Early Ordovician conodonts of East and North Greenland

M. Paul Smith
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Early Ordovician conodonts of East and North Greenland

M. Paul Smith
Frontispiece

North-eastern shore of Ella Ø, northern East Greenland. Massively weathering Ordovician limestones of the Cape Weber Formation are exposed in a large scale Caledonian structure which contains the Eleanore Bay Supergroup (Proterozoic), Tillite Group (Late Proterozoic) and Cambrian—earliest Ordovician shallow marine sediments in its core. The sequence is overlain with angular unconformity by Devonian clastic sediments which are present in the poorly exposed ground towards top right.
Contents

Introduction ........................................ 5
Stratigraphic background .......................... 6
East Greenland ........................................ 6
Description of localities ............................ 9
PF 770824–1 ......................................... 9
North Greenland ....................................... 9
Description of localities ............................ 10
JEM 790627–1 ........................................ 10
JSP 800630–5 .......................................... 10
JSP 800630–6 .......................................... 10
JSP 800702–1 .......................................... 10
Biosratigraphy ........................................ 13
Development of Early Ordovician conodont
biozonation ........................................... 13
Biosratigraphy of the Cape Weber Formation 15
Biosratigraphy of the Danmarks Fjord and
Amdrup Members ..................................... 15
Biosratigraphy of the Pyramideplateau Member 17
Conodont Colour Alteration .......................... 17
East Greenland ........................................ 17
North Greenland ....................................... 18
Apparatus nomenclature .............................. 18
Taxonomic comments ................................. 18
Systematic descriptions .............................. 19
Genus Aloxoxonus nov ................................. 19
Aloxoxonus staufferti Furnish 1938 .............. 19
Aloxoxonus sp. A ...................................... 20
Aloxoxonus sp. B ...................................... 20
Genus Bergstroemognathus Serpagli 1974 .... 21
Bergstroemognathus extendus (Graves &
Ellison 1941) ......................................... 21
Genus Chionoconus nov ............................... 22
Chionoconus avangna sp. nov ...................... 22
Genus Cordyloodus Pander 1856 ................. 24
Cordyloodus sp. nov. A ................................ 24
Genus Cristodus Repetski 1982 .................... 25
Cristodus loxoides Repetski 1982 ............... 25
Cristodus? sp. A ....................................... 25
Genus Diaphorodus Kennedy 1980 .............. 26
Diaphorodus delicatus (Branson & Mehl 1933) 26
Diaphorodus? russoi (Serpagli 1974) ............ 26
Diaphorodus sp. nov. A .............................. 26
Diaphorodus? sp. B ................................... 27
Genus Drepanodon Pander 1856 ................. 27
Drepanodon arcaitrus Pander 1856 .............. 28
Drepanodon concavus (Branson & Mehl 1933) 28
Drepanodon? costatus Abaimova 1971 .......... 30
“Drepanodus” sp. A .................................. 31
“Drepanodus” sp. B .................................. 31
Drepanodon? sp. C .................................... 31
Genus Drepanoistodus Lindström 1971 ......... 31
Drepanoistodus aff. forceps (Lindström 1955) 31
?Drepanoistodus suberecutus (Branson & Mehl
1933) .................................................. 31
Drepanoistodus sp. A ................................ 32
Genus Eucharodus Kennedy 1980 ............... 32
Eucharodus apion sp. nov ........................... 32
Eucharodus parallelus (Branson & Mehl 1933) 33
Eucharodus toomeyi (Ethington & Clark
1964) ................................................... 35
Eucharodus xyron? (Repetski 1982) .............. 35
Genus Fahraeusodous Stouge & Bagnoli 1988. 35
Fahraeusodous marathonensis (Bradshaw 1969) 36
Genus Fryxellodontus Miller 1969 .............. 37
“Fryxellodontus” sp. A .............................. 37
Genus Glyptocodon Kennedy 1980 .............. 38
Glyptocodon quadruplicatus (Branson & Mehl
1933) ................................................... 38
Genus Histiodella Harris 1962 ................. 40
Histiodella donnæ Repetski 1982 ............... 40
Histiodella? sp. A .................................... 40
Genus Juanognathus Serpagli 1974 ............. 41
Juanognathus variabilis Serpagli 1974 ......... 41
Juanognathus sp. nov. A ............................ 41
Genus Jumudontus Cooper 1981 ............... 41
Jumudontus gananda Cooper 1981 ............. 41
Genus Oepikodus Lindström 1955 .............. 41
Oepikodus communis (Ethington & Clark
1964) ................................................... 42
Oepikodus sp. A ...................................... 45
Oepikodus sp. B ...................................... 45
Genus Oistodus Pander 1856 ..................... 46
“Oistodus” ectyphus sp. nov ....................... 46
Genus Oneotodus Lindström 1955 .............. 46
Oneotodus costatus Ethington & Brand 1981. 46
“Oneotodus” mitra Abaimova 1971 ............ 48
Oneotodus sp. A ...................................... 48
Genus Parapanderodus Stouge 1984 .......... 48
Parapanderodus striatus (Graves & Ellison
1941) ................................................... 49
Genus Protapanderodus Lindström 1971 ....... 52
Protapanderodus elongatus Serpagli 1974 .... 52
Protapanderodus gradatus Serpagli 1974 .... 52
Protapanderodus cf. gradatus Serpagli 1974 ... 53
Protapanderodus leonardi Serpagli 1974 ....... 53
Genus Protapriorioides McTavish 1973 ........ 54
Protapriorioides papilosus (van Wamel 1974) 54
Genus Pieracontiodus Harris & Harris 1965 ... 55
Pieracontiodus brasonii (Ethington & Clark
1982) ................................................... 56
Genus Reuterodus Serpagli 1974 ............... 58
?Reuterodus andinus Serpagli 1974 ............ 58
Genus Scalpellodus Dzik 1976 ................. 59
Scalpellodus? narvalensis sp. nov ............... 59
Scalpellodus? sp. A .................................. 61
Genus Scandodus Lindström 1955 .............. 61
“Scandodus” ethingtoni sp. nov .................. 61
Genus Sclopolodus Pander 1856 ............... 62
“Sclopolodus” emarginatus Barnes & Tuke
1970 ................................................... 63

Meddelelser om Grønland, Geoscience 26 - 1991

3
“Scolopodus” filosus Ethington & Clark 1964 63
Scolopodus quadratus Pander 1856? 63
Scolopodus sp. A 64
Genus Semiacontiodus Miller 1969 64
Semiacontiodus sp. A 64
Genus Toxotodus nov. 64
Toxotodus amphigius sp. nov. 64
Toxotodus cariae (Repetski 1982) 65
Genus Tropodus Kennedy 1980 65
Tropodus australis (Serpagli 1974) 66
Tropodus comptus (Branson & Mehl 1933) 66
Tropodus? sp. A 69
Tropodus sp. B 69
Genus Ulrichodina Furnish 1938 69
Ulrichodina abnormalis (Branson & Mehl 1933) 69
Ulrichodina simplex Ethington & Clark 1982 71
Ulrichodina wisconsinensis Furnish 1938 71
Ulrichodina sp. nov. A 72
Ulrichodina sp. B 72
Genus Variabiloconus Landing, Barnes & Stevens 1986 72
Variabiloconus bassleri (Furnish 1938) 73
Genus Wandelia nov. 73
Wandelia guyi sp. nov. 74
Wandelia candidisphaera sp. nov. 75
Wandelia sp. A 75
Genus novum A 75
Gen. nov. A sp. nov. A 75
Gen. nov. A sp. nov. B 76
Acknowledgements 76
References 77
Early Ordovician conodonts of East and North Greenland

M. PAUL SMITH

Conodonts of middle to late Canadian (Early Ordovician) age are described from the Cape Weber Formation of Ella Ø, East Greenland, from the Danmarks Fjord and Andrup Members (Wandel Valley Formation) of Kronprins Christian Land, eastern North Greenland, and the Pyramideplateau Member (Wandel Valley Formation) of Peary Land, central North Greenland. A total of 33 genera and 73 species are systematically described and of these, four new genera (Aloxocosuris, Chionocosuris, Toxotodus and Wandelia) and eight new species (Chionococonus avangna, Eucharodus apion, “Oistodus” ectyphus, Scalpellodus? narhvalensis, “Scandodus” ethingtoni, Toxotodus amphigynus, Wandelia guyi and W. candidisphaera) are recognised. The faunas are coniform-dominated and typical of shallow water Midcontinent Realm assemblages found throughout most of North America.

