VP 3550–3553 from GGU sample 82738.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Other material. About 50 fragments from GGU sample 82736 and 82738.

Description. A few shield fragments and trunk scales show similar ornamental features without any elevated tubercles. Shield fragments are poorly preserved and only reach a size of about 1 mm (Fig. 27E–J). Better preserved trunk scales reach about 1.5 mm in length (Fig. 27A, B, D). The upper surface of the shield fragments is flat and smooth with predominantly regular rows of large pore openings. Some specimens show that this surface is composed of welded individual elongated units of the superficial layer, separated by pores and combining superficial tissue (Fig. 27I). Cavities of the vascular system are visible at the broken edges.

The scales are also poorly preserved, but show the same general crown morphology with a smooth upper surface perforated by large pore openings (Fig. 27A, B). In crown view, the scales are rhomboidal. The surface is concave and bends down anteriorly towards the distinct base. A distinct neck is visible anteriorly as a shallow furrow, both on the lateral crown wall and the base. The base is low with a broad rounded brim and projects out anteriorly.

In basal view, the visceral surface of the scales and shield varies from smooth to bumpy and concave to convex, with a few round openings (Fig. 27D). The tissue often has a reticulate structure in visceral view, which is common in osteostracans.

Visible morphological structures at the broken edges may indicate a superficial layer of dentine-like tissue, a middle layer of spongy bone and a basal layer of laminar bone.

Remarks. Dermal ornamentation of osteostracans is little studied and the material under discussion can only be compared with fragments that Gross (1961) referred to as *Zenaspis* ? sp. indet. from erratics in north Germany. Several specimens of the latter differ by showing clear individual elongated units rather than a continuous smooth upper surface. However, this ornamentation, composed of a smooth superficial layer pierced by pores, is found in many different groups of osteostracans and it is not diagnostic of *Zenaspis*. Osteostraci indet. may be more similar to the non-cornuate osteostracan *Hemicyclaspis* (P. Janvier, personal communication 1999).

Occurrence. Pridoli–Lochkovian, Hall Land, North Greenland.

Osteostraci? indet.

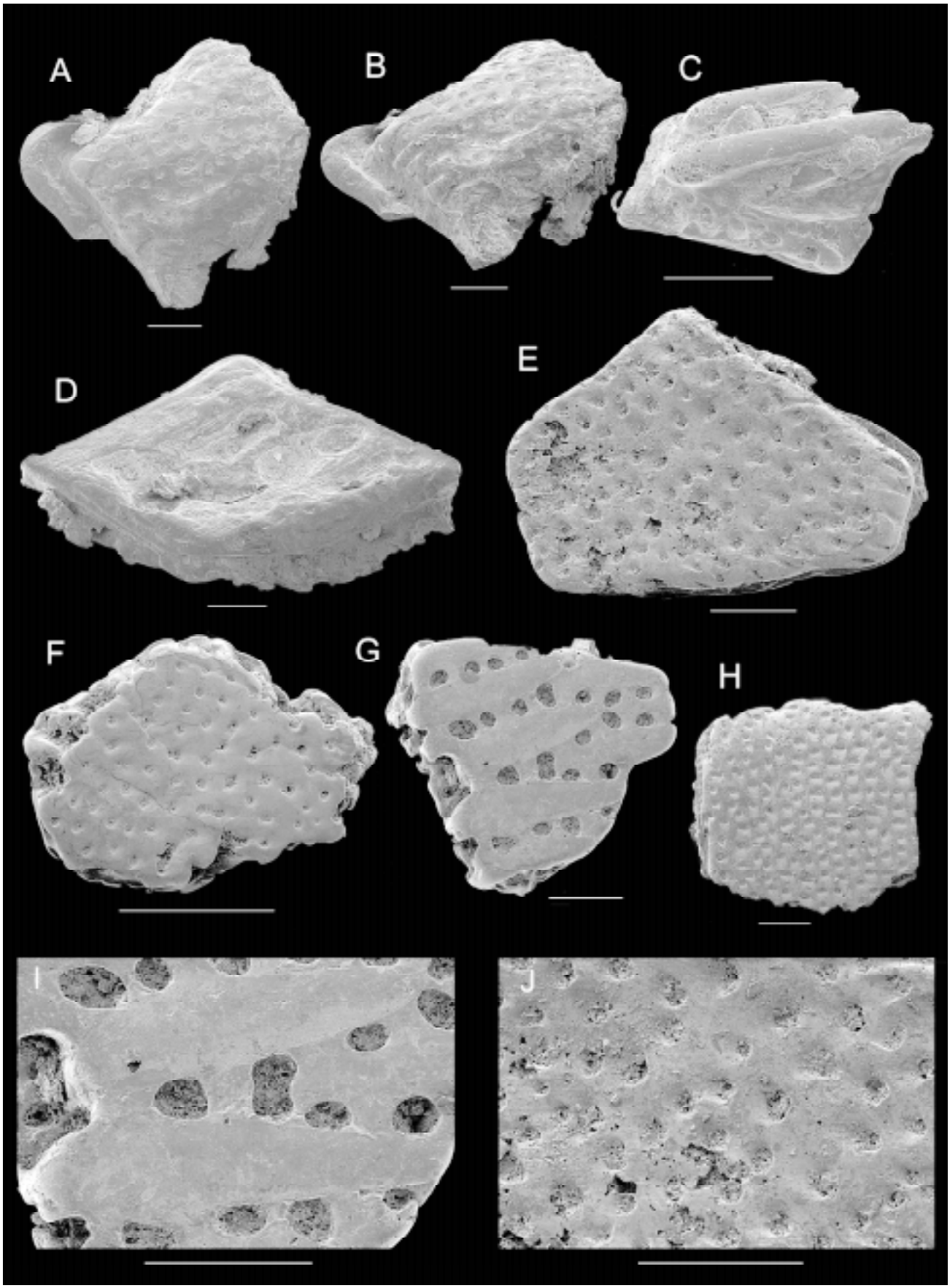
Fig. 27C

Figured material. MGUH VP 3547 from GGU sample 319264.

Other material. One specimen from GGU sample 82738.

Locality and age. The Halls Grav and Monument lo-

Fig. 27. Osteostraci indet. and Osteostraci? indet. SEM photomicrographs. Scale bars equal 0.2 mm.
A, **B**, **D**–**J**. Osteostraci indet. **A**: Trunk scale in crown view, MGUH VP 3550. **B**: Trunk scale in oblique crown view, MGUH VP 3550. **D**: Trunk scale in basal view, MGUH VP 3551. **E**: Shield fragment in external view, MGUH VP 3549. **F**: Shield fragment in external view, MGUH VP 3548. **G**: Shield fragment in external view, MGUH VP 3552. **H**: Shield fragment in external view, MGUH VP 3553. **I**: Shield fragment in external view, close up on surface, MGUH VP 3552. **J**: Shield fragment in external view, close up on surface, MGUH VP 3549.
C: Osteostraci? indet. Trunk scale in oblique crown view, MGUH VP 3547.
MGUH VP 3547, 3548 from GGU sample 319264, Monument; MGUH VP 3549 from GGU sample 82736, Halls Grav; MGUH VP 3550–3553 from GGU sample 82738, Halls Grav.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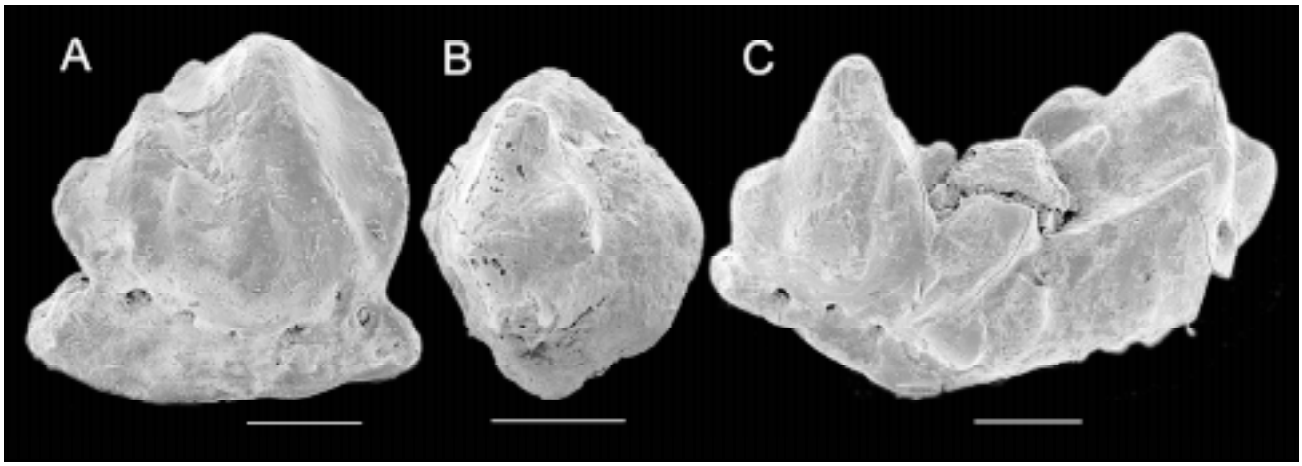


Fig. 28. Chondrichthyes indet. SEM photomicrographs. Scale bars equal 0.1 mm.
A: Unit with three odontodes in anterior view, MGUH VP 3554. **B**: Single odontode in crown view, MGUH VP 3555. **C**: Unit with many odontodes in oblique crown view, MGUH VP 3556.
All specimens from GGU sample 319264, Monument.

calities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian, (Pridoli–Lochkovian).

Description. This second type is completely different from the more common Osteostraci indet. and is only represented by two rhomboidal scales with elevated elongated tubercles, which are slightly wider in the anterior part (Fig. 27C). Each scale has three tubercles, one longer median and two shorter lateral. The basal part follows the general morphology of the scale and does not show any specialization. No clear neck is developed, but in crown view the anteriorly attached scale has a tubercle-free anterior area for overlap by the previous scale. In basal view the scale is concave with a bumpy surface.

The scarcity of present material prohibits histological investigation.

Occurrence. Pridoli–Lochkovian, Hall Land, North Greenland.

Chondrichthyes

Chondrichthyes indet.

Fig. 28

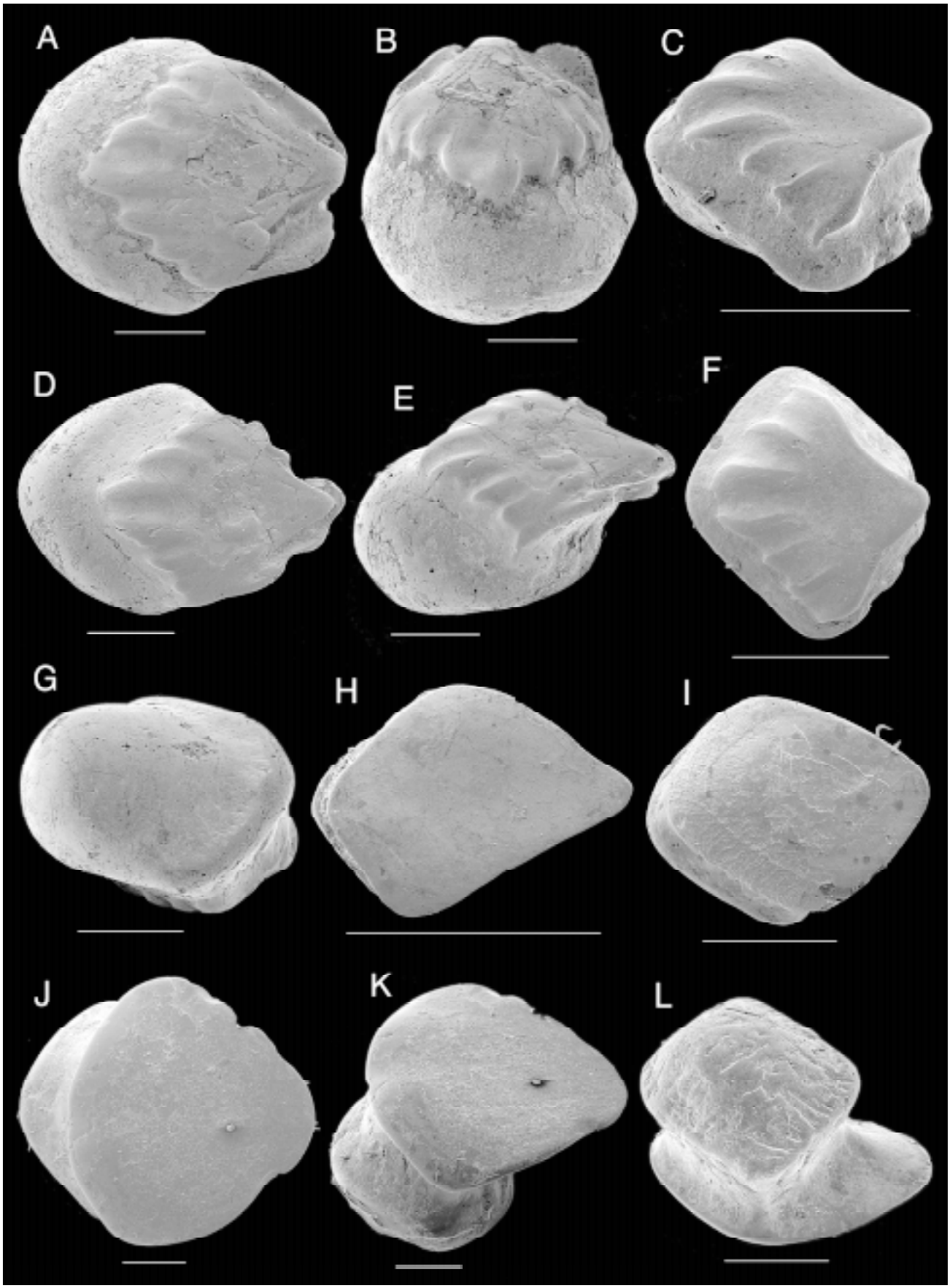
Figured material. MGUH VP 3554–3556 from GGU sample 319264.