The conodont faunas from the Cape Weber Formation on Ella Ø are referred to three biozones: the manitouensis Biozone, Fauna D and the communis Biozone. Those from the lower members of the Wandel Valley Formation are representative of uppermost Fauna D and the communis Biozone. There is a discussion of potential zonal and subzonal schemes for deep and shallow-water biofacies.

Fused clusters of Oepikodus communis (Ethington & Clark) and Parapanderodus striatus (Graves & Ellison) are described from the Cape Weber Formation and are amongst the oldest euconodont natural assemblages recorded. Their implications in terms of apparatus reconstruction and architecture are discussed.

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Early Palaeozoic sediments in Greenland are confined to two principal areas: the Franklinian Basin of North and North-West Greenland and a second basin now incorporated in the Caledonian East Greenland fold belt. Outcrop in the latter occurs as a narrow north-south belt in the fjord region (Fig. 1), stretching from Canning Land (71°36’N) to C. H. Ostenfeld Nunatak (72°22’N) (Henriksen & Higgins 1976). The initial Early Cambrian transgression resulted in the deposition of tidally dominated quartz arenites which pass upwards into sandy shales and then to silty limestones, reflecting a diminishing elastic supply. The majority of the succession is dominated by limestones and dolomites, with shallow subtidal limestones as the most common facies association. The whole sequence bears strong resemblance to those at other localities in a similar position on the eastern margin of the Laurentian craton, particularly northwestern Scotland and western Newfoundland (Swett & Smit 1972). The youngest sediments preserved are of early Middle Ordovician age (Smith 1982) and provide a maximum age limit for the onset of Caledonian deformation.

The Franklinian Basin was initiated in latest Proterozoic time with the deposition of mudstones, sandstones and conglomerates deposited initially on a storm-dominated shelf and subsequently in more shallow water inshore environments (Peel 1982; Higgins et al. in press). Following this stage of development, the basin differentiated into two parts: an east-west trending shallow marine platform fringing the craton and, to the north, a deep water trough. The boundary between the two varied in character with time from a gradual outer shelf-slope-trough transition to an escarpment and bypass zone. Sedimentation in the trough was characterised alternately by starved basin sediments and by sand turbidites with carbonate breccias derived from the platform.

After a major phase of Early Cambrian clastic deposition on the platform, carbonate sedimentation was dominant until the early Silurian (Llandovery) and was closely paced with subsidence. Until Middle Ordovician time, a cyclic alternation of shallow subtidal and intertidal facies associations was dominant. A major transgression in the Middle Ordovician resulted in a more consistently subtidal succession through into the Silurian. In late Llandovery time, the platform founndered in response to loading by Caledonian nappe sheets in eastern North Greenland. As a consequence of
the associated inundation, carbonate deposition was largely replaced by hemipelagic mudstones with turbiditic siltstones and was maintained only locally along a belt of isolated mounds. Deposition was brought to an end by the Middle to Late Devonian Ellesmerian Orogeny and the youngest sediments of the Franklinian Basin preserved in North Greenland are of Pridoli age (Peel 1982; Higgins et al. in press).

During the Early Ordovician, conodonts attained a diversity which was not to be equalled at any subsequent stage in their history (Sweet 1985). It is therefore surprising that there has been relatively little study directed at this interval, particularly of those faunas from the North American Midcontinent Realm. When Ethington & Clark (1971) collated all previous work, they were able to record only seven systematic accounts although subsequently there have been the major contributions of, for example, Kennedy (1980), Miller (1980), Cooper (1981), Ethington & Clark (1982) and Repetski (1982). Yet Early Ordovician conodonts perhaps remain the most understudied, despite their importance in establishing morphological trends which were to persist until the Triassic. There is an especial lack of systematic descriptions based on long, continuous sections although notable exceptions to this are the sections at Ibex, Utah (Ethington & Clark 1982) and El Paso, Texas (Repetski 1982). The Greenland sections provide an opportunity to test the taxonomy and faunal succession established in these areas at sites up to 5500 km distant and on the opposite margin of the craton.

Stratigraphic background

East Greenland

The Canadian in East Greenland is represented by the uppermost Dolomite Point, Antiklinalbugt, Cape Weber and lowermost Narwhale Sound Formations. Depending upon which horizon is selected by the International Commission on Stratigraphy as defining the base of the Ordovician, the Cambro-Ordovician boundary on Ella Ø (Fig. 1) occurs either at 27–37 m below the top of the Dolomite Point Formation (base of intermedius Biozone) or close to the Dolomite Point–Antiklinalbugt boundary (base of lindstromi Biozone) (Miller & Kurtz 1979). Further to the north on C. H. Ostenfeld Nunatak the base of the lindstromi Biozone occurs slightly lower in the sequence, within the uppermost part of the Dolomite Point (Miller & Kurtz 1979). Prior to these conodont studies a substantial unconformity encompassing late Middle–Late Cambrian time had been postulated to occur between the Dolomite Point and Antiklinalbugt Formations (Cowie 1961, 1971).

The Early Ordovician succession was first described by Koch (1929) who distinguished two units, the Eskimo Hut and Cape Weber Formations. Poulsen (1930) reassigned the upper part of the Eskimo Hut Formation to the Cape Weber Formation and included the lower part in the Cass Fjord Formation, a unit originally described in Washington Land, western North Greenland (Poulsen 1927). The inclusion of East Greenland sediments within this formation was maintained until Peel & Cowie (1979) noted the differences in the respective sequences and on account of the substantial distance of East Greenland from the type area erected a new unit, the Antiklinalbugt Formation.

Conodonts from the Antiklinalbugt Formation were noted by Kurtz & Miller (1981). Although studied to date only at a reconnaissance level, some diachrony is evident. On Ella Ø, the formation ranges from the base of the lindstromi Biozone to the upper part of the manitouensis Biozone whereas further north it ranges from low in the lindstromi Biozone to the base of the communis Biozone (Kurtz & Miller 1981; unpublished GGU collections).

The Cape Weber Formation was originally thought to rest disconformably on an erosion surface of the Antiklinalbugt Formation (Poulsen 1930), but subsequent work (Cowie & Adams 1957 and others) showed the boundary to be conformable. The formation has been studied in detail at only three localities: Ella Ø (Cowie & Adams 1957), Albert Heim Bjerge (Cowie & Adams 1957; Hambrey et al. 1988) and C. H. Ostenfeld Nunatak (Frykman 1979; Hambrey et al. 1988). It is over 1000 m thick and is composed of massive, pale grey limestones and dolomitic limestones (Cowie & Adams 1957). Intraformational conglomerates are common, especially near the base, as is chert, which is most abundant in the middle part of the unit. The uniform character and gradational nature of lithological changes prevented Cowie & Adams (1957) from erecting formal subdivisions, although they did record a broad division into a lower group of banded limestones, dolomitic in part, a middle group of massive and highly silicified limestones and an upper group of heavily dolomitised limestones. On Albert Heim Bjerge, a distinctive 85 m unit of thickly bedded, fissiliferous black limestones was described from the middle of the formation.