Other material. Few poorly preserved specimens from GGU sample 319264.

Locality and age. The top of Monument, Hall Land, North Greenland, Chester Bjerg Formation, Early Devonian (Lochkovian).

Description. Chondrichthyes indet. includes odontodes which are found isolated or grown together to larger units (Fig. 28). Each odontode is very small and the largest unit, including about 5 variable sized scales, does not exceed 0.5 mm. Isolated odontodes have a round or slightly rhomboidal base (Fig. 28B). The base is low and in basal view either flat, concave or convex, sometimes exposing a tiny pulp opening. A high

Fig. 29. *Nostolepis* and *Gomphonchus*. SEM photomicrographs. Scale bars equal 0.2 mm.
A–**G**. *Nostolepis halli* sp. nov. **A**: Scale in crown view, holotype, MGUH VP 3567. **B**: Scale in anterior view, holotype, MGUH VP 3567. **C**: Scale in oblique crown view, MGUH VP 3568. **D**: Scale in crown view, MGUH VP 3569. **E**: Scale in oblique crown view, MGUH VP 3569. **F**: Scale in crown view, MGUH VP 3568. **G**: Scale in oblique basal view, MGUH VP 3570.
H–**L**. *Gomphonchus* cf. *G. sandelensis*. **H**: Scale in crown view, MGUH VP 3563. **I**: Scale in crown view, MGUH VP 3562. **J**: Scale in crown view, MGUH VP 3564. **K**: Scale in oblique crown view, MGUH VP 3564. **L**: Scale in oblique basal view, MGUH VP 3565.
MGUH VP 3562 from GGU sample 319264, Monument; MGUH VP 3563–3565, 3567–3570 from GGU sample 82738, Halls Grav.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inclination characterizes the tri-partite crown, which has the shape of a three-cusped tooth. A narrow and smooth median section is flanked by two wide, but shorter, lateral wings. The crown narrows towards the base, forming a short but pronounced neck. Several large canal openings perforate the neck on both sides. When the scales are grown together, differentiation of the base is not visible, and only the different crown units are seen. One well preserved specimen shows a group of three scales with welded bases (Fig. 28A). The main part is formed by a large scale, with two smaller scales growing on the anterior part. Another specimen shows a row of overlapping scales of different sizes with several large neck canal openings on both the anterior and posterior side (Fig. 28C).

Remarks. Since few scales were available, histological investigations were not made. Chondrichthyes indet. may be a growing polyodontodia of *Ctenacanthus* type in the scheme of Karatajute-Talimaa (1992).

Some vertebrate remains of unknown origin, treated under Incertae Sedis may also be comparable with true chondrichthyans (Fig. 43D, H, J).

Occurrence. Lochkovian, Monument, Hall Land, North Greenland.

Acanthodii

Order Climatiida Berg 1940
Family Climatiidae Berg 1940

Genus *Nostolepis* Pander 1856

Type species. *Nostolepis striata* Pander 1856, Late Silurian (Pridoli), Ohesaare Formation, Saaremaa, Estonia.

Diagnosis. Small and large scales with smoothly downbent anterior part of crown; neck less pronounced in anterior part; crown anteriorly ornamented by posteriorly converging or parallel strongly expressed ridges and ribs; superpositional growth with simple mesodentine in crown and irregular branching tubules rising from radial, circular and ascending vascular canals; cellular bone in base usually with numerous cell cavities.

Species content. *Nostolepis striata* Pander 1856; *N. alta* Märss 1986a; *N. applicata* Vieth 1980; *N. arctica* Vieth 1980; *N. athleta* Valiukevicius 1994; *N. costata* Goujet 1976; *N. curiosa* Valiukevicius 1994; *N. curta* Valiukevicius 1994; *N. gaujensis* Valiukevicius 1998; *N. gracilis* Gross 1947; *N. guangxiensis* Wang Nian-zhong 1992; *N. infida* Valiukevicius 1994; *N. kernavensis* Valiukevicius 1985; *N. lacrima* Valiukevicius 1994; *N. laticristata* Valiukevicius 1994; *N. matukhini* Valiukevicius 1994; *N. minima* Valiukevicius 1994; *N. multangula* Valiukevicius 1994; *N. multicostata* Vieth 1980; *N. robusta* (Brotzen 1934); *N. spina* Valiukevicius 1994; *N. taimyrica* Valiukevicius 1994; *N. tareyensis* Valiukevicius 1994; *N. tcherkesovae* Valiukevicius 1994.

Range. Early Silurian (Wenlock) – Middle Devonian (Eifelian).

Nostolepis halli sp. nov.

Fig. 29A–G; Fig. 30

Derivation of name. In honour of Charles Francis Hall, the leader of the U.S. North Polar Expedition 1871–73, who died and was buried in Hall Land. Also referring to the main fossil locality close to his grave.

Holotype. MGUH VP 3567 from GGU sample 82738 (Fig. 29A, B).

Figured material. MGUH VP 3567–3571, 3631 from GGU sample 82738.

Other material. About 60 scales from GGU samples 82734, 82736, 82737, 82738 and 298937.

Locality and age. The Halls Grav locality, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian (Pridoli).

Diagnosis. Homogeneous set of medium-sized scales, about 1 mm, with low rhomboidal crown, bent down anteriorly towards base and anteriorly diffuse neck; crown smoothly ridged anteriorly with intermediate furrows; lateral wings folded up; large convex base, displaced anteriorly, with lower posterior part; mesodentine tissue in crown with irregular branching tubules; cellular bone in base with few osteocyte cavities and process tubules.

Scale morphology. Like the other acanthodians, the scales of *Nostolepis halli* sp. nov. are quite poorly preserved. They are brown-yellow to dark brown, medium sized and vary in length from about 0.5–1 mm.

The set of scales is homogeneous and no clearly differentiated scale types seem to be present.

The rhomboidal or sector-shaped crown is smooth, flat or slightly convex (Fig. 29A–F). Postero-lateral crown margins are straight and meet in a posteriorly pointing crown apex. Smaller specimens may have postero-lateral margins that make a curve towards the centre of the scale before they meet (Fig. 29C, F). On a slightly lower level, at the postero-lateral sides, a small dorso-lateral wing is visible on each side in the best preserved specimens (Fig. 29A, B, D, E). The wing is folded along a median line with its lateral margins pointing upward. This in cross section V-shaped wing is characteristic of the species. Anteriorly 7–10 smooth ridges separated by short, shallow furrows run backwards towards the centre of the upper crown surface. They converge slightly but do not join before they disappear in the flat crown surface. The ridges are also evenly distributed on each side of an imaginary median line and bend gently down towards the neck and the base. Due to the presence of ribs and furrows, the anterior crown margin appears crenulated or notched in a dorsal view. On the upper crown surface it is often possible to see each layer of growth. The crown is higher posteriorly, which gives a slightly posteriorly rising inclination. Posteriorly the low neck is much more pronounced than in the indistinct lower anterior part. The neck is smooth and neither pore openings nor neck furrows are visible. The transition between the neck and the anterior crown furrows is very gentle and the neck is only pronounced near the lower ends of the intermediate ridges. Usually the base is much wider than the crown and is much higher anteriorly. A large part of the swollen displaced base projects at the front.

Scale histology. The upper crown surface in most scales of *Nostolepis halli* is poorly preserved but overlapping, sometimes visible in the antero-dorsal upper part of the crown, indicating a superpositional type of growth; up to seven growth lamellae are visible and superposed on the embryonic scale (Fig. 30A). Each lamella in the crown contains irregular branching tubules of mesodentine type (Fig. 30B). The proportionally large base is composed of layers of cellular bone with round or flattened osteocyte cavities and tubules of irregularly distributed short branching processes (Fig. 30A). The flattened cavities are, together with associated tubules, generally arranged along the longitudinal axis of the basal layers. Each layer or zone is laminated and continuous with one on the crown. Long tubules

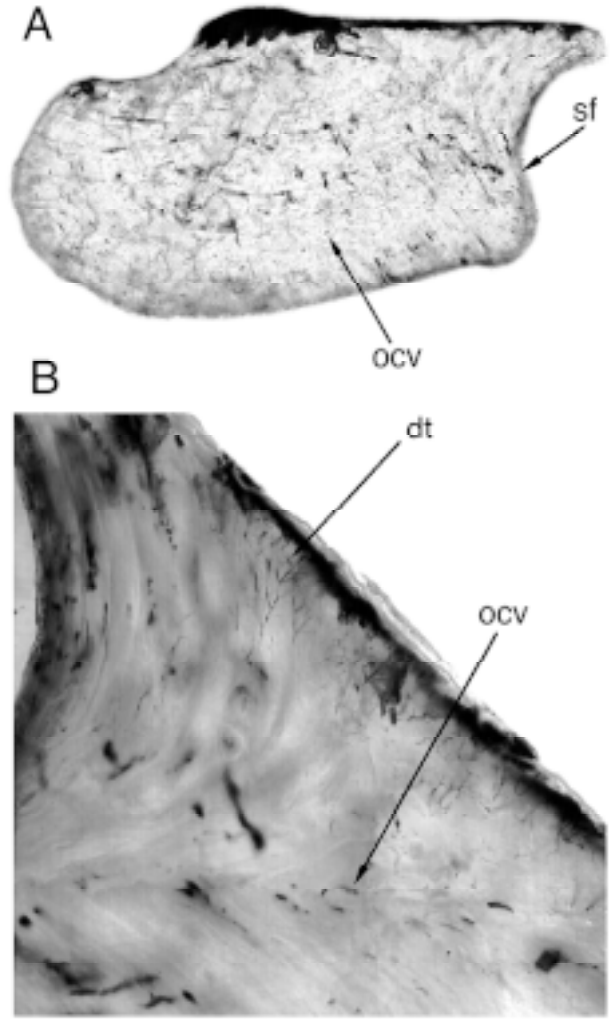


Fig. 30. *Nostolepis halli* sp. nov. Histology of the scale.
A: Scale in vertical longitudinal section, MGUH VP 3571, × 98.
B: Scale in vertical longitudinal section, close up of crown, MGUH VP 3631, × 325.
All specimens from GGU sample 82738, Halls Grav.
dt: dentine tubules; **ocv**: osteocyte cavities; **sf**: tubules of Sharpey's fibres.

of Sharpey's fibres are developed perpendicular to these basal layers.

Scale dimensions. Length 0.5–1.1 mm; width 0.5–1.0 mm.

Remarks. The Greenland species is delimited from comparable species by the up-bent shape of the lateral wing. Lateral structures of other species of *Nostolepis* are instead expressed as vertical, diagonal or horizontal ribs. The smaller *Gomphonchus* cf. *G. hoppei*, reported by Vieth (1980) from the Lochkovian strata of the Canadian Arctic, has a general morphology more similar to *N. halli* than the traditional *G. hoppei*. Its

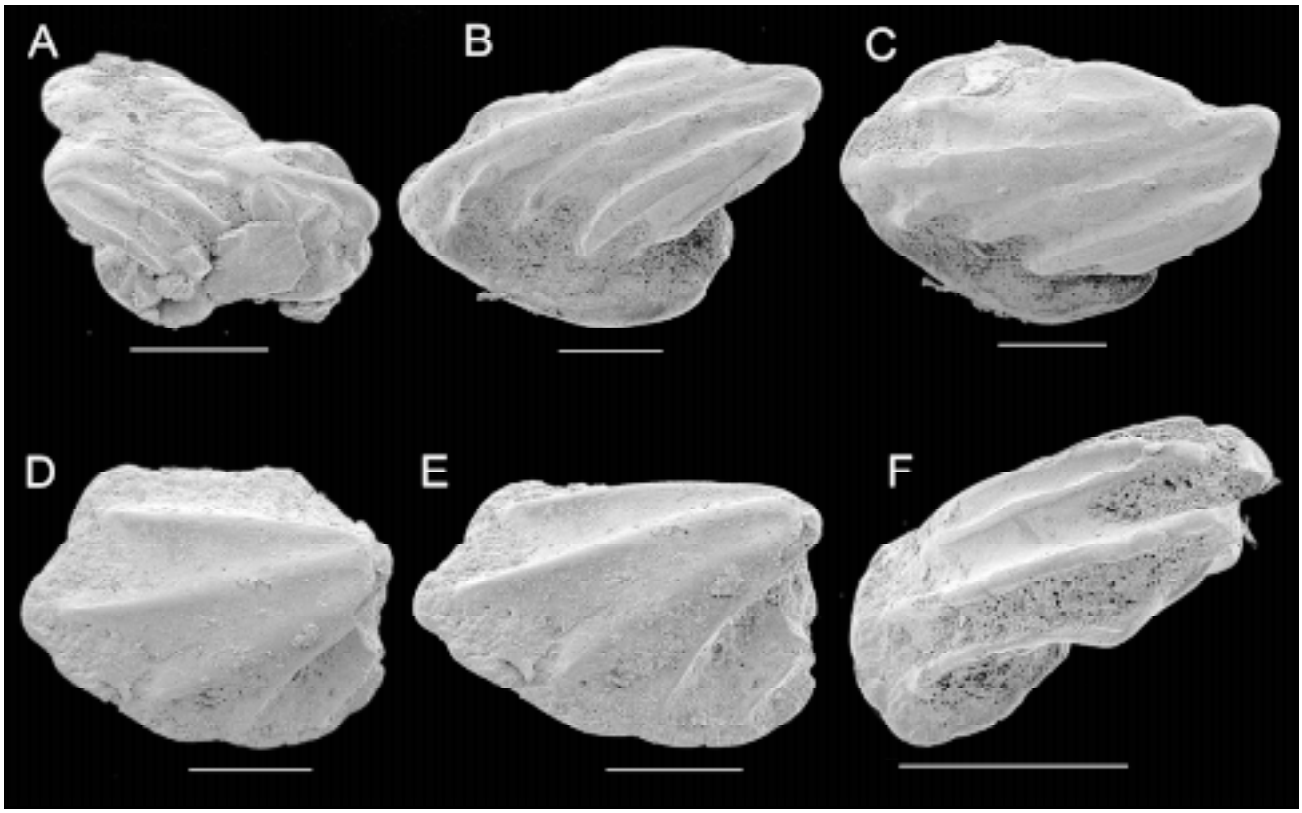


Fig. 31. Climatiida indet. SEM photomicrographs. Scale bars equal 0.2 mm.
A: Head? scale in oblique crown view, MGUH VP 3558. **B**: Trunk scale in oblique crown view, MGUH VP 3560. **C**: Scale in crown view, MGUH VP 3560. **D**: Scale in crown view, MGUH VP 3557. **E**: Scale in oblique crown view, MGUH VP 3557. **F**: Scale in oblique crown view, MGUH VP 3559.
MGUH VP 3557–3559 from GGU sample 82736, Halls Grav; MGUH VP 3560 from GGU sample 82738, Halls Grav.