The macrofauna of the Cape Weber Formation is sparse and, for the greater part, fragmentary. Poulsen (1937) considered the age to be late Canadian on the basis of the trilobite fauna. Cowie & Adams (1957) reported well-preserved material only from the “Black Limestones” on Albert Heim Bjerge. These faunas were correlated with Zone J faunas from the Pogonip Group of Nevada (Hintze 1952) and the Garden City Formation of Utah (Ross 1951).

The Narwhale Sound Formation was erected by Poulsen (1930) and conformably overlies the Cape Weber Formation. The lower part of the formation comprises massive, coarsely crystalline dolomites and calcareous dolomites with an extremely sparse macrofauna. Poulsen (1937) interpreted the age as Chazyan. The lowest part of the formation on Ella Ø contains the gastropod...
Fig. 1. Cambro-Ordovician outcrops in central and northern East Greenland. Early Ordovician erratic blocks are present on Cecilia Nunatak.

_Ceratopea billingsi_ which indicates that the Canadian-Whiterockian boundary must occur somewhat above the base at this locality (Yochelsen 1964). The first Whiterockian conodonts appear 95 m above the base, where _Pteraconiodus cryptodens_ is present (Smith 1985). Younger Ordovician sediments are preserved only to the north, on Albert Heim Bjarne and C. H. Ostenfeld Nunatak, where the Heimbjerge Formation conformably overlies the Narwhale Sound Formation (Cowie & Adams 1957). Conodont faunas (Smith 1982, 1985) indicate that at these localities the top of the Narwhale Sound Formation is of _holodentata_ Biozone (Middle Whiterockian) age in the zonal scheme of Sweet (1984). The top of the Heimbjerge Formation extends into the _sweeti_ Biozone (Late Whiterockian) on C. H. Ostenfeld Nunatak (Smith 1982, 1985) where it is truncated and overlain by Devonian clastic sediments.
Fig. 2. Vertical aerial view of section PF 770824–1 on Ella Ø, northern East Greenland.
Description of localities
PF 770824–1. – The section was collected on Ella Ø (Fig. 2) by P. Frykman with an average sampling interval of 17.5 m and extends from the base to the top of the Cape Weber Formation (Fig. 3). The boundary between banded limestones and the main limestones occurs between 152 and 200 m. The top of the main limestones occurs at approximately 970 m, at the last abundant occurrence of chert before dolomites are recorded. The boundary between the Cape Weber and Narwhale Sound Formations occurs in a 40 m unexposed section and the last occurrence of typical Cape Weber lithologies is at 1165 m. There are 230 m of Narwhale Sound Formation preserved beneath the unconformable Kap Kolthoff Supergroup of Devonian age (Yeats & Friend 1978).

North Greenland

Early Ordovician sediments cropping out from eastern Freuchen Land in the west to Kronprins Christian Land in the east (Fig. 4) are assigned to the Wandel Valley Formation of the Ryder Gletscher Group (Peel & Smith 1988). The formation name was introduced by Troelsen (1949) for the “greyish blue limestones with poorly preserved fossils” noted by Koch (1923). A Canadian age was suggested by Troelsen on the basis of specimens of the gastropod Ceratopea, the identifications of which were confirmed by Yochelsen & Peel (1975). The formation was redescribed in detail by Christie & Peel (1977) who informally recognised lower, middle and upper members. These units were subsequently formalised by Peel & Smith (1988), who erected the Pyramid plateau and Vestervig Elv Members for the lower/middle and upper members respectively.

Coeval carbonate sediments in Kronprins Christian Land were included by Adams & Cowie (1953) within their embrace Centrum Limestone. Subsequently, this interval was divided into the Danmarks Fjord Dolomite (Fränkl 1955) and the Amdrup Formation (Cowie 1971; modified by Scrutton 1975). The equivalence of these units to the Wandel Valley Formation was recognised by Peel (1980a) and Peel et al. (1981) who redefined them as members. An upper member remained unnamed and was formalised as the Alexandrine Bjerke Member by Peel & Smith (1988).

The Wandel Valley Formation overlies the underlying Cambrian and Proterozoic units and rests on progressively older strata to the southeast (Ineson & Peel 1980; Peel 1986). The angular discordance is not large at outcrop scale. In Freuchen Land and western Peary Land it generally overlies the Middle-Late Cambrian Tavens Iskappe Group and progressively overlies this unit to rest on the underlying Early-Middle Cambrian Brønlund Fjord Group in southern Peary Land. It rests on the Early Cambrian Buen Formation in the Hagen Fjord area, and around Danmark Fjord on the Proterozoic Kap Holbæk Formation (Peel 1986).

The lower part of the Pyramid plateau Member in Peary Land comprises pale weathering, thin-to-medium-bedded dolomites with planar to wavy silty laminae, thin beds of intraformational conglomerate and chert nodules. These alternate with and are subsequently succeeded by dark grey-brown, burrow-mottled crystalline dolomites and limey dolomites in medium to thick beds (Christie & Peel 1977; Peel & Smith 1988). The presence of Ceratopea unguis and C. ankylosa indicates a late Canadian age for the member (Yochelsen & Peel 1975).

The Vestervig Elv Member conformably overlies the Pyramid plateau Member and marks a change back to light grey weathering, parallel to wavy laminated dolomites and dolomicrites with intraformational conglomerates and chert nodules. Macrofossils are very scarce within this unit but conodonts indicate that the Canadian-Whiterockian boundary occurs at or just above the member boundary (Smith 1985; Peel & Smith 1988).

The lowest unit of the Wandel Valley Formation in Kronprins Christian Land, the Danmarks Fjord Member, is a brown weathering, grey to dark grey dolomite with undulating laminar or lenticular bedding. The laminated horizons often show small, domed stromatolites. Black cherts are common and thin beds of intraformational conglomerate and oolite occur throughout. No macrofauna has been recovered from the Danmarks Fjord Member. Although the dolomite was originally...
considered to be of Ordovician age (Adams & Cowie 1953; Fränkl 1955) an Early Cambrian age was subsequently presumed (Cowie 1961, 1971). Conodonts from the member (Smith & Peel 1986) verified the late Canadian age postulated by Peel et al. (1981).

The Amdrup Member conformably overlies the Danmarks Fjord Member and is composed of dark weathering, dark grey, medium to thick-bedded burrow-mottled limestones and dolomitic limestones. Thin lenticular, scoured beds of skeletal grainstones are common, as are intraformational conglomerates and black chert nodules (Peel & Smith 1988). The member contains a moderately abundant and diverse macrofauna which includes gastropods, brachiopods, trilobites and cephalopods. Peel (1980b) recorded Ceratopea billingsi, the late Canadian species recorded also from the Narwhale Sound Formation on Ella Ø (Yochelsen 1964). The trilobite Ceratopeltis latilimbata was described from the lowest beds of the member by Fortey & Peel (1983) and Fortey (1986) documented trilobite faunas from the lower part of the member which he correlated with Ross-Hintze Zone H.

The Alexandrine Bjerge Member conformably overlies the Amdrup Member and is of similar lithology to the Vestervig Elv Member of Peary Land. As with the Vestervig Elv Member no macrofauna has been recorded, but conodonts indicate that the bases of the two members are approximately synchronous (Peel & Smith 1988).

Description of localities
JEM 790627-1. – The section was collected by J. E. Mabillard in Børglum Elv, central Peary Land at the type locality of the Pyramideplateau Member (Section D of Christie & Peel 1977) (Fig. 5). The member is 130 m thick at this locality and was sampled on average at 10 m intervals (Fig. 7).

JSP 800630-5 & JSP 800630-6. – Four samples collected by J. S. Peel on the west side of Kap Holbæk, the reference locality for the Danmarks Fjord Member (Peel & Smith 1988) (Fig. 6: locality B).