illustrated histology suggests it is probably also of *Nostolepis* but its lateral ridges are clearly different from the wings of *N. halli*.

Occurrence. Pridoli, Halls Grav, Hall Land, North Greenland.

Climatiida indet.
Figs 31, 32

Figured material. MGUH VP 3557–3559 from GGU sample 82736, MGUH VP 3560, 3561 from GGU sample 82738.

Other material. About 35 scales from GGU sample 82734, 82736, 82737, 82738.

Locality and age. The Halls Grav locality, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian (Pridoli).

Scale morphology. The small and variably shaped climatiid scales are a rare component of the collections from the Halls Grav locality. The crown has a high inclination from the larger base and narrows towards the posteriorly pointing end (Fig. 31). In upper view, the crown is convex or almost flat with ridges which converge posteriorly. The scales may have as many as eight ridges converging from the base towards the posterior crown apex. One scale type has a cone-shaped crown with distinct ridges, converging from the base to the slightly posteriorly pointing apex (Fig. 31D, E). Some of the ridges run more at the lateral areas. The neck is mostly weakly developed. Another type, probably from the body, has a flatter more elongated or rhomboidal crown with less inclination and a more pronounced neck (Fig. 31B, C). In this type, the ridges run more on the median upper surface of the crown with only very few on the lateral areas. They bend down anteriorly towards the neck and lateral ridges are much shorter. In basal view the posteriorly overhanging crown is almost smooth and shows only

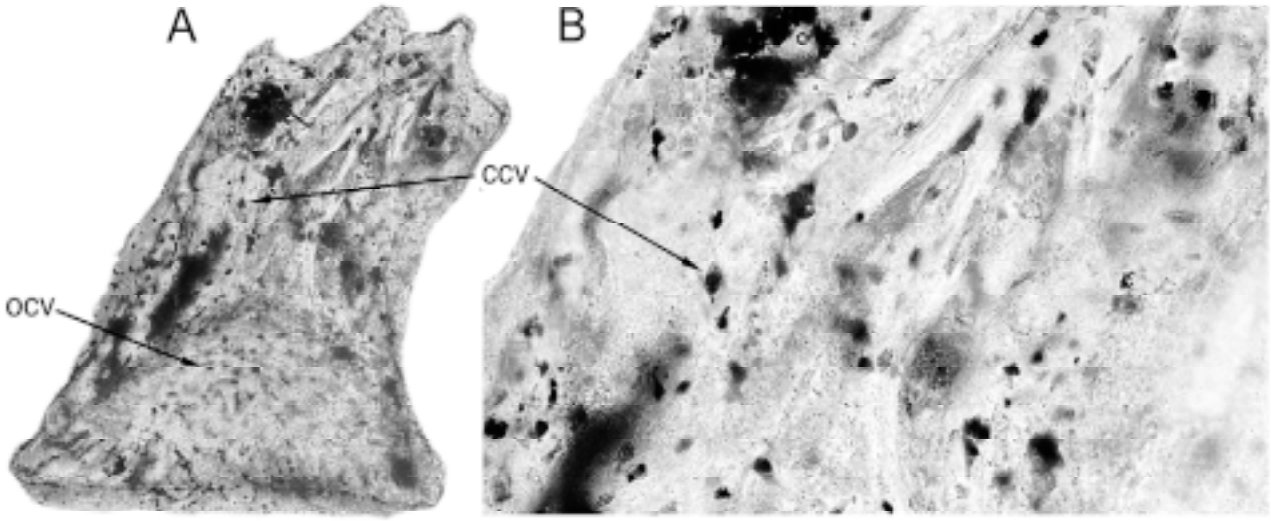


Fig. 32. Climatiida indet. Histology of scale.
A: Scale in vertical longitudinal section, MGUH VP 3561, × 177. **B**: Scale in vertical longitudinal section, close up of crown, MGUH VP 3561, × 590.
MGUH VP 167 from GGU sample 82738, Halls Grav.
ccv: cavities in crown; **ocv**: osteocyte cavities.

very weak striations. All scales have a round or irregular base which is often very thin. In basal view the scales are flat, convex or just slightly concave. Less regular scales, almost triangular in outline, appear to be composed of three smaller welded scales (Fig. 31A) and may be derived from the head region.

Scale histology. The large embryonic scale has perhaps only one or two growth zones added on the top and sides (Fig. 32). The base of the embryonic scale has many round osteocyte cavities with bone cell processes (Fig. 32A). Sharpey's fibres are present in the lower part of the base. The crown is poorly preserved in available sections but shows several rounded cell cavities with spreading tubules (Fig. 32B).

Scale dimensions. Length 0.3–0.7 mm; width 0.2–0.6 mm.

Remarks. Although the histological information is limited, it indicates similarities with the most primitive acanthodian structures found in *Euthacanthus* Powrie 1864 from the Lower Devonian of Scotland (Denison 1979). Morphologically these scales are more similar to *Climatius* Agassiz, 1845 and *Nostolepis* Pander 1856. The base of *Climatius* has no (or very few) bone cell cavities (Ørvig 1967; Denison 1979).

Occurrence. Pridoli, Halls Grav, Hall Land, North Greenland.

Order Ischnacanthida Berg 1940
Family Ischnacanthidae Woodward 1891

Genus *Gomphonchus* Gross 1971

Type species. *Gomphodus sandelensis* Pander 1856 (type by monotypy); Late Silurian (Pridoli), Ohesaare Formation, Saaremaa, Estonia.

Diagnosis. Small and large scales (0.3–1.3 mm) with low or convex base, often displaced anteriorly; low or elevated rhomboidal crown with low inclination; smooth or ornamented with radiating ridges and furrows; superpositional growth with dentine in crown; cellular and acellular bone in base and outer enameloid layer on crown; long fine branching ascending vascular canals rising from neck towards crown centre in each dentine growth layer; fine network of horizontal and radial canals in crown.

Species content. *Gomphonchus sandelensis* (Pander 1856); *G. alveatus* Vieth 1980; *G.*? bogongensis Burrow 1997; *G. hoppei* (Gross 1947); *G. liujingensis* Wang Nian-zhong 1992; *G. tauragensis* Valiukevicius 1998; *G.*? *turnerae* Burrow 1995.

Range. Early Silurian (Wenlock) – Early Devonian (Emsian).

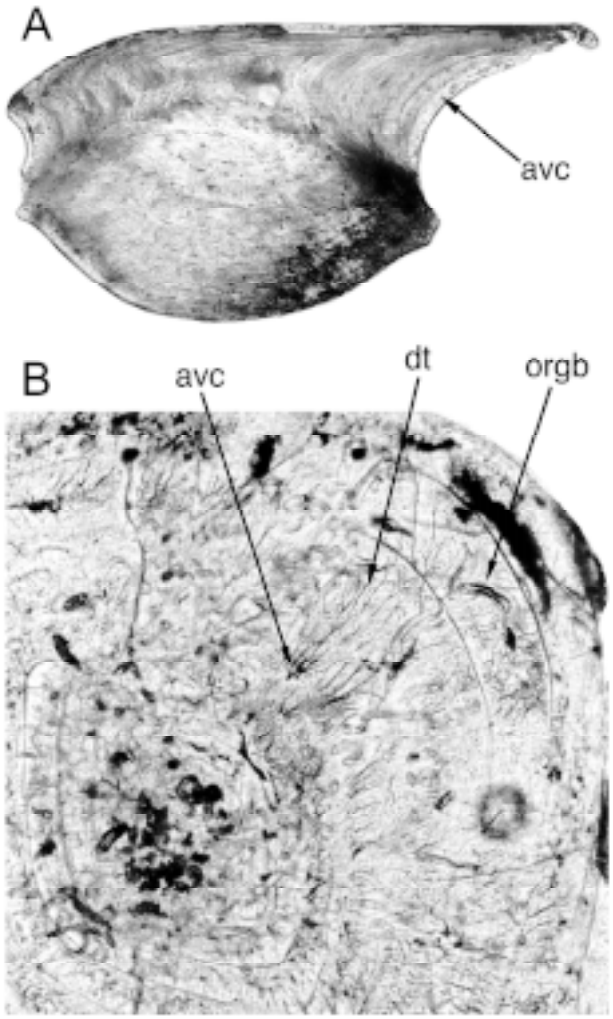


Fig. 33. *Gomphonchus* cf. *G. sandelensis*. Histology of the scale. **A**: Scale in vertical longitudinal section, MGUH VP 3566, × 216. **B**: Scale in horizontal crown section, MGUH VP 3632, × 191. All specimens from GGU sample 82738, Halls Grav.
avc: ascending vascular canals; **dt**: dentine tubules; **orgb**: organism borings or burrows.

Remarks. Gross (1971) concluded, contrary to earlier views (Gross 1947), that several specimens of the type species, *G. sandelensis*, have bone cells in the basal tissue. Often specimens lack this distinct character, probably due to differences in preservation. J. Valiukevicius (1995; personal communication 1998) suggests that *Gomphonchus* may have both cellular and acellular bone in the base.

***Gomphonchus* cf. *G. sandelensis* (Pander 1856)**
Fig. 29H–L, I; Fig. 33

Syntypes. *Gomphodus sandelensis*, Pander 1856, table. 6, fig. 15–17. Late Silurian (Pridoli), Ohesaare Formation, Saaremaa, Estonia. The types have been lost.

Figured material. MGUH VP 3562 from GGU sample 319264, MGUH VP 3563–3566, 3632 from GGU sample 82738.

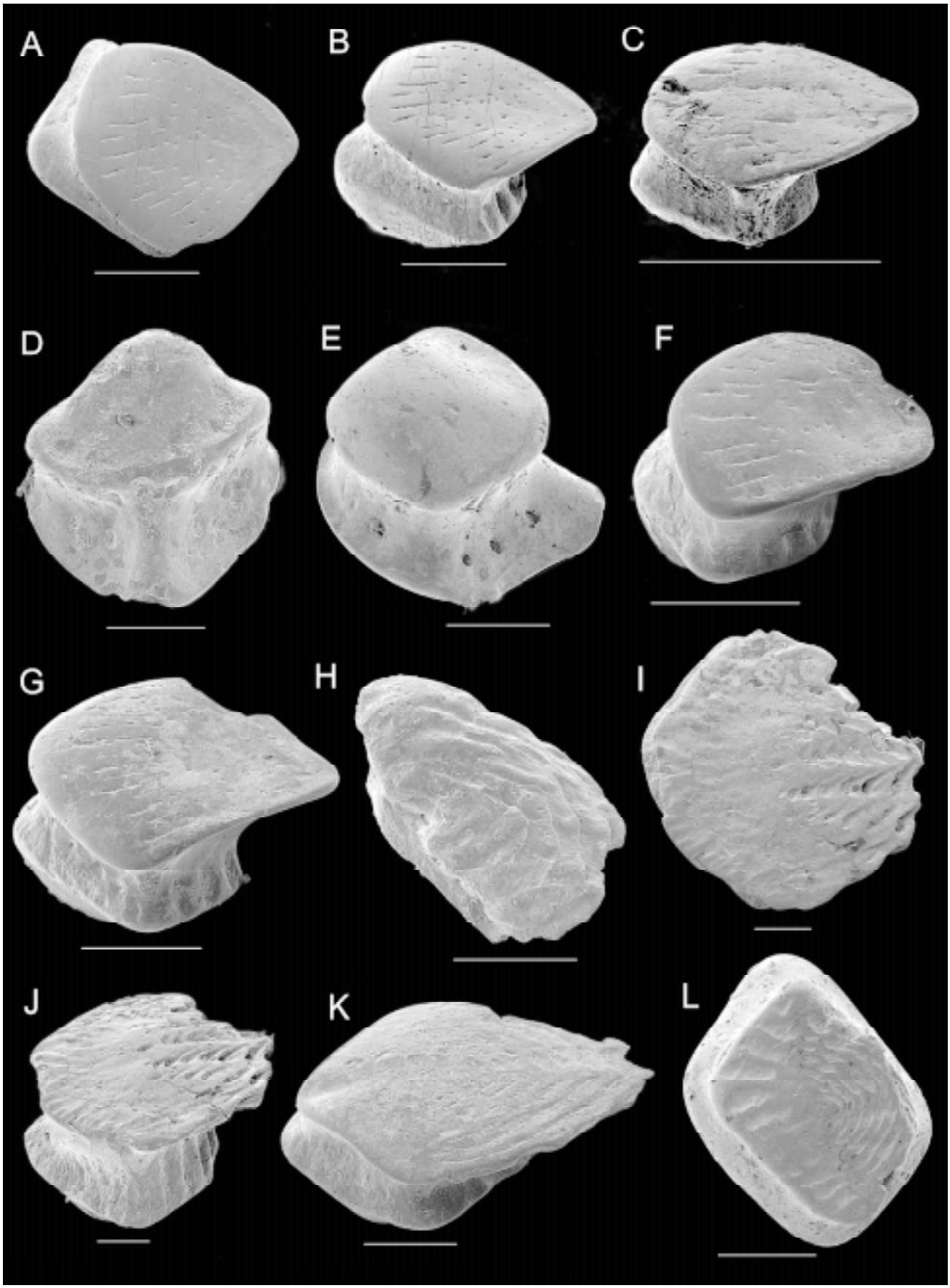
Other material. Hundreds of specimens from GGU samples 82734, 82736, 82737, 82738, 298937 and 319264.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Diagnosis. Small and large scales (0.3–1.2 mm) with low inclined and flat rhomboidal crown; smooth or anteriorly ridged upper crown surface; crown bending slightly down anteriorly; neck high and distinct with posterior vertical ridges; base convex, often displaced anteriorly; superpositional growth with long, fine, little branching, ascending vascular canals; acellular bone in the base.