JSP 800702-1. – The section was collected by J. R. Ineson and J. S. Peel on the east side of Danmark Fjord (Fig. 6: section A). It runs through the Danmarks Fjord Member (6 m), the Amdrup Member (194 m) and into the Alexandrine Bjerge Member with a sampling interval of 10–15 m (Fig. 7). The locality is a reference section for the Amdrup Member (Peel & Smith 1988).
Fig. 5. The Wandel Valley Formation in Børglum Elv, showing the position of section JEM 790627–1 at the type locality of the Pyramide plateau Member. BF, Brønlund Fjord Formation. WV, Wandel Valley Formation, BR, Børglum River Formation.
Fig. 6. The Wandel Valley Formation around Danmark Fjord. A. cliffs on the eastern side of Danmark Fjord showing the Wandel Valley Formation (WV) overlain by the Sjælland Fjælde (SF) and Børglum River (BR) Formations. For scale, the Sjælland Fjælde Formation is approximately 120 m thick. B. view across Kap Holbæk and Danmark Fjord towards western Kronprins Christian Land. Profile A is section JSP 800702–1 and B shows the position of localities JSP 800630–5 and 800630–6. A. Amdrup Member. AB. Alexandrine Bjerge Member. BR. Børglum River Formation. FS. Fyns Sø Formation (Proterozoic). KH. Kap Holbæk Formation (Proterozoic). SF. Sjælland Fjælde Formation. WV. Wandel Valley Formation. SF. Sjælland Fjælde Formation. BR. Børglum River Formation.
Fig. 7. Stratigraphic logs of sections JEM 790627–1, Børglum Elv, Peary Land, and JSP 800702–1, Kronprins Christian Land, showing sample positions. DFM, Danmarks Fjord Member.

Biostratigraphy

Development of Early Ordovician conodont biozonation

In the interval between the first description of Early Ordovician conodonts from North America (Branson & Mehl 1933) and the first provisional attempt at establishing a biostratigraphic framework (Ethington & Clark 1971) only six systematic descriptions of similar faunas were published and correlation was carried out by simple subjective comparison. The scheme proposed by Ethington & Clark (1971) synthesized what was known about distribution and incorporated five informal “Faunas” which were essentially assemblage zones. Twelve additional faunas were proposed by Sweet et al. (1971) for the Middle and Upper Ordovician, although it was subsequently shown that the oldest of these, Fauna 1, overlaps to a significant degree with Fauna E (Fig. 8).

Ethington & Clark (1982) systematically described and documented in detail the distribution of conodonts through the Canadian (= Ibexian) Series type section in the Ibex area of westernmost Utah. A more refined, though still provisional, zonation was produced to replace Faunas B–E. Biostratigraphic intervals defined by the first appearance of one or more species were named and a precise correlation was possible with the Ross-Hintze trilobite-brachiopod zones established in the same sections (Hintze 1952; Hintze in Ross et al. 1982) (Fig. 8). It is pertinent to note here that the Canadian – Whiterockian boundary for this study is taken at the first appearance of the brachiopod Orthidiella, as recommended by Ross et al. (1982: 12). This has the consequence of placing the first appearance of the brachiopod Orthambonites subalata and the trilobite Ecetnonotus in the uppermost Canadian although they too have been considered to be Whiterockian indicators by Ross (1951, 1970). The first appearance of Orthidiella at Ibex is close to that of Pteracontiodus cryptodens (Mound) (Ross et al. 1982) and this species is taken as the conodont index for the base of the Whiterockian Series.

Intervals of post-proavus Biozone/pre-Orthidiella age. The Ibex area was situated close to the margin of the Laurentian craton (Ethington 1979) and relatively deep water biofacies are thus represented in parts of the sequence (Ethington & Repetski 1984). In consequence, many of the species used to define the faunal intervals, particularly in the late Canadian, are not present in more widespread shallow water biofacies. As a result they have limited application as zonal indices for the whole craton and it would be advantageous to base the biozonation on species with a wider distribution, both in an ecological and a geographical sense. Once the framework was established it would be possible, if necessary, to overlay separate deep and shallow water subzonations whilst retaining an ease of correlation between the two.

Some of the informal zonal intervals of Ethington & Clark (1971, 1982) have now been replaced by formal terms. A formal and more detailed zonation of the
Upper Cambrian and lowermost Ordovician was put forward by Miller (1978, 1988). The *proavus* and *intermedius* biozones are equivalent to Fauna A of Ethington & Clark (1971) and Fauna B has been replaced by the *lindstromi* and *angulatus* biozones.

Fauna C was replaced by the *Loxodus bransoni* Interval in the Ibex study (Ethington & Clark 1982). Although this species is geographically widespread it is a rare component in collections (Ethington & Repetski 1984) and Landing et al. (1986) instead proposed a zone based on the first appearance of the characteristic species *Rossodus manitouensis* Repetski & Ethington 1983, a more common species in all but the shallowest water environments. The zone is approximately equivalent to the *Loxodus bransoni* Interval although *R. manitouensis* ranges rather lower than *L. bransoni* (Ethington & Clark 1982; Taylor & Landing 1982), substantially reducing the length of the *angulatus* Biozone. Further work is necessary to determine whether the use of both zones is appropriate.

Ethington & Repetski (1984) proposed the *communis* Biozone to replace Fauna E. The base was placed at the first appearance of *Oepikodus communis* (Ethington & Clark 1964) and the top at that of a new species of *Plectodina* which is introduced at approximately the same level as *P. cryptodens* (Ethington & Repetski 1984).

These developments leave only Faunas D and its equivalent intervals, the *Glyptoconus quadraplicatus aff. S. rex* Interval, without any formal basis. Although the characteristic species *G. quadraplicatus* is extremely widespread and common, the remaining three taxa are less so. The most satisfactory solution is probably to erect a *quadraplicatus* Biozone which could be subzoned using *A. deltatus*, *M. dianae* or shallow water species. A detailed restudy of the “Fauna C-D” boundary is currently under way (Ethington et al. 1987; Ethington pers. comm.) to determine in detail the faunal succession and to analyse its biomere-like character. As a result, it is not appropriate to erect here a new *quadraplicatus* Biozone and Fauna D is retained, although with a base more rigidly defined on the first appearance of *G. quadraplicatus*. 

Biostratigraphy of the Cape Weber Formation

On Ella Ø, the first occurrence of *G. quadraplicatus*, and hence the base of Fauna D as defined here, is at 64 m above the formation base. Below this the low diversity faunas are characteristic of the *manitouensis* Biozone and comprise *Variabiloconus bassleri* (Furnish), a species which does not range above the zone (Ethington et al. 1987), together with *Cordylodus* sp. nov. A, “*Drepandus*” sp. A and *Semiacontiodus* sp. A (Fig. 9).

The only species introduced at the same level as *G. quadraplicatus* is *Eucharodus parallellus* (Branson & Mehl), followed by *Aloxconus staufferi* (Furnish) and *Aloxconus* sp. B at 76 m. The majority of characteristic Fauna D taxa are introduced between 134 m and 178 m but then few species make their first appearances in the upper part of the zone. The major exceptions to this are *Eucharodus toomeyi* (Ethington & Clark) (342 m), *Protopanderodus leonardii* Serpagli (342 m), *P. elongatus* Serpagli (430 m) and *P. gradatus* Serpagli (438 m). Ethington & Clark (1982) recorded all three of the *Protopanderodus* species only from the *communis* Biozone but Repetski (1982) did record *P. elongatus* and *P. leonardii* from Fauna D, the former from low in the zone.

The first appearance of *O. communis* is at 514 m and the majority of Fauna D species range through into the *communis* Biozone for a considerable distance. An exception is *A. staufferi* which is last seen 27 m above the base of the zone. Only one species, *Wandelia guyi* gen. et sp. nov., is introduced relatively low in the *communis* Biozone, although in the Wandel Valley Formation it first appears with *Cristodus loxoides* Repetski and below the first appearance of *O. communis*. A large number of species are introduced 846 m above the formation base, in what is probably an environmentally controlled event, and this high diversity interval persists until 992 m. Those species occurring in this interval include *Bergstroemognathus extensus* (Graves & Ellison), *Jumudon­thus gananda* Cooper, *Fahraeusodus marathonensis* (Bradshaw) *Protopriioniodus papiliosus* (van Wamel), *Pteracontiodus bransoni* (Ethington & Clark), *?Reut­erodius andinus* Serpagli and *Toxododus carlae* (Repetski). The presence of both *J. gananda* and *?R. andinus* in this interval indicates a position above the base of the *?R. andinus*/*J. gananda* Interval of Ethington & Clark (1982). This unit would have wide application if formalised as the *J. gananda* Sub-biozone. The next youngest interval in Ethington & Clark’s scheme is that of *P. aranda*/*J. jaanussoni*, but neither of these indices is present.

The uppermost part of the formation again yields collections of low diversity and is dominated by species which originated in Fauna D. Some samples contain no *communis* Biozone indices and demonstrate the care needed in applying Fauna D as a biostratigraphic interval in shallow water/restricted biofacies. A small number of the species originating in Fauna D continue across the Cape Weber – Narwhale Sound boundary, accompanied by only one species originating in the *communis* Biozone, *?R. andinus*. The low diversity reflects the environmentally restricted character of the basal Narwhale Sound Formation on Ella Ø. The first White­rockian species to appear is *Pteracontiodus cryptodens* at 95 m above the boundary. Conodonts from the Cape Weber Formation on Albert Heim Bjerge (unpubl. GGU collections) indicate that the diachronism observed in older formations persists through to this level. The basal part of the formation there contains conodonts representative of Fauna D rather than the *man­itouensis* Biozone. Similarly, the Cape Weber – Nar­whale Sound boundary is younger on Albert Heim Bjerge with White­rockian species, including *P. cryptoden­s*, first appearing 912 m above the base of the Cape Weber Formation (unpublished GGU collections).

Biostratigraphy of the Danmarks Fjord and Amdrup Members

The majority of the species in the Canadian part of the Wandel Valley Formation are long-ranging, hyaline, con­form species, although a few albide conform and a very few ramiform-pectiniform species are also present. Most of the species in the lower 50 m of the Danmark Fjord section (JSP 800702–1) are typical long-ranging Fauna D taxa (Fig. 10) which continue into the *commu­nis* Biozone. Two of the species which appear low in the formation, *Cristodus loxoides* Repetski and *P. bransoni*, are known to have first appearances in high Fauna D (Ethington & Clark 1982; Repetski 1982) and delimit a maximum age for the formation. *O. communis* itself first appears at 55 m together with *P. papiliosus*.

Recent data suggest that *C. loxoides* may have substantial potential as a zonal index. In the Wandel Valley Formation, the first appearance, at 20 m, of *C. loxoides* is 35 m below that of *O. communis*. This relationship is maintained in the El Paso Group of westernmost Texas where *C. loxoides* first appears 42 m below the range base of *O. communis* (Repetski 1982). The western Newfoundland platform and slope sequences permit correlation of these range bases the graptolite biozonation. In the platform sequence, *C. loxoides* first appears together with *O. communis* at the base of the Catoche Formation (St. George Group) (Stouge 1982), and within the *Tetragraptus approximatus* graptolite zone (Williams et al. 1987). In the equivalent sediments of the slope sequence, the Factory Cove Member of the Cow Head Group, the single occurrence of *C. loxoides* is 32 m below the range base of *O. communis*, and is coincident with the base of the *T. approximatus* Zone (Stouge & Bagno!i 1988; Williams & Stevens 1988). If the base of Arenig is taken at the base of the *T. approximatus* Zone, the characteristic species *C. loxoides* appears to be a reasonable conodont index for the lower
Fig. 9. Conodont range chart of selected species from the Cape Weber Formation, Ella Ø (section PF 770824–1).

Fig. 10. Conodont range chart of selected species from the Danmarks Fjord and Amdrup Members, Kronprins Christian Land (section JSP 800702–1).
Boundary of that series in Laurentia although further work is needed to establish the degree of precision of this correlation.

In summary, the base of the Wandel Valley Formation in Kronprins Christian Land is likely to be of late Canadian/basal Arenig age, or latest Fauna D in conodont terms. However, if the first appearance of O. communis in the section is above the true range base owing to environmental constraints, a lowest communis Biozone age is also possible.

Few species are introduced in the upper part of the member but those which are include F. marathonensis, B. extensus, Juanognathus variabilis and a number of Protopanderodus species. Few taxa cross the Amdrup–Alexandrine Bjerge boundary and the first Whiterockian species, Drepanoistodus angulensis Ethington & Clark, is introduced 60 m above it. The presence of D. angulensis together with Protoprioniodus aranda Cooper indicates that the Canadian – Whiterockian boundary occurs below this point, in the lowest 60 m of the Alexandrine Bjerge Member.

Biostratigraphy of the Pyramideplateau Member

The Pyramideplateau Member of Peary Land is dominated by long-ranging shallow water species to an even greater degree than the Kronprins Christian Land members (Fig. 11). W. guyi is again present with C. loxoides at the base of the member, and there is no evidence for diachronicity between Kronprins Christian Land and Peary Land.

As with the Amdrup Member, only a few species cross the boundary into the overlying member. The first Whiterockian species, Chosonodina rigbyi Ethington & Clark, D. angulensis and Trigonodus? sinuosus (Mound) are introduced 48 m above, in the Vestervig Elv Member. The co-occurrence of these species indicates a position within the altifrons Biozone of Sweet (1984) (Harris & Repetski pers. comm.) and shows that the Canadian – Whiterockian boundary, as in Kronprins Christian Land, occurs at or just above the base of the upper member.

Conodont Colour Alteration

The colour alteration of conodonts in response to heating has been known for many years (Ellison 1944; Lindström 1964) but was not systematically studied and quantified until the work of Epstein et al. (1977). Unaltered conodont elements were experimentally heated and the alteration process was discovered to be both time and temperature dependent. A scale of conodont colour alteration indices (CAI 1–8) was proposed which corresponded to colour changes from pale yellow (CAI 1) through light and dark brown to black (CAI 5), and from black to grey (CAI 6), white (CAI 7) and eventually clear (CAI 8). In the initial study only CAI 1–5 were experimentally calibrated but subsequent work (Rejebian et al. 1987) has extended the calibration to CAI 6–8.

East Greenland

CAI values for Ordovician rocks from the Caledonian fold belt are surprisingly low. Late Canadian to Whiterockian conodonts from Ella Ø, Albert Heim Bjerge
and C. H. Ostenfeld Nunatak (Fig. 1) have values of 1, 1 and 2 respectively. These indicate minimum temperatures of < 50-90°C (CAI 1) and 60-140°C (CAI 2) (Epstein et al. 1977). Late Canadian coniform elements recovered from erratic blocks on north Cecilia Nunatak in Inner Gletscherland (Fig. 1) do have a higher CAI of 4 (190-300°C) and indicate the presence of more highly metamorphosed Ordovician carbonates to the west, underneath the Inland Ice. These higher values suggest that the western margin to the fold belt is further to the west than previously suspected and supports recent structural data (Manby & Hambrey 1988).

North Greenland

Canadian conodonts from Børglum Elv, Peary Land, have a CAI of 2 (60-140°C) and those from sections in Danmark Fjord are 3 (110-200°C). These values conform well with the compilation of all Ordovician-Silurian localities in North Greenland (Armstrong 1983). The contoured map for all data features a south to north increase in CAI from 1+ to 5 with isotherms trending W-E across North Greenland before swinging through 90° to run down the East Greenland Caledonides. The E-W trending CAI isotherms are in close agreement with those derived by palynomorph Thermal Alteration Index and pyrolysis studies (Christiansen et al. 1985).