Scale morphology. Scales of *Gomphonchus* cf. *G. sandelensis* are very rare and vary in colour from yellow-brownish to darker brown. They are poorly preserved, often with broken crown edges, and are represented by one main morphotype. Scale length equals crown length and varies between 0.2 and 1.0 mm. The crown is rhomboidal in shape with rounded corners. The

Fig. 34. *Poracanthodes*. SEM photomicrographs. Scale bars equal 0.2 mm.
A–**G**. *Poracanthodes* cf. *P. punctatus*. **A**: Scale in crown view, MGUH VP 3572. **B**: Scale in oblique crown view, MGUH VP 3572. **C**: Scale in oblique crown view, MGUH VP 3573. **D**: Scale in postero-basal view, MGUH VP 3574. **E**: Scale in oblique basal view, MGUH VP 3575. **F**: Scale in oblique crown view, MGUH VP 3576. **G**: Scale in oblique crown view, MGUH VP 3577.
H–**L**. *Poracanthodes* cf. *P. porosus*. **H**: Scale in oblique crown view, MGUH VP 3583. **I**: Scale in crown view, MGUH VP 3596. **J**: Scale in oblique crown view, MGUH VP 3596. **K**: Scale in oblique crown view, MGUH VP 3582. **L**: Scale in crown view, MGUH VP 3584.
MGUH VP 3572–3577, 3584 from GGU sample 82738, Halls Grav; MGUH VP 3582 from GGU sample 82736, Halls Grav; MGUH VP 3583, 3596 from GGU sample 319264, Monument.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anterior corner is more rounded than the pointed posterior end. The most anterior part of the crown often bends down slightly towards the base. Often concentric layers are evident, due to abrasion, on the smooth crown surfaces, which are flat or slightly convex. The clear bilateral symmetry is often lost in these scales (Fig. 29H). From the flat dorsal surface and the sharp edges, the crown slopes with a low angle towards the crown centre and bends back again, forming a quite distinct and high neck. The neck is evenly high all around the scale, given by very little or no visible inclination. Posteriorly, the lower part of the neck has vertical ribs with intervening openings of the dentine canals. Small dentine canal or tubule openings are visible all around the neck. The junction between the neck and the base is characterized by a well marked rim. In basal view, the base is oval or rhombic with rounded corners and often clear concentric striping. The high vaulted base is narrower than the crown, often with the swelling displaced anteriorly.

Scale histology. Many scales are poorly preserved and the histological structures are often disturbed by irregular canals formed by boring organisms (Fig. 33B). *G.* cf. *G. sandelensis* has a superpositional type of growth with at least 8 layers superposed on the embryonic scale (Fig. 33A). Narrow ascending canals in each dentine layer divide and send off few side-branches of finer tubules (Fig. 33B). Osteocyte cavities are not clearly visible in the base. Numerous tubules of Sharpey's fibres in the base run radially and perpendicularly from the outer surface towards the centre.

Scale dimensions. Length 0.2–1.0 mm; width 0.2–1.0 mm.

Remarks. *G.* cf. *G. sandelensis* differs from the type material by not having the distinct neck ribs anteriorly and the anterior ribs of the upper crown surface. A few scales from the Halls Grav locality are found which might come from the head region. The true taxonomical affinity, however, is unknown and they could be related to any of the acanthodian scale taxa.

Occurrence. *G.* cf. *G. sandelensis,* Pridoli–Lochkovian, Hall Land, North Greenland; *G. sandelensis,* Wenlock–Pridoli, Saaremaa, Estonia and Latvia; Ludlow, Gotland, Sweden; Pridoli, Scania, Sweden; Pridoli, Timan-Pechora region, north-eastern part of European Russia; Pridoli, erratic boulder, Germany; Lower Devonian, Arctic Canada; Lochkovian, Spain.

Genus *Poracanthodes* Brotzen 1934

Type species. *Poracanthodes punctatus* Brotzen 1934. Lower Devonian? erratic boulder (Bey. 36), the lowlands of northern Germany. Later designated as type species by Gross (1971), see also Valiukevicius (1992).

Diagnosis. Large and small scales with flat rhomboidal crown; ornamented crown with short parallel or radial ridges on anterior part, alternatively unornamented; posterior part of crown smooth or often with concentric grooves and multicuspidate ridges; pore canal system with radial pore, arcade pore and pore canals; pore canals open on upper crown surface with numerous pores arranged in radial or concentric rows; crown composed of dentine and mesodentine; base composed of acellular bone or bone with osteocyte cavities. (Modified from Valiukevicius 1992.)

Species content. *Poracanthodes punctatus* Brotzen 1934; *P. gujingensis* Wang Nian-zhong & Dong Zhizhong 1989; *P. menneri* Valiukevicius 1992; *P. porosus* Brotzen 1934; *P. subporosus* Valiukevicius 1998.

Range. Late Silurian (Ludlow) – Early Devonian (Lochkovian).

Remarks. For a long time *Poracanthodes* was considered to represent lateral line scales of *Gomphonchus* (Gross 1971; Denison 1979), an idea subsequently changed by the find of articulated specimens of *Poracanthodes menneri* with a complete squamation of poracanthodiform scales (Valiukevicius 1992). Valiukevicius (1995) also introduced a *Poracanthodes* type of histology for scales, including several genera such as *Poracanthodes*, *Gomphonchus* (only *G. hoppei*), *Ectopacanthus* and *Lietuvacanthus*. This grouping is not stable for taxonomical usage since, for example, several species within *Poracanthodes* differ by either having superpositional or areal growth which should serve as a character to split up the now well established genus *Poracanthodes*. Revision is also prompted by the presence of cellular or acellular bone tissue. Vergoossen (1997) proposed a taxonomical revision of poracanthodid acanthodians but this cannot be completely adapted, since his reassignment of the type species *Poracanthodes punctatus* to *P. porosus* and the new *Brotzenolepis punctatus* is inadmissible following the International Code of Zoological Nomenclature (Ride *et al*. 1985, Article 61a) and thereby not valid. Although the validity of the genus *Poracanthodes* has

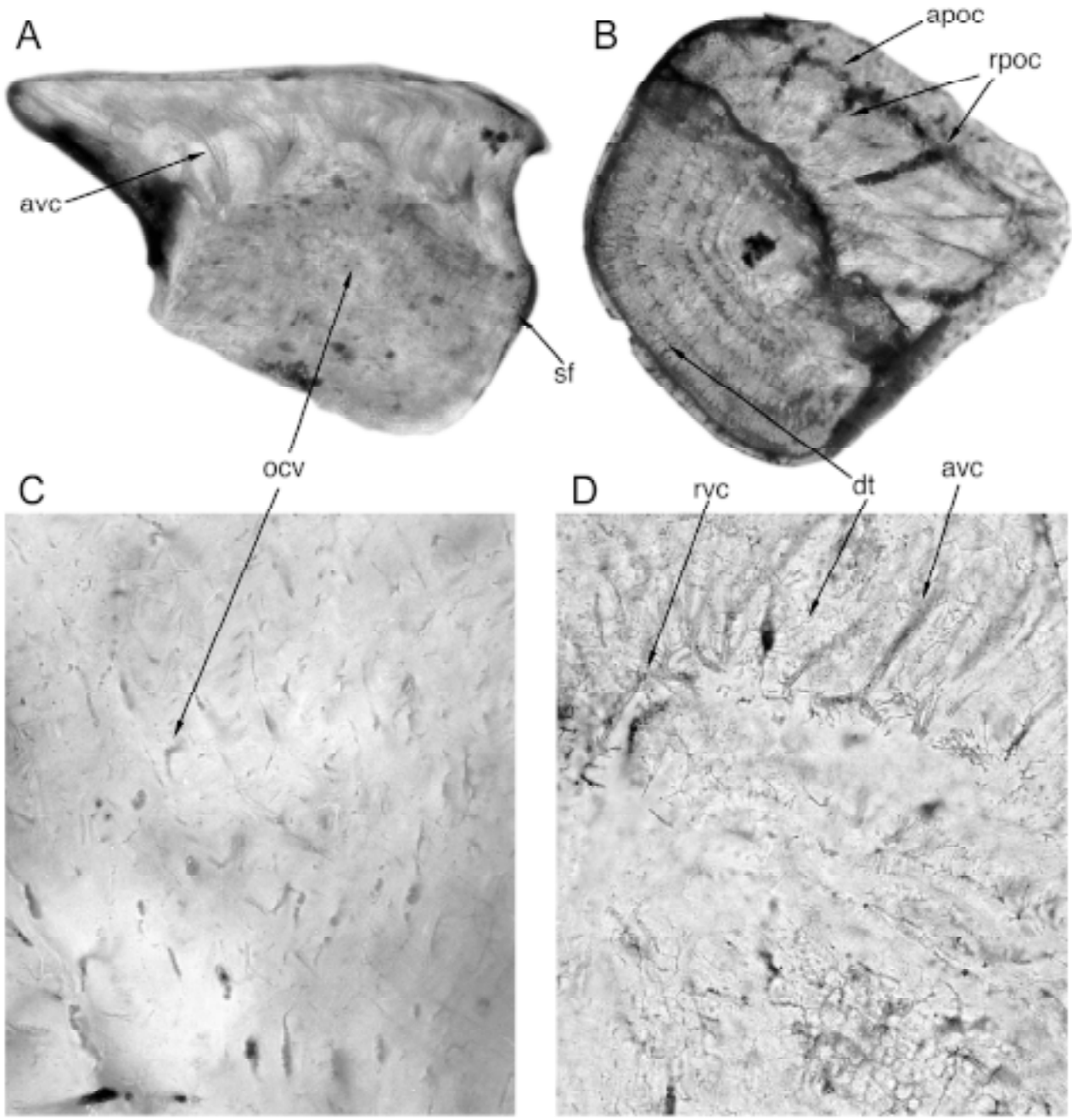


Fig. 35. *Poracanthodes* cf. *P. punctatus*. Histology of the scale.
A: Scale in vertical longitudinal section, MGUH VP 3578, × 174. **B**: Scale in horizontal crown section, MGUH VP 3579, × 152. **C**: Scale in vertical longitudinal section, close up of basal tissue, MGUH VP 3580, × 548. **D**: Scale in vertical longitudinal section, close up of crown, MGUH VP 3581, × 514.
All specimens from GGU sample 82738, Halls Grav.
apoc: arcade pore canals; **avc**: ascending vascular canals; **dt**: dentine tubules; **ocv**: osteocyte cavities; **rpoc**: radial pore canal; **rvc**: radial vascular canals; **sf**: tubules for Sharpey's fibres.

been questioned, it became definitely valid when Valiukevicius (1992) designated *P. punctatus* as the type species.

Poracanthodes cf. *P. punctatus* Brotzen 1934

Fig. 34A–G; Fig. 35

1986a *Poracanthodes* aff. *punctatus* Brotzen – Märss, p. 57, plate 32, figs 6, 7, 9.

Syntypes. Poracanthodes punctatus, Brotzen 1934, plate 3, figs 1, 8. Lower Devonian? erratic boulder (Bey. 36), the lowlands of northern Germany. The material seems to be lost.

Figured material. MGUH VP 3572–3581 from GGU sample 82738.

Other material. Hundreds of specimens from GGU samples 82734, 82736, 82737, 82738, 298937, 298960 and 319264.