Apparatus nomenclature

Following the initial attempts at Bergström & Sweet (1966) and Webers (1966) to apply multielement rather than form taxonomy to Ordovician conodonts, a variety of nomenclatural schemes have been devised for designating the element types of apparatuses. The most commonly encountered are those of Jeppsson (1971), Klapper & Philip (1971), Sweet & Schönlaub (1975) and Barnes et al. (1979), but the scheme of Sweet & Schönlaub (1975), as modified by Sweet (1981), has gained the widest usage and is used here for ramiform-pectiniform apparatuses.

The notational scheme of Sweet & Schönlaub has also been applied to the apparatuses of coniform species, most notably by Barrick (1977), Orchard (1980) and Cooper (1981). Before this scheme can be applied to coniform apparatuses it should, however, first be demonstrated that the element types are homologous with those in ramiform-pectiform apparatuses. Whilst this has been done for taxa with prioniodontid affinities (e.g. Diaphorodus) it has not been demonstrated for true coniform apparatuses. In particular, there is no evidence that elements assigned to the P position in coniform apparatuses (Orchard 1980; Cooper 1981) are homologous with the pectiform elements conventionally assigned to that position. Furthermore, the evidence from natural assemblages indicates that the overall architectures of coniform and ramiform-pectiniform apparatuses are dissimilar (Aldridge et al. 1987; Smith et al. 1987; Smith 1990).

The only nomenclatural schemes designed specifically for coniform apparatuses are those of Barnes et al. (1979) and so far as is possible these are used here. Type I apparatuses exhibit cross-sectional symmetry transition from laterally compressed or rounded (s element) to asymmetrical (t) to antero-posteriorly compressed (u). Intermediates between these element types may be present in more plastic apparatuses. Type III apparatuses are here slightly redefined from the concept of Barnes et al. (1979). They are composed of laterally compressed elements in which element types are distinguished by recurvature and, in some genera, the distribution of costae, which may form a transition series. They are distinguished from Type I by having all elements laterally compressed. Natural assemblages of P. striatus (Figs 29, 30), a Type I apparatus, show significant differences in apparatus architecture to Type III apparatus assemblages such as Panderodus (Smith et al. 1987) and Besselodus (Aldridge 1982). Whereas the latter are laterally juxtaposed in half apparatus rows, the former exhibit more complex element interrelationships which mirror element morphology (see P. striatus – Remarks). These differences in apparatus architecture may represent a fundamental phylogenetic division within the coniform euconodonts.

Taxonomic comments

The initial attempts at producing a suprageneric classification of conodonts (Ulrich & Basler 1926; Branson & Mehl 1944; Hass 1962) were on a form taxonomic basis and consequently have little biological validity. The first attempt at a zoological classification was that of Lindström (1970) and this was expanded upon to produce that used in the second conodont Treatise (Robison 1981). This classification predates a number of key systematic studies of Canadian faunas (Kennedy 1980; Cooper 1981; Ethington & Clark 1982; Repetski 1982) and with the addition of the problems noted by Fahrhau (1984) is of little validity for genera in this interval. As a result, suprageneric classification is not employed in this study. A major study of phylogenetic relationships will be necessary before a valid zoological classification of Early Ordovician conodonts can be achieved.

Where open nomenclature is used, the notation is essentially that of Richter (1943, 1948), reviewed by Matthews (1973). As remarked upon by Bengtson (1988), the precise usage by authors of the terms aff., cf. and ? varies and that used here is in accordance with his recommendations. The use of quotation marks around a genus to indicate obsolence or use in a form taxonomic sense follows the suggestions of Jeppsson & Merrill (1982). Where appropriate, use is made of Bengt-
Systematic descriptions

Genus *Aloxoconus* nov.

Type species. — *Acontiodus staufferi* Furnish, 1938: 326.

Derivation of name. — alox (Gr.), furrow; konos (Gr.), cone; with reference to the grooved posterior face.

Diagnosis. — Apparatus unimembrate. Elements antero-posteriorly compressed, anterior face convex, posterior face concave or flat, may bear a median ridge or pair of ridges. Cusp erect to proclined. Basal cavity outline ovate, long axis transverse. Hyaline or albid.

Remarks. — Following Furnish’s (1938) description of *Acontiodus staufferi* a majority of authors followed the practice of assigning the species to *Acontiodus* in a form sense although it has become increasingly clear that there is no phylogenetic relationship to that genus. *Acontiodus* was considered by Austin et al. (1981) to be a possible junior synonym of *Acodus* Pander which itself was treated as a nomen dubium by Kennedy (1980). Other authors have assigned the species to *Scolopodus* whilst continuing to interpret it as having a unimembrate apparatus. The apparatus of *Scolopodus sublaevis*, the type species, is however multimembrate and exhibits symmetry transition. Landing (1981) included Furnish’s species in *Scolopodus quadruplicatus* Branson & Mehl together with the elements described as *Scolopodus triplicatus* and *Scolopodus robustus* by Ethington & Clark (1964). The distribution and morphology of *S. quadruplicatus*, *S. triplicatus* and *S. robustus*, indicates that they are conspecific and they were grouped together as *Glyptoconus quadruplicatus* by Kennedy (1980). In the Greenland collections the distribution of *A. staufferi* shows no particular association with *G. quadruplicatus*; in relative terms the former is exceedingly scarce, although they are both members of the same shallow water biofacies. Indeed *A. staufferi* does not appear to be conapparatal with any other element and is hence interpreted as a unimembrate species in need of a generic name.

Furnish (1938) also described two similar, though older, elements as *Acontiodus iowensis* and *A. propinquus*. Landing (1981) included both in a single species, *Semiacontiodus iowensis*, together with an albid *A. staufferi-like* element and an un-named asymmetrical element. Landing et al. (1986) retained the binomen but included only *A. iowensis* and *Oistodus mehli* Furnish as, respectively, the symmetrical and asymmetrical elements of a *Semiacontiodus* apparatus. However, *A. iowensis* and *A. staufferi* are strikingly similar and differ only in details of the posterior ridge and in white matter development. Specimens of *A. iowensis* with a bifid posterior ridge have frequently been assigned to the form taxon *A. staufferi*. There are three possible interpretations of the relationship between the two elements: 1) they are structural homoeomorphs and not phylogenetically related, 2) the older species *A. iowensis* evolved into the younger by loss of the asymmetrical element and white matter, 3) *A. iowensis* is not associated with an asymmetrical element and evolved into *A. staufferi* by loss of white matter and a change in the proportion of bifid to non-bifid posterior ridges. Only in the latter case could *Acontiodus iowensis* be assigned to *Alaokoconus*. Landing et al. (1986) reported three asymmetrical elements and five symmetrical elements in their small collection but there was no distributional relationship. Collections from Greenland (GGU, unpublished) and Utah (R. L. Ethington, pers. comm.) do not support the inclusion of an asymmetrical element and for this reason the third, most parsimonious, postulate is adopted here and *A. iowensis* is reassigned to *Aloxoconus* pending further work.

*Aloxoconus* thus includes *A. staufferi* and *A. iowensis* together with *A. propinquus* and a number of species described in open nomenclature.