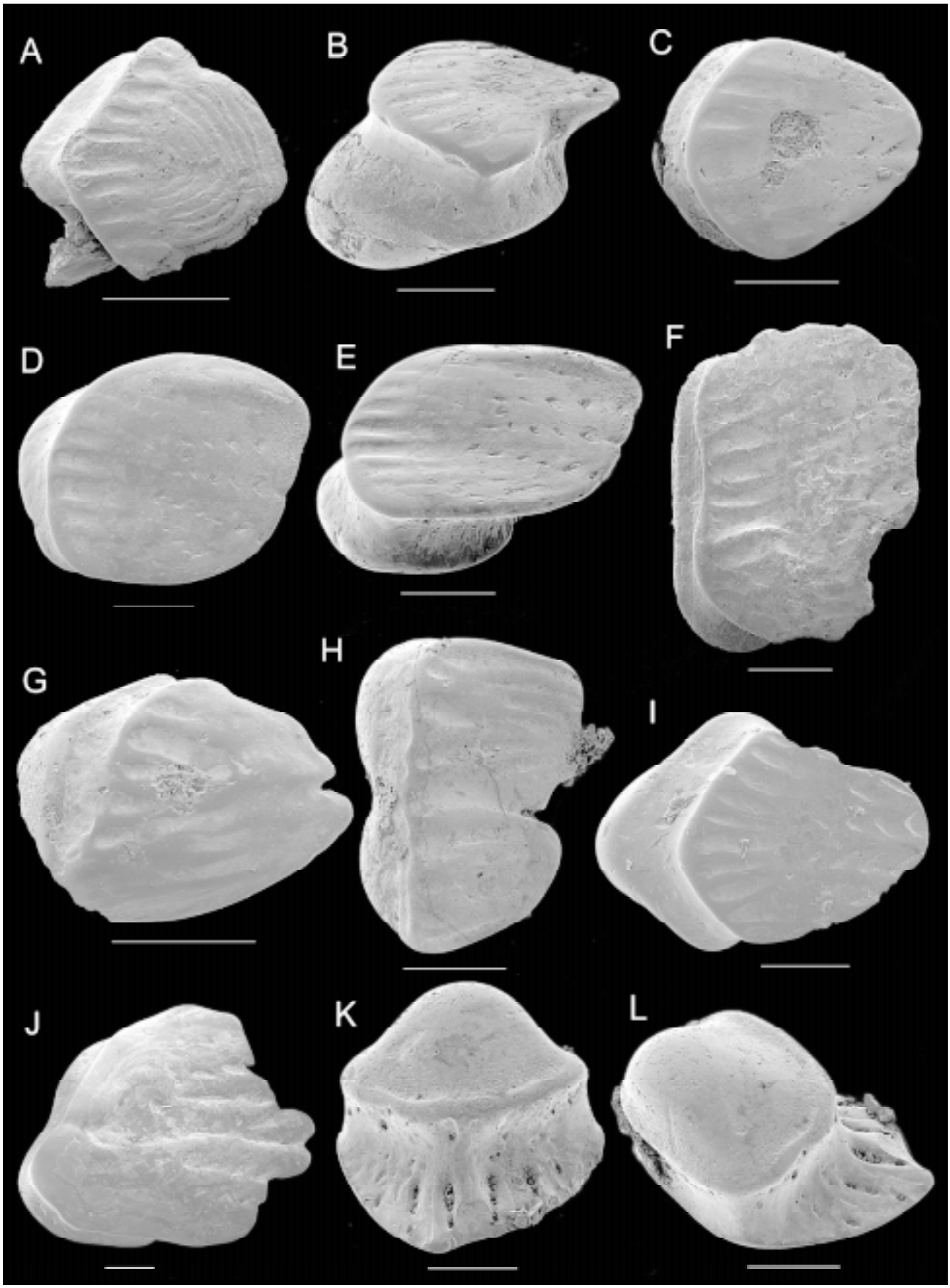
Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Diagnosis. Small and large poracanthodid scales with rhomboidal crown; anterior crown margin round or angular; anterior part smooth, rarely with short ridges, often with median sulcus; crown surface with concentric rows of tiny pores, parallel to the postero-lateral crown margins; high neck with posterior openings for radial pore canals above openings for vascular canals; superpositional type of growth; pore canal system with radial pore canals connected by arcade pore canals; pore canals run from arcade canal to openings in the upper crown surface.

Scale morphology. Scales of *Poracanthodes* cf. *P. punctatus* vary in colour from dirty white to amber brown or dark brown. They are quite well preserved and highly variable in size, 0.2–0.9 mm in length. The crown shape is smoothly rhomboidal with a rounded anterior outline and a longer, pointed posterior part (Fig. 34A–C, F, G). The crown has a very low inclination but anteriorly the flat or slightly convex crown bends down slightly towards the base. Small pores are visible on the otherwise smooth upper surface. They have an almost concentric orientation in the posterior part, following the growth lamellae. Pores on the central anterior part of the upper crown surface are arranged along narrow slits or furrows of different length. They have an antero–posterior orientation and may be difficult to separate morphologically from the anterior part of the more concentric rows. Just below the acute margins, the crown gets narrower, forming a high distinctive neck. Large openings of four or six radial canals are visible on the part of the neck that joins the lower side of the crown (Fig. 34D, E). Smaller vascular canal openings, on a lower level on the neck, occur posteriorly where vertical slits or furrows are also developed at the basal part of the neck. The base is round or rhomboidal and follows the shape of the crown. The base and the neck are clearly separated by a brim. Posteriorly the crown is larger and projects over the base. The anteriorly displaced base, which seldom projects anteriorly, is usually higher in the frontal part. Growth lines are sometimes clearly visible at the basal surface.

Scale histology. The scales show superpositional growth with up to nine lamellae superposed on the embryonic scale, but due to their thinness these are sometimes difficult to detect in the upper posterior part of the crown. External morphological characters also suggest superpositional growth. The crown is composed of dentine with narrow ascending vascular canals rising from the basal part in each growth zone (Fig. 35A). These dentine canals branch into fine dentine tubules, forming a complex and multibranched dentine pattern (Fig. 35D). Each ascending canal joins with the dentine canal in the next lamellae by larger horizontal dentine canals. These radial vascular canals must not be confused with the larger radial pore canals that belong

Fig. 36. *Poracanthodes* cf. *P. porosus*. SEM photomicrographs. Scale bars equal 0.2 mm.
A: Scale in crown view, MGUH VP 3585. **B**: Scale in oblique crown view, MGUH VP 3586. **C**: Scale in crown view, MGUH VP 3587. **D**: Scale in crown view, MGUH VP 3588. **E**: Scale in oblique crown view, MGUH VP 3588. **F**: Scale in crown view, MGUH VP 3597. **G**: Scale in crown view, MGUH VP 3589. **H**: Two joint scales in crown view, MGUH VP 3590. **I**: Scale in crown view, MGUH VP 3591. **J**: Scale in crown view, MGUH VP 3592. **K**: Scale in postero-basal view, MGUH VP 3593. **L**: Scale in oblique basal view, MGUH VP 3593.
MGUH VP 3585–3593 from GGU sample 82738, Halls Grav; MGUH VP 3597 from GGU sample 319264, Monument.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to the pore canal system of porosiform acanthodian scales. The pore canals are best visible as openings on the crown surface where they form the typical pattern of *P.* cf. *P. punctatus*. Four or six large radial pore canals extend from the centre and open on the neck, close to the lower crown surface (Fig. 35B). On a slightly higher level concentric arcade pore canals are developed, following each growth lamellae. The base has growth layers parallel to the subsurface, composed of cellular bone with round or spindle-shaped osteocyte cavities (Fig. 35C) which are arranged along the boundaries of the individual layers. The basal tissue also contains fibres and short multibranched canals. Perpendicular to the layers and the parallel fibres both long and short tubules of Sharpey's fibres are developed.

Scale dimensions. Length 0.2–0.9 mm; width 0.2–1.0 mm.

Remarks. *Poracanthodes punctatus* Brotzen 1934 from erratic boulders of the North German lowlands differs from present material by not having clear narrow longer slits on the anterior part of the crown surface. Other specimens from erratic boulders of similar age also lack this character and may also differ by having a deeper sulcus in the anterior part of the crown (Gross 1947, 1971; Märss 1986a). Scales from the Late Silurian (Pridoli) Kaugatuma Stage of Estonia, referred by Märss (1986a) to *P.* aff. *P. punctatus*, are morphologically similar to the scales from North Greenland.

Some of the head scales of unknown affinity (Fig. 43A–C) may belong to *Poracanthodes* cf. *P. punctatus* or other acanthodian taxa.

Occurrence. *Poracanthodes* cf. *P. punctatus*, Pridoli–Lochkovian, Hall Land, North Greenland; *Poracanthodes punctatus*, Pridoli–Lochkovian, Estonia and Latvia; Pridoli, Manbrook, Welsh Borderland, Great Britain; Early Devonian, erratic boulder, lowlands of northern Germany.

Poracanthodes cf. *P. porosus* Brotzen 1934

Fig. 34H–L; Fig. 36; Fig. 37

1976 '*Gomphodus*' and '*Poracanthodes*' types – Bendix-Almgreen, fig. 443G–I, K.

Holotype. *Poracanthodes porosus* Brotzen 1934, plate 3, fig. 2, Lower Devonian? erratic boulder (Bey. 36), lowlands of northern Germany. Material seems to be lost.

Figured material. MGUH VP 3582 from GGU sample 82736, MGUH VP 3584–3595 from GGU sample 82738, MGUH VP 3583, 3596, 3597 from GGU sample 319264.

Other material. Thousands of scales are available from GGU samples 82734, 82736, 82737, 82738, 298937, 298953, 298954, 298960, 298963 and 319264.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Diagnosis. Small and large scales with superpositional or areal growth; rhomboidal crown with smooth or ridged anterior part; zigzag growth pattern on posterior part of crown; upper crown surface with radial rows of large pores; pore canal system with pore canals which run from the wide radial pore canals towards upper crown surface; radial pore canal openings on the upper part of the neck.

Scale morphology. Scales of *Poracanthodes* cf. *P. porosus* are very common in all the vertebrate yielding samples from the Chester Bjerg Formation. They are badly preserved and the posterior part of the crown is usually broken or completely destroyed. The colour of the scales varies from white to dark brown within the same sample. There is a high variability in size among this morphologically homogeneous group of scales, but it is still possible to detect several basic types.

The most common type has a posteriorly protruding crown which may be smoothly rhomboidal or rounded and sometimes with a more irregular shape (Fig. 36C–L), which may be due to two scales that have grown together (Fig. 36H). The crown is usually flat with a very low plane inclination, but it may be slightly convex or concave (Fig. 36D, E, G, H). Up to six rows of pore openings run radially or longitudinally from the centre towards the posterior margin of the otherwise smooth crown surface, but clear pores are absent in some specimens (Fig. 36G, H). Up to eight wider, deeper furrows with intermediate ridges are developed and extend from the centre towards the anterior crown margin. The upper crown surface often appears heavily worn and the ornamentation is only weakly visible. In some specimens it is possible to detect a faint zigzag growth pattern in the posterior part of the crown (Fig. 36C, I). The well pronounced neck is quite low and perforated by small and larger pores in the anterior part (Fig. 36K, L). The smaller

pore openings are concentrated on a median level, representing the openings of radial vascular canals. The larger openings are arranged in short slit-like rows on the lower side of the crown and towards the neck. They represent the radial pore canal and associated pore canals. The anteriorly protruding base is strongly convex and separated from the crown and its neck by a well marked rim. The anterior part of the concentrically striped base is higher and more vaulted than the posterior part.

A few scales have a more elongated rhomboidal shape of the crown and show a clear zigzag pattern in the posterior part of the crown (Fig. 34K). The anterior part is smooth, often with a marginal sulcus.

A second scale type differs mainly by the ornamentation of the upper crown surface. It lacks the weak zigzag pattern in the posterior part of the crown. Instead these scales have concentric grooves parallel to the postero-lateral margins (Fig. 34L; Fig. 36A). The pore canal openings are still arranged radially and perpendicular to these grooves. In the anterior part of the crown up to eight regular wide furrows with intermediate ridges are developed.

The third distinct scale type has a more rounded crown with short irregular and weakly developed ridges on the anterior part of the upper crown surface (Fig. 34I, J). Pore canal openings are arranged in radial rows that run from the centre towards the posterior margin. Between the rows are ridges, which are cut by concentric growth lines that give an overlapping zigzag growth pattern. The scales have neck pores and ridges on the posterior part of the clear and relatively high neck.