(Aloxoconus) staufferi Furnish 1938

Fig. 12 a, b

- 1938 *Acontiodus staufferi* Furnish – 326, pl. 42: 11–12, fig. 1 K
v non 1964 *Acontiodus staufferi* Furnish – Ethington & Clark: 686–688, pl. 113: 4, 9
non 1965 *Acontiodus staufferi* Furnish – Ethington & Clark: pl. 2: 14
v non 1965 *Acontiodus staufferi* Furnish – Mound: 12–13, pl. 1: 22
1970 *Acontiodus staufferi* Furnish – Barnes & Tuke: 84, pl. 19: 2, 3
v non 1971 *Acontiodus staufferi* Furnish – Ethington & Clark: pl. 1: 14
non 1971 *Scolopodus staufferi* (Furnish) – Druce & Jones: 94–95, pl. 18: 8–9
non 1971 *Scolopodus staufferi* (Furnish) – Jones: 67, pl. 6: 7a–c
non 1971 *Acontiodus staufferi* Furnish – Greggs & Bond: 1463, pl. 1: 1, 2
1975 *Acontiodus staufferi* Furnish – Abaimova: 51–52, pl. 2: 8–10, fig. 6: 14, 17
1980 "Acontiodus" staufferi Furnish – Kennedy: pl. 2: 38
1980 Acontiodus iowensis Furnish – Grether & Clark: pl. 1: 46
1980 Acontiodus staufferi Furnish – Grether & Clark: pl. 1: 49
v non 1982 "Acontiodus" staufferi Furnish – Ethington & Clark: 24, pl. 1: 24
1982 Acontiodus staufferi Furnish – Repetski: 15, pl. 4: 4a-5d
p 1982 Scolopodius staufferi (Furnish) – Moskalenko: 139-140, pl. 25: 14 only (non pl. 25: 10a & b)
non 1985 Acontiodus staufferi Furnish – Stouge, Bagnoli & Albani: pl. 1: 4
1988 "Acontiodus" staufferi Furnish – Stouge & Bagnoli: 112, pl. 1: 3

Remarks. – A. staufferi, as first described by Furnish (1938) from the Shakopee Dolomite of Wisconsin, included some specimens with an unmodified posterior ridge and others with bifid posterior costae. Many subsequent identifications of the species have been in error and document variants of A. iowensis from older units, of manitouensis Biozone age. The principal difference between the two species is in the degree of albidity, A. iowensis being almost entirely albid, and perhaps also in the proportion of bifid specimens. Specimens described by Ethington & Clark (1964) as A. staufferi are here assigned to Aloxoconus sp. A. The material most closely similar to that from Greenland was described by Barnes & Tuke (1970).

Range. – A. staufferi occurs from the base up to 30 m in the Wandel Valley Formation in Børglum Elv and up to 55 m in Kronprins Christian Land; also from 76 to 543 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 28.

Aloxoconus sp. A

Fig. 12 c

v 1964 Acontiodus staufferi Furnish – Ethington & Clark: 687, pl. 113: 4, 9
v 1982 Scolopodiform C, Ethington & Clark: 107, pl. 12: 14, fig. 29
p 1988 Parapanderodus emarginatus (Barnes & Tuke) – Stouge & Bagnoli: 126-127, pl. 7: 2 only (non pl. 7: 1, 3)

Remarks. – These specimens differ from A. staufferi in being more antero-posteriorly compressed, having sharper posterior costae and lacking the flared and lipped basal margin. Stouge & Bagnoli (1988) included the element in the apparatus of "Scolopodius" emarginatus (Barnes & Tuke) together with an element identical to the s element of Parapanderodus striatus (Graves & Ellison). Both of these elements are considerably more abundant than Aloxoconus sp. A in the Greenland samples, and there is no support for an apparatus of this composition.

Range. – A. sp. A ranges from 12 m to 45 m in the Wandel Valley Formation of Kronprins Christian Land and occurs at 128 m in Børglum Elv. The species is also found at 424 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 5.

Aloxoconus sp. B

Fig. 12 d


Description. – Cusp erect to slightly proclined. Anterior margin rounded. Lateral faces flat, converging anteriorly, terminated posteriorly by postero-lateral costae. Posterior face concave or with a shallow, v-shaped groove. Basal outline approximately circular. Basal margin straight or lipped. Basal cavity moderately deep,
conical, apex just anterior of centre. Hyaline, may be faintly striate.

Remarks. – The morphology is similar to *A. propinquus* Furnish but, as noted by Landing & Barnes (1981), the type specimens are albid whereas these are hyaline. Furthermore, no specimens with a median posterior costa, as illustrated by Furnish (1938: pl. 42: 15), were recovered from Greenland.

The specimens described as *A. propinquus* by Ethington & Clark (1982) are very similar to *A. sp. B* but are albid and occur at lower stratigraphic levels. *A. sp. B* may prove to be a posteriorly acostate component of the apparatus of *A. staufferi* since the overall morphology of the two elements is very similar.

Range. – *A. sp. B* occurs from the base up to 121 m in the Wandel Valley Formation in Børglum Elv and at 45 m in Kronprins Christian Land. A single specimen was found at 76 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 8.

Genus *Bergstroemognathus* Serpagli 1974


Type species. – By original designation, *Oistodus extensus* Graves & Ellison, 1941: 13.

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**Bergstroemognathus extensus** *(Graves & Ellison 1941)*

Fig. 13 a–g

<table>
<thead>
<tr>
<th>Year</th>
<th>Reference Details</th>
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<td>1941</td>
<td><em>Oistodus extensus</em>, Graves &amp; Ellison: 13, pl. 1: 16, 28</td>
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<td>Indeterminable specimen, Graves &amp; Ellison, pl. 1: 20</td>
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<td><em>Rhipidognathus?</em> n. sp. – Bergström et al.: fig 1 K</td>
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<td>1976</td>
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<td>1988</td>
<td><em>Bergstroemognathus extensus</em> (Graves &amp; El- lison) – Stouge &amp; Bagnoli: 113, pl. 1: 6–13</td>
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Fig. 13. *Bergstroemognathus extensus* (Graves & Ellison). a: inner lateral view of segminate M element, × 40, MGUH 18.708, GGU 240011. b: posterior view of alate Sa element, × 60, MGUH 18.709, GGU 240014. c: inner lateral view of bipennate S element, × 60, MGUH 18.710, GGU 240015. d: lateral view of bipennate S element, × 60, MGUH 18.711, GGU 240014. e: lateral view of bipennate S element, × 60, MGUH 18.712, GGU 240014. f: lateral view of bipennate S element, × 60, MGUH 18.713, GGU 240015. g: lateral view of bipennate S element, × 60, MGUH 18.714, GGU 240013.
Remarks. — The trimembrate apparatus consists of a geniculate segminate M element, an alate Sa element and bipennate S elements. Bergström (1981: W134–135) considered the third element to be tertiopedate but the third, lateral, process, is simply a downward extension of the basal margin rather than a true process. The morphology of the alate and segminate elements is consistent with previous descriptions in all but denticule numbers. The Greenland specimens have up to twelve denticles on the alate element and eighteen on the segminate element. This is rather more than on those described by Serpagli (1974) who cited up to seven and twelve denticles respectively.

The bipennate element is variable both in terms of symmetry and denticulation. The anterior process is always denticulate, bearing from two to five denticles. The posterior process may be adenticulate and bear a thin keel or have up to three denticles. If a keel is present, small incipient denticles may be found at its anterior end. The anterior and posterior processes may be in the same plane or the element may be strongly laterally bowed. Studies on larger collections may show that a systematic transition takes place within this element.

The specimen figured by Bergström et al. (1972) is fragmentary but may be part of an alate element. The specimens figured by Cooper (1981) differ in having broader, more laterally discrete denticles and may represent a different species. Bultynck & Martin (1982) illustrated a typical segminate element. The two bipennate specimens figured by Stouge (1982) have very well developed anterior processes and extremely short posterior processes. This type of element has also been recovered from Greenland. In addition to the references cited in the synonymy list, B. extensus has also been reported from Washington Land (Kurtz & Miller, GGU int. rept.).

Range. — B. extensus occurs between 916 m and 1052 m up to the Cape Weber Formation on Ella Ø and ranges from 103 m to 195 m in the Wandel Valley Formation in Kronprins Christian Land.

Number of specimens. — 3 alate Sa, 12 bipennate S, 14 segminate M.

Genus Chionoconus nov.


Type species. — Chionoconus avangna sp. nov.

Derivation of name. — chion (Gr.), snow; konos (Gr.), cone; with reference to both the geographical location and the albid character of the type species.

Diagnosis. — Apparatus trimembrate. p element with erect cusp, anterior keel and expanded inner face. q element with more reclined and curved cusp, unexpanded base. r element geniculate, anterior margin keeled, inner face carinate. Albid.