Scale histology. The first and most common type of scale has superpositional growth with at least six layers superposed on the embryonic scale. The second type probably has superpositional growth while the third type most likely has areal growth. The dentinous crown has ascending vascular canals rising from the basal part which branch into finer dentine tubules in each growth zone (Fig. 37A). The pore canal system of these porosiform scales is characterized by up to six wide radial pore canals (Fig. 37B). Several wide pore canals extend from the radial pore canals towards the upper crown surface, where they are visible as large pore openings. No arcade canals are found in the North Greenland forms. The radial pore canals open on the lower crown surface, close to the neck (Fig. 36K, L). The smaller openings of the radial vascular canals open on the neck. The base has growth layers composed of

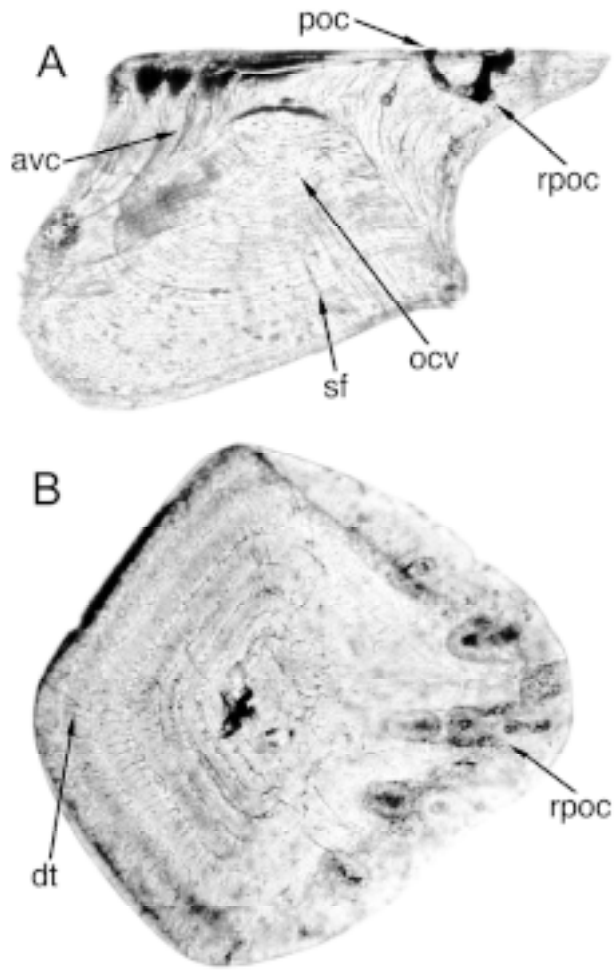


Fig. 37. *Poracanthodes* cf. *P. porosus*. Histology of the scale. **A**: Scale in vertical longitudinal section, MGUH VP 3594, × 122. **B**: Scale in horizontal crown section, MGUH VP 3595, × 127. Both specimens from GGU sample 82738, Halls Grav. **avc**: ascending vascular canals; **dt**: dentine tubules; **ocv**: osteocyte cavities; **poc**: pore canals; **rpoc**: radial pore canal; **sf**: tubules for Sharpey's fibres.

cellular bone with round or spindle-shaped osteocyte cavities parallel to the subsurface (Fig. 37A). Both long and short tubules of Sharpey's fibres are developed perpendicular to the layers and the parallel fibres.

Scale dimensions. Length 0.2–1.0 mm; width 0.2–1.0 mm.

Remarks. Valiukevicius (1992) showed that the variability among scales from different parts of the body of *Poracanthodes menneri* from the Lower Devonian of Severnaya Zemlya is not notably large which, together with histological characters, suggests that scales referred here to *P.* cf. *P. porosus*, probably belong to several species. The three basic types of *P.* cf. *P. porosus*

from the Chester Bjerg Formation mainly differ in the ornamentation in the anterior part of the crown and by growth type. The first and most common type shows regular ridges and furrows on the anterior part of the crown. This type is similar to *Poracanthodes subporosus* Valiukevicius 1998 by appearing to have superpositional growth, but differs notably by the anterior crown ornamentation. The second scale type (Fig. 34L, 36A) has the same regular anterior ridges and furrows, but differs from the first type by having concentric grooves without any clear radially oriented pores. These two types may together be sufficiently diagnostic to establish a new taxon, but since poracanthodid taxonomy is still controversial, it is preferable to keep their affinity open for future revision of the group. There are, however, a few scales that show closer morphology to *P. porosus* s.s. The last described morphotype (Fig. 34I, J) is similar to scales of specimens of *P. menneri* found in the Lower Devonian of Severnaya Zemlya (Valiukevicius 1992). Related isolated scales are also found in the eastern Baltic and the central Urals (Märss 1997).

Occurrence. *Poracanthodes* cf. *P. porosus*, Pridoli–Lochkovian, Hall Land, North Greenland; *Poracanthodes porosus*, Pridoli–Lochkovian, Estonia and Latvia; Lower Devonian, erratic boulders, Germany; Pridoli, Manbrook, Welsh Borderland, Great Britain.

Acanthodii indet.
Spine fragments
Figs 38–40

Figured material. MGUH VP 3598 from GGU sample 82736, MGUH VP 3599–3603 from GGU sample 82738, MGUH VP 3604, 3605 from GGU sample 298937.

Other material. Hundreds of small fragments, mostly poorly preserved, from GGU samples 82734, 82736, 82737, 82738, 298937, 298954, 298963 and 319264.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Morphology. Despite the fragmental preservation of the fin spines from the Chester Bjerg Formation, the ornamentation of smooth longitudinal ribs suggests a common morphology. These fragments are derived from both the proximal and distal parts of the spines and show different stages of development (Figs 38, 39).

A well preserved proximal fragment of an assumed juvenile spine, triangular in cross section, exposes a quite short maybe broken base and a posteriorly wide open central pulp cavity (Fig. 38C, D). Five broad, evenly sized, spine ribs run parallel towards the broken terminations. The ribs have a characteristic smooth surface and are rounded in cross section. The distal part of this particular spine is lacking but the equivalent stage is represented by many other fragments, with five to seven slender ribs that converge towards the apex (Fig. 38E, G–I). Fragments from the distal part have a closed central cavity and a posterior shallow furrow or slit of variable width and size. They are often round or oval in cross section, but can also be triangular and more laterally flattened. It is difficult to tell if the several types of fragments that represent distal terminations are from old or young spines. Several larger fragments with seven ribs have similar cross sections and the same gross morphology, but they represent the middle part of older spines (Fig. 40).

Most fragments have the same general morphology with evenly sized ribs that in the most distal part converge and join to form wider ribs. Some fragments, however, from distal and other parts have ribs of variable size. The variation may involve smaller ridges occurring as striations on the larger anterior ribs (Fig. 38G) or larger lateral ridges (Fig. 38H, I). Some fragments are slightly curved.

One slender fragment has narrow noded ribs, which is a character common for spines of climatiids (Fig. 38A, B). Between each rib small pore holes are visible.

Histology. Due to the fragmental preservation it is difficult to define old or young spine fragments by only looking at the general morphology. Old scales have an immature proximal part and mature middle and distal parts. Most spines under discussion seem to be quite young and histological characters indicating maturity are mainly visible in distal fragments.

The superficial layer, forming the main part of the ribs, is the same in all fragment types (Fig. 40) and is composed of dentinous tissue with irregular branching tubules and rare joining lacunae. This dentine or perhaps mesodentine-like superficial layer gradually turns into a middle layer with concentrically laminated vascular canals. Usually this tissue, sometimes referred to as trabecular dentine (Denison 1979) but more correctly as osteodentine (Ørvig 1967), forms the main

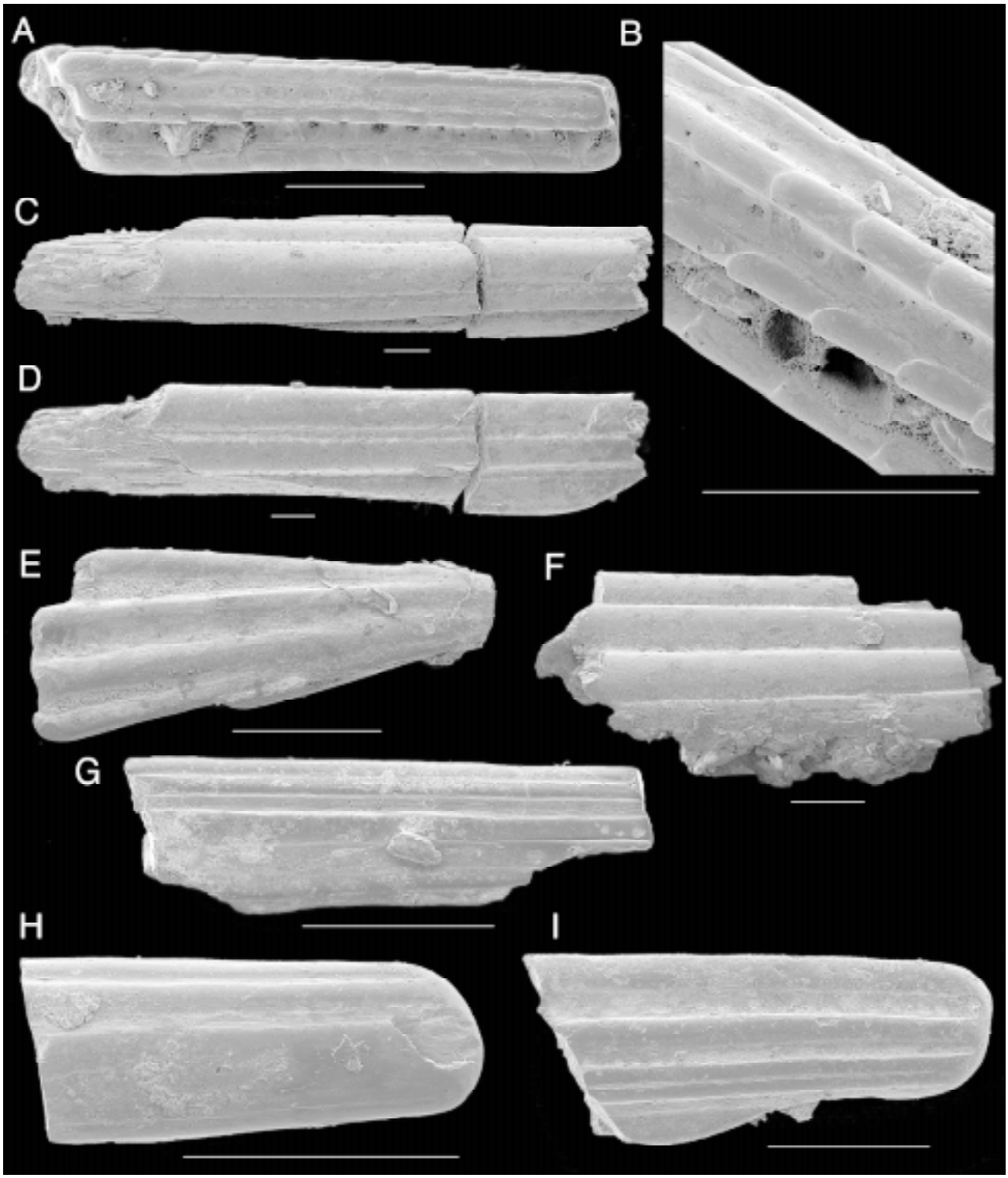


Fig. 38. Acanthodian fin spine fragments. SEM photomicrographs. Scale bars equal 0.5 mm.
A: Fragmental middle part in postero-lateral view, MGUH VP 3599. **B**: Fragmental middle part in postero-lateral view, close up of noded ribs, MGUH VP 3599. **C**: Fragmental proximal part in anterior view, MGUH VP 3604. **D**: Fragmental proximal part in lateral view, MGUH VP 3604. **E**: Fragmental middle part in lateral view, MGUH VP 3605. **F**: Fragmental distal part in lateral view, MGUH VP 3600. **G**: Fragmental distal part in lateral view, MGUH VP 3598. **H**: Fragmental distal part in lateral view, MGUH VP 3601. **I**: Fragmental middle part in lateral view, MGUH VP 3602.
MGUH VP 3598 from GGU sample 82736, Halls Grav; MGUH VP 3599–3602 from GGU sample 82738, Halls Grav; MGUH VP 3604, 3605 from GGU sample 298937, Halls Grav.

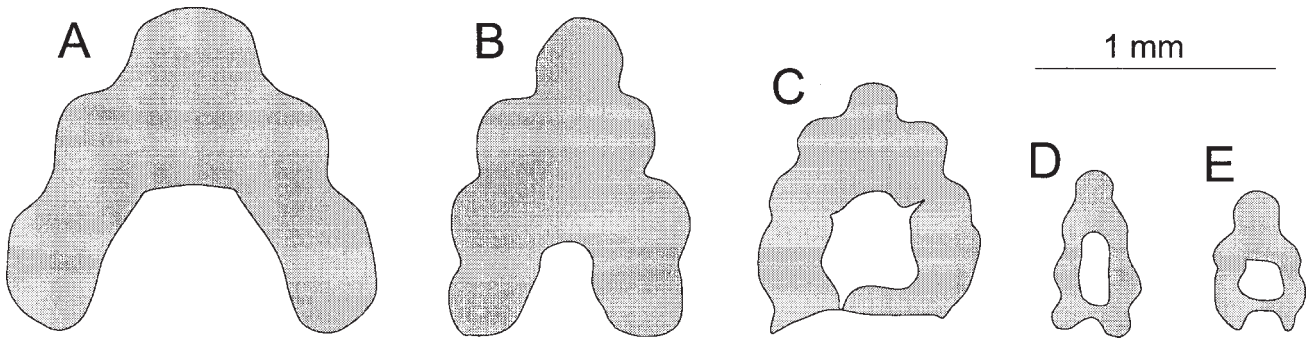


Fig. 39. Schematic illustration showing fin spine cross sections and the different stages of development. Scale bar equals 1 mm. **A**: Proximal part of immature spine. **B**: Proximal part of slightly matured spine. **C**: Middle part of immature spine. **D**: Distal part of immature spine. **E**: Distal part of slightly matured spine.

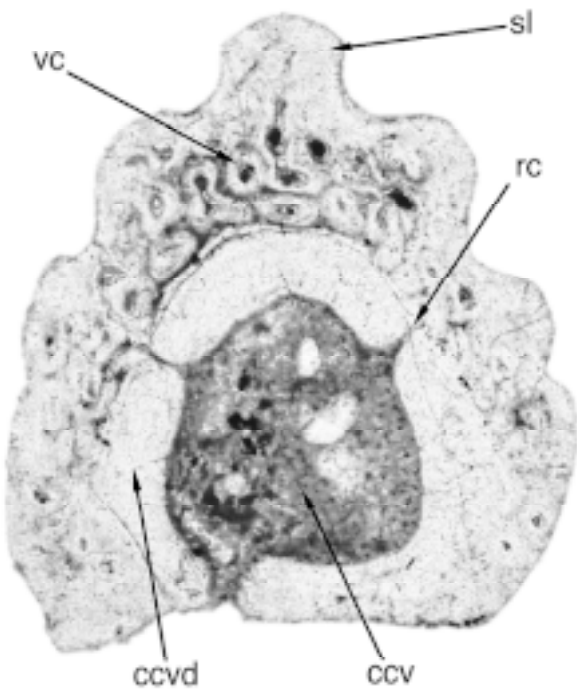


Fig. 40. Histology of acanthodian fin spine. Cross section, MGUH VP 3603 from GGU sample 82738, Halls Grav, × 82.
ccv: central cavity; **ccvd**: central cavity denteon; **rc**: radial canals; **sl**: superficial layer; **vc**: vascular canals.

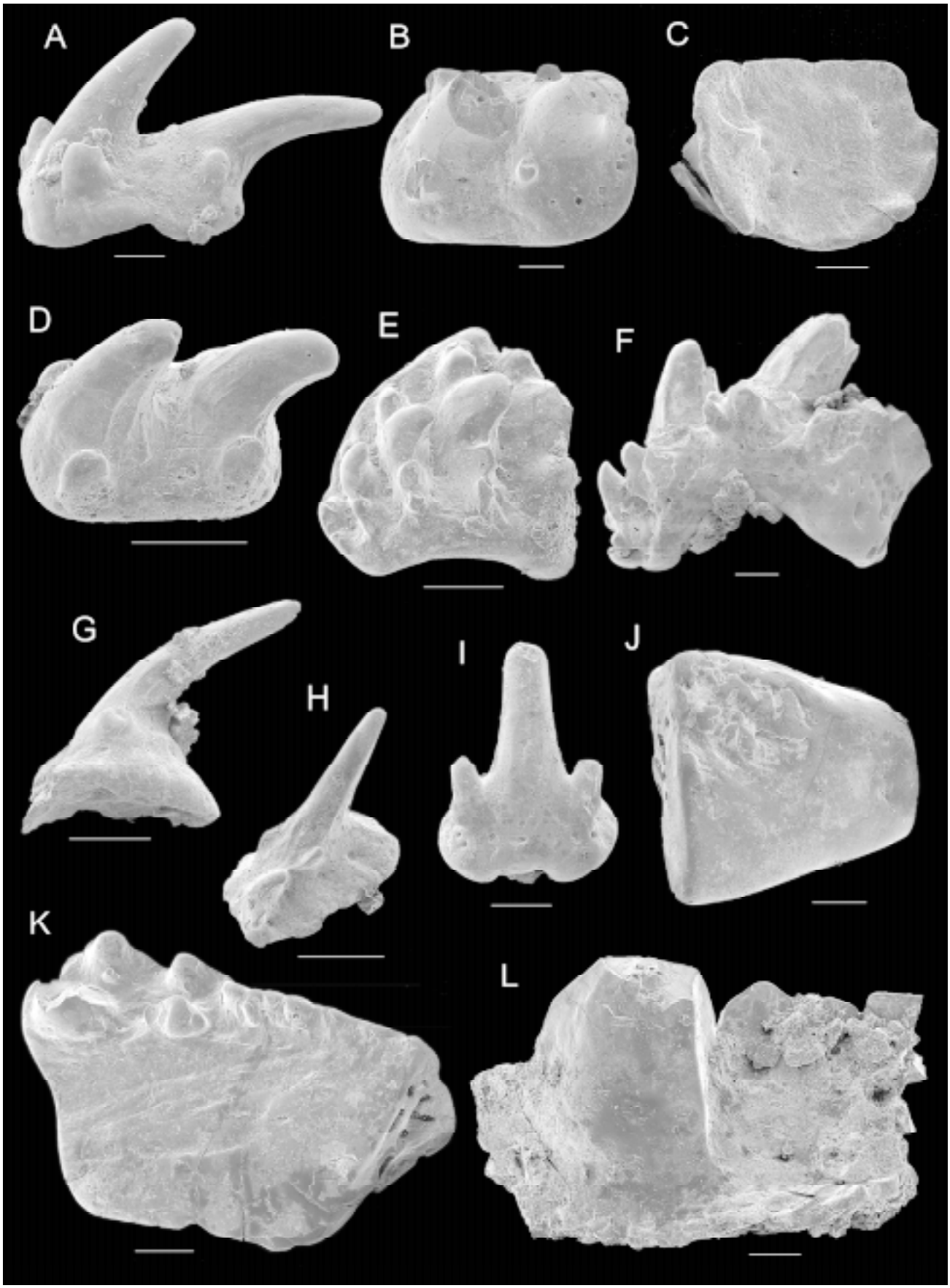
bulk of the immature spine and slightly less of the mature one. The vascular canals are predominantly longitudinal and parallel to longitudinal supporting fibres. Larger canals are concentrated in the anterior region of the spine and they may be enlarged or a number may unite to form a subcostal-like canal. It is also possible to detect differently oriented shorter canals that connect these larger canals.

Fragments from immature parts of a spine have a very thin basal layer of cellular bone lining the either open or closed central cavity. The central cavity, however, is filled by central cavity denteon at maturity. Radial canals extend from the central cavity towards the middle layer and may sometimes merge with the vascular canals.

Remarks. Despite the uniform type of morphology the spines from Chester Bjerg Formation show quite pronounced differences due to the size and maturity of the spines. There may be true taxonomical differences or reflect variation between spines from different positions on the body.

The general morphology is similar to spines of Ischnacanthidae, Acanthidae and smooth-ribbed spines of uncertain origin often placed within *Onchus* (Denison 1979). However, many different types with a wide

Fig. 41. Acanthodian dental elements. SEM photomicrographs. Scale bars equal 0.2 mm.
A: Tooth whorl in lateral view, MGUH VP 3611. **B**: Tooth whorl in oblique upper view, MGUH VP 3606. **C**: Tooth whorl in visceral view, MGUH VP 3615. **D**: Tooth whorl in oblique upper view, MGUH VP 3607. **E**: Tooth whorl in oblique upper view, MGUH VP 3608. **F**: Tooth whorl in lateral view, MGUH VP 3616. **G**: Single tooth element in lateral view, MGUH VP 3609. **H**: Single tooth element in lateral view, MGUH VP 3610. **I**: Single tooth element in anterior view, MGUH VP 3612. **J**: Fragment of posterior part of a jaw bone in upper view, MGUH VP 3613. **K**: Fragment of middle part of a jaw bone in postero-lateral view, MGUH VP 3617. **L**: Fragment of anterior part of a jaw bone in inner lateral view, MGUH VP 3614.
MGUH VP 3606–3610 from GGU sample 82736, Halls Grav; MGUH VP 3611–3614 from GGU sample 82738, Halls Grav; MGUH VP 3615, 3616 from GGU sample 298937, Halls Grav; MGUH VP 3617 from GGU sample 319264, Monument.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time range have been referred to *Onchus*, suggesting an unsatisfactory taxonomic situation. Several of these species probably belong to *Gomphonchus*. According to Gross (1971) *Gomphonchus* is completely built up by dentine and mainly characterized by unornamented smooth ridges. The material from Greenland should therefore be of *Gomphonchus* type, but Gross (1971) included *Poracanthodes* within *Gomphonchus*, an idea now changed by the find of articulated *Poracanthodes menneri* (Valiukevicius 1992). *Gomphonchus*, as defined by Gross (1971), is known to have spines with an inserted base, while *Poracanthodes* does not (Valiukevicius 1992). The presence of *Poracanthodes* and *Gomphonchus* scales in the North Greenland material leaves the position of the spines open to discussion.

The rarity of the single spine fragment with ornamented ridges may suggest a close relation with *Nostolepis* or Climatiida indet. scales found in the same sample. Although it is unusual for Ischnacanthidae to have noded or tuberculate fin-spine ridges (Denison 1979), Gross (1971) figured such fragments referred to *Gomphonchus* from erratic boulders in Germany.

Occurrence. Pridoli–Lochkovian, Hall Land, North Greenland.

Dental elements
Figs 41, 42

1976 Tooth whorls of '*Gomphodus*' ('*Plectrodus*') type – Bendix-Almgreen, fig. 443L, M.
1976 *Nostolepis* sp. fragments of dentigerous jawbones – Bendix-Almgreen, fig. 443O, P.

Figured material. MGUH VP 3606–3610 from GGU sample 82736, MGUH VP 3611–3614, 3618 from GGU sample 82738, MGUH VP 3615, 3616 from GGU sample 298937, MGUH VP 3617 from GGU sample 319264.

Other material. Several hundred tooth whorls, single teeth and jaw bone fragments from GGU samples 82734, 82736, 82737, 82738, 298937, 298953, 298954, 298960, 298963 and 319264.

Locality and age. The Halls Grav and Monument localities, Hall Land, North Greenland, Chester Bjerg Formation, Late Silurian – Early Devonian (Pridoli–Lochkovian).

Tooth whorl description. Tooth whorls of the main type are bilaterally symmetrical, with a series of teeth on a curved base. They show little curvature and have only two three-cusped tooth rows on each whorl (Fig. 41A–D). They range greatly in total size, 0.5–1.5 mm in length, but the main proportions are preserved even in the smallest specimens. The tooth rows are usually equal in size, but the anterior tooth row may be slightly smaller than the other. Each row has a long slender main central cusp and a pair of smaller side cusps. The main cusp curves posteriorly and is about five times higher than the shorter and more robust side cusps. Small weakly developed ridges or striae run proximally along the main cusp. In some specimens one pair of longer lateral ridges is developed, running almost along the whole length of the main cusp. All cusps are round or oval in cross section, with a wider proximal part. The base of the whorl is round, elongated or square and usually deeply concave in basal view (Fig. 41C). Large canal openings are visible on the upper as well as the lower surface of the base. On the upper surface they are often visible as a ring along the margins of the basal part of the whorls. Due to the poor preservation and delicate structures, many specimens are found with broken cusps, exposing the central pulp canal. The colour is usually pale brown but may vary from white to dark brown.

A few specimens differ mainly by having three or four tooth rows and several variably sized side cusps. They are often irregularly oriented and the whole whorl tends to be less symmetrical (Fig. 41F). The side cusps point in different directions and decrease in size laterally. The main cusp is short and robust with small, pronounced, longitudinal ridges. The difference in height between the main cusp and the largest side cusps is less than four times. The more curved base is only anteriorly to posteriorly concave and almost convex transversely.

A third symmetric type, represented by one broken specimen, is found with at least five tooth rows (Fig. 41E). This type is much lower than the previous ones and the total number of tooth rows is unknown due to posterior breakage of the only well preserved specimen. Each row has a robust main central cusp and two pairs of side cusps, decreasing in size laterally. The size of the cusps in each row also decreases anteriorly and the cusps at front are very tiny. The base is wide, flat and less curved than the second type, with few visible canal openings.

In the large main tooth cusp in the first and most common tooth whorl, dentine surrounds a large central pulp cavity (Fig. 42), with branching dentine tubules radiating towards the outer surface which may

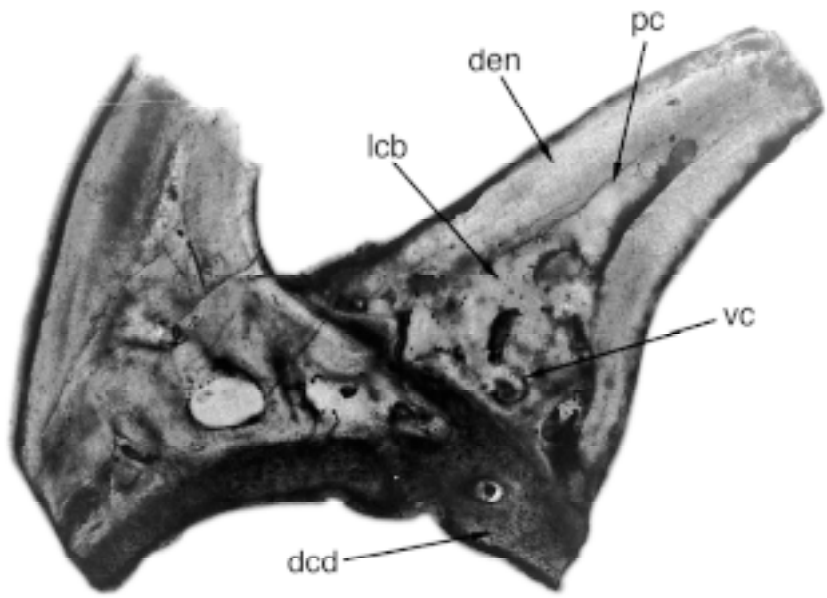

Fig. 42. Histology of acanthodian tooth whorl. Vertical longitudinal section, MGUH VP 3618 from GGU sample 82738, Halls Grav, × 91.
dcd: dense cellular bone; **den**: dentine; **lcb**: light cellular bone; **pc**: pulp canal; **vc**: vascular canal.

show a thin shiny enameloid layer. Proximally the pulp canal branches into a net of vascular canals surrounded by dentine and light cellular bone in the main body of the tooth whorl. The thin layer of basal tissue is composed of more dense cellular bone, penetrated by a few short canals.

Single tooth description. The single tooth type resembles a modified tooth whorl having only one row of cusps (Fig. 41G–I). The main single central cusp is slender and very long. It is smooth, straight or curved and has a weak striation on the proximal part. On each side and around the many times longer central cusp two, or rarely up to four smaller cusps are developed. These side cusps are not necessarily symmetrically oriented around the main cusp. A central pulp cavity is exposed when the apex of the cusps is broken (Fig. 41B). The sloping upper side of the base is round and thin, exposing large canal openings on the dorsal surface. In basal view, the base has canal openings on the deeply concave surface. Histologically, these teeth have the same basic structures seen in tooth whorls.

Jaw bone description. Jaw bones are very poorly preserved and it is difficult to find a consistent morphology among all the small fragments. One of the best preserved fragments is about 1.5 mm long and represents a fragment of the middle part of a jaw (Fig. 41K). Teeth are located on the outer half of the main jaw bone. Half the length of the lateral margin has one row of small tightly packed mono-cusped teeth, while the anterior half has two rows of two larger, separated, three-cusped teeth. Each of these consists of one larger main cusp and two smaller side cusps. Each cusp is heavily worn and more rounded than subtriangular. The inner teeth are slightly larger than the marginal ones. The jaw bone has a vertical lateral outer side and an inner side that slopes gently antero-laterally in the posterior part. In the inner anterior part the slope is initially more vertical, forming an almost L-shaped cross-section. In basal view, the jaw-bone fragment is almost square with a concave basal surface. On the broken anterior and posterior ends, several large pores and cavities after the vascular system are visible. Both marginal rows of teeth are in line with the vertical outer lateral side of the jaw bone.

Another fragment shows the anterior broken part of the jaw with a large tooth cusp and a posterior row of smaller side cusps (Fig. 41L). The fragment is 1.8 mm long. The slightly broken main cusp is 0.5 mm high, about 75% of the total jaw height, and has a subtriangular parabasal section with straight lateral and posterior sides, forming an almost perpendicular postero-lateral corner. The antero-lateral side is more rounded between the other two sharp corners. In width, the main cusp forms almost the whole part of the supporting jaw bone, which is triangular in cross section. Three laterally flattened side cusps run posteriorly along the outer lateral edge and vertical side. They have an elliptical parabasal section and are about 1/3 of the main cusp height.

A fragment from the posterior part of a jaw (Fig. 41J) is broken at both ends and is about 0.9 mm long and 1.0 mm wide. In upper view, it has a trapezoid-like shape and is narrower posteriorly. It is smooth and convex on the upper surface, with a flattened anterior area bearing small irregular rounded denticles. The denticles are very low and seem to be heavily worn. The whole fragment, however, is quite low and flat or slightly concave in basal view. Spaces after the cancellous vascular system are visible at the broken ends.

Remarks. Tooth whorls of the most common type, with only two three-cusped tooth rows (Fig. 41A–D), were referred to as *Gomphodus* by Bendix-Almgreen (1976), and are similar to the symmetric multiple tooth whorls of *Gomphonchus* (Gross 1957). The enclosed basal concavity suggests that the presence of only two tooth rows is original and not a result of breakage; this is also the dominant preservational state. Although reported by Bendix-Almgreen (1976), this form has apparently not been recorded by earlier workers. Gross (1967b) suggested that less curved whorls in *Gomphonchus* were symphysial, while heavily curved whorls with many rows where located somewhere in the mouth cavity. The evidence for this is not unambiguous and, as pointed out by Ørvig (1973), there are no clear ideas about the relation between tooth whorls and jaw bones in early ischnacanthids or climatiids. Whorls can be symphysial, located in the mouth cavity or even in the branchial region (Gross 1971; Ørvig 1973). Faunal composition and the proportion of acanthodian scales suggest that most dental elements described in this paper are ischnacanthids represented by *Gomphonchus* and poracanthodian scales. The high number of whorls or 'semi' whorls of the first type in comparison with the low number of preserved jaw bones, suggests that tooth whorls are from the mouth cavity or possibly even from the branchial region. No whorls of the type described as *Nostolepis* by Gross (1971) have been found in the material from Hall Land.

The two other types of tooth whorl, rare and with a higher number of rows, may be similarly interpreted. They are more similar to the whorls illustrated by Gross (1957) as *Gomphodus*. Burrow (1995) argued that an asymmetric tooth whorl may be parasymphysial, but not ankylosed to the jaw bone, like the tooth whorls of, for example, dipnoans. This explanation can be invoked for the rare multiple tooth whorls under discussion, but the differences between the types of tooth whorl may reflect not only different position, but also different taxonomical affinity.

The single teeth fragments from Greenland are more or less of one type and are closely related in shape and histology to the whorls with two teeth rows, indicating a common origin.

The anterior dental jaw bone fragment (Fig. 41L) is similar to the anterior part of jaw bones earlier attributed to *Nostolepis* (Gross 1957, 1971). The subtriangular parabasal section of the main cusp was originally a character differentiating it from *Gomphonchus* Gross (1957, 1971). He also based this on the idea that very few higher taxa were present in his material from the Beyrichienkalk and those present thereby fell conveniently into either *Gomphonchus* or *Nostolepis*. However, as pointed out by Denison (1976, 1979), the histology does not support this idea, since the jaw-bone attached teeth show no indication of mesodentine, which is characteristic of scales, fin spines and tooth whorls of *Nostolepis*. Gross (1971) regarded *Poracanthodes* to be specialized scales of *Gomphonchus*, but the find of the articulated *Poracanthodes menneri* described by Valiukevicius (1992) suggests that the diversity was higher than Gross (1971) originally believed. *Poracanthodes menneri* (Valiukevicius 1992) has a subtriangular parabasal section in the larger main cusps, suggesting that poracanthodiformes could contain *Nostolepis*-type jaw bones as defined by Gross (1971). This is supported by the occurrence of poracanthodiform scales and *Nostolepis*-type jaw bone fragments from

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Fig. 43. Incertae sedis. SEM photomicrographs. Scale bars equal 0.2 mm.

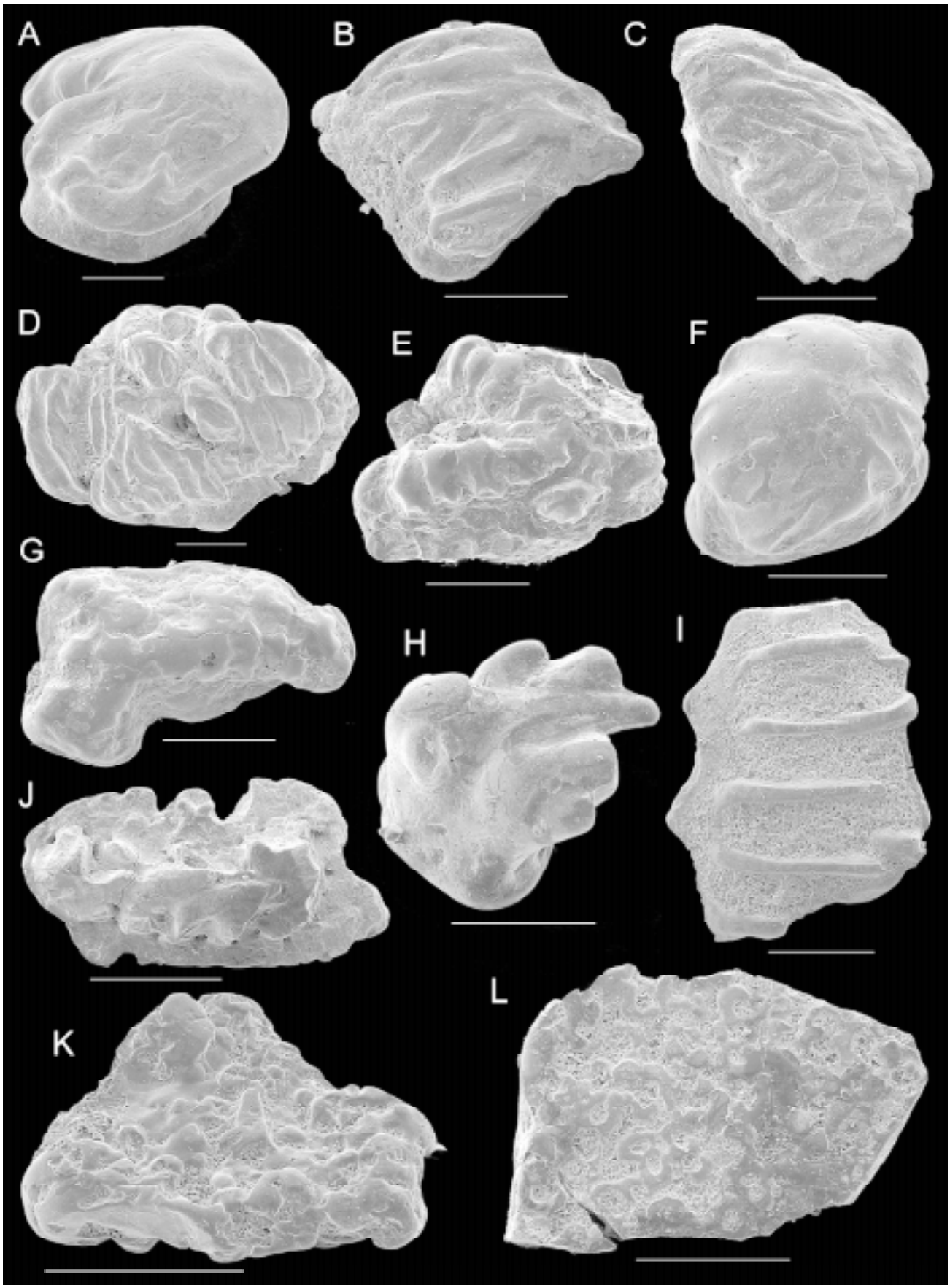
A–**C**, **E**–**G**. Acanthodian scales and tesserae. **A**: Scale in oblique crown view, MGUH VP 3619. **B**: Scale in oblique crown view, MGUH VP 3623. **C**: Scale in oblique crown view, MGUH VP 3628. **E**: Tesserae in crown view, MGUH VP 3620. **F**: Scale in oblique crown view, MGUH VP 3624. **G**: Tesserae in oblique crown view, MGUH VP 3625.

D, **H**, **J**. ?Chondrichthyans. **D**: Unit of odontodes in oblique crown view, MGUH VP 3629. **H**: Unit of odontodes in oblique crown view, MGUH VP 3621. **J**: Unit of odontodes in crown view, MGUH VP 3630.

I: Pisces indet. Plate in upper view, MGUH VP 3626.

K, **L**. ?Actinopterygian. **K**: Plate fragment in upper view, MGUH VP 3627. **L**: Plate fragment in upper view, MGUH VP 3622.

MGUH VP 3619 from GGU sample 82736, Halls Grav; MGUH VP 3620–3627 from GGU sample 82738, Halls Grav; MGUH VP 3628–3630 from GGU sample 319264, Monument.


A
B
C
D
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H
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K
L

Late Silurian beds of Cornwallis Island, Arctic Canada (Burrow 1995; Burrow *et al*. 1997). Assignment to *Nostolepis* cannot be completely excluded since dental jaw bone is known in *Nostolepis*-like articulated acanthodians (J. Valiukevicius, personal communication 1998). Ørvig (1973) suggested, and Valiukevicius (1992), demonstrated that the upper jaw of ischnachantids also has teeth, indicating that the anterior fragment described here may be from the upper or lower jaw.

The posterior jaw fragment, whether it is from the upper or lower jaw, is similar to Silurian and lower Devonian ischnacanthids described by Gross (1971) and Burrow (1995), but the ornamentation is much more worn.

The bone fragment from a probably middle part of a jaw may belong to the same jaw type as the anterior and the posterior fragments, but the teeth are quite different. This difference may be taxonomic, but can also reflect a positional difference.

Occurrence. Pridoli–Lochkovian, Hall Land, North Greenland.

Incertae sedis

Fig. 43

Figured material. MGUH VP 3619 from GGU sample 82736, MGUH VP 3620–3627 from GGU sample 82738, MGUH VP 3628–3630 from GGU sample 319264.

Other material. Hundreds of unidentified fragments from all GGU samples processed, see Fig. 4.

Remarks. Some of the more distinctive of the many poorly preserved remains found in the residues of the Chester Bjerg Formation are mentioned here.

Several of the fragments may represent scales from the head region of acanthodians (Fig. 43A–C, F). They all have irregular ornamentation on the crown which merges into the neck anteriorly. The ornamentation may vary but the scales have the same general morphology. Some rare remains with irregular ornamentation may also be specialized scales or tesserae of acanthodians (Fig. 43E, G).

Polyodontodia-like remains (*sensu* Karatajute-Talimaa 1992) usually occur as single specimens and cannot with certainty be assigned to the true chondrichthyans (Fig. 43D, H, J). The odontodes are different in all these remains and can be rounded or three-cusped, but they all possess the characteristic neck canals.

One fragmental plate or scale has several smooth, high and narrow, elongate tubercles on a low compact basal layer (Fig. 43I). Several fragments or plates with compact tissue have irregularly shaped tubercles of similar tissue (Fig. 43K, L). These tubercles are heavily worn and show no distinctive features. They show some similarity with indeterminate fragments from Gotland, loosely assigned to *Andreolepis hedei* (Fredholm 1988).

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