Remarks. — Only the type species can be assigned to Chionoconus with certainty. The apparatus or apparatuses represented by Paltodus sweeti, Scandodus robustus, Oistodus hunickeni and Scandodus americanus of Serpagli probably belong here although more work is necessary to ascertain the exact composition of the apparatus or apparatuses of this group of elements.

Chionoconus is distinguished from the majority of Canadian genera in being trimembrate. Of those genera which have trimembrate apparatuses, Chionoconus is distinguished from Oistodus in being acostate and lacking a trichonodelliform element. The type species of Scandodus, S. furnishi, Lindström, is distinct in lacking a true geniculate element (Bergström 1981: W144). Drepanoistodus shares with Chionoconus an erect p element, a reclined/recurved q element and a geniculate r element, but the presence of the distinctive anterior keel and anticusp in the p and q elements and the markedly straight cusps are sufficient to consider the two as separate genera. Furthermore, the q element of Chionoconus does not display the range of variation which is now being recorded in Drepanoistodus (Dzik 1983; Smith, Aldridge & Fortey unpublished collections).

In a radical reinterpretation of the genus Tropodus, Bagnoli et al. (1988) and Stouge & Bagnoli (1988) included the p and r elements of C. avangna as P and M elements of T. comptus. This revision, which included taxonomic alterations to other Tropodus species, is discussed in detail under that genus but it may be noted here that the absence of C. avangna from many localities where T. comptus is present does not support this interpretation.

Chionoconus avangna sp. nov.

Fig. 14 a–h

1970 Distomodus kentuckyensis Branson & Branson – Lee: 317, pl. 7: 11, 12
? 1971 Acontidodus onestensis Furnish – Druce & Jones: 56–57, pl. 12: 5a–7c only, (non pl. 12: 3a–4b)
? 1971 Oistodus inequalis Pander – Druce & Jones: 76, pl. 12: 10a–13b, fig. 25a
? 1974 Acodus delciatus Lindström – Viira 41, pl. 2: 28, fig. 16a–c
v 1982 Oistodus inequalis Pander – Ethington & Clark: 67–68, pl. 7: 7, fig. 15
v 1982 “Scandodus” sp. 1 – Ethington & Clark: 96–97, pl. 11: 6, 7, fig. 22
1982 Acodus? sp. cf. A. delicatus Branson & Mehl – Stouge: 33, pl. 4: 1, 2, 5

Meddelelser om Grønland, Geoscience 26 · 1991
1983 *Scandodus cf. robustus* Serpagli – Ni in Zeng et al.: pl. 11: 15

1983 *Triangularodus bravibasis* (Sergeeva) (sic) – Ni in Zeng et al.: pl. 11: 17

1988 *Tropodus comptus* (Branson & Mehl) – Bagnoli et al.: 215–216, pl. 41: 8, 11 (non pl. 41: 9, 10)

1988 *Tropodus comptus* (Branson & Mehl) – Stouge & Bagnoli: 141–142, pl. 16: 1, 2

Derivation of name. – Avangná (Greenlandic), North Greenland.

Type material. – The holotype is MGUH 18.716, a p element, from sample GGU 239968 collected 164 m above the base of the Cape Weber Formation on Ella Ø (section PF 770824–1). Paratypes are MGUH 18.715 (p element) and MGUH 18.718 (q element) from GGU 274955 collected 55 m above the base of the Wandel Valley Formation in section JSP 800702–1, Danmark Fjord; MGUH 18.717 (p element) and MGUH 18.721 (r element) from GGU 274950 collected 130 m above the base of the Wandel Valley Formation in section JSP 790627–1, Børglum Elv, Peary Land.

Diagnosis. – p element with anterior keel and broad spatulate anticusp; basal cavity strongly expanded on inner face only. q element with unexpanded base and anterior keel. The keels of both p and q elements may be deflected laterally. r element with characteristically extended antero-basal corner and basal cavity with strongly expanded inner face.

Description. – p element

Cusp erect. Upper edge of base short, straight, sharp-edged, meeting posterior margin of cusp at angle of 90° or rather less. Posterior margin keeled, nearly straight. Anterior margin keeled; keel higher than on posterior

![Image of Chionocoilinus avangna](https://via.placeholder.com/150)

Fig. 14. *Chionocoilinus avangna* gen. et sp. nov. a: inner lateral view of p element (paratype), × 40, MGUH 18.715, GGU 274955. b: inner lateral view of p element (holotype), × 40, MGUH 18.716, GGU 239968. c: inner lateral view of p element (paratype), × 40, MGUH 18.717, GGU 274950. d: inner lateral view of q element (paratype), × 40, MGUH 18.718, GGU 274955. e: outer lateral view of q element (paratype), × 40, MGUH 18.719, GGU 239984. f: inner lateral view of r element (paratype), × 60, MGUH 18.720, GGU 226394. g: inner lateral view of r element (paratype), × 40, MGUH 18.721, GGU 274950. h: outer lateral view, same specimen.

Meddelelser om Grønland, Geoscience 26 · 1991
margin, deflected inwards, narrowing distally, proximally produced as large, rounded anticusp which may be deflected outwards. Outer face flat or gently rounded. Inner face with carina one third from anterior margin. Basal margin straight or distinctly angular, angle just to posterior of anticusp. Basal outline equilaterally triangular with one corner on inner face. Outer face unexpanded, inner side strongly expanded, some specimens with costa along maximum curvature of inner face. Basal cavity shallow, asymmetrically triangular in profile, anterior margin in line with posterior margin of anticusp, posterior margin parallel to upper edge of base.

q element
Cusp reclined. Upper edge of base very short, with a low keel; junction with posterior margin angular or sharply curved. Posterior margin sharp to keeled, gently curved. Anterior margin keeled, deflected inwards; short angular anticusp may be developed. Outer face flat to gently rounded. Inner face rounded, keel deflected inwards. Outer face of basal cavity unexpanded, inner side strongly expanded, some specimens with costa along maximum curvature of inner face. Basal cavity shallow, asymmetrically triangular in profile, anterior margin in line with posterior margin of anticusp, posterior margin parallel to upper edge of base.

r element
Geniculate. Upper edge of base extremely short, keeled. Posterior margin straight, keeled. Anterior margin keeled, straight or slightly curved, may be deflected inwards. Outer face gently rounded, inner face carinate. Antero-basal corner extended, basal margin straight. Base unexpanded on outer face, greatly expanded on posterior part of inner face as continuation of carina, extended as narrow slit to antero-basal corner.

Intermediate specimens of p–q or q–r morphology are common. All specimens are albid above the basal region.

Remarks. — The p element of C. avangna has been figured by Tipnis et al. (1978) and Ethington & Clark (1982: pl. 11: 6, 7). The element figured as O. inaequalis by Ethington & Clark (1982: pl. 7: 7) is morphologically close to the r element of C. avangna, but has a much longer range than Scandodus sp. 1, the p element, and may include two or more similar elements.

Oistodus sp. 6 of Ethington & Clark (1982), from the House Limestone, resembles the r element but is substantially older than the Greenland specimens. As suggested by Ethington & Clark (1982), the specimens may be conspecific with O. inaequalis of Druce & Jones (1971) and together with Acontiodus onoeotensis of the latter authors may constitute the apparatus of an older, but related, species.

Triangulodus cf. T. brevibasis (Sergeeva) of Repetski (1982) contains some very similar elements to those in C. avangna. The erect scandiform, acodiform and drepanodiform elements compare closely with the p and q elements. The r element (oistodiform of Repetski) is, however, very different and, in addition, elements corresponding to his trichonodelliform and distacodiform elements are not present in the Greenland collections.

Range. — C. avangna occurs from the base to the top of the Pyramideplateau Member (Wandel Valley Formation) in central Peary Land and the lower two members in Kronprins Christian Land. On Ella Ø the species has a range from 164 m to 1010 m.

Number of specimens. — 134 p, 174 q, 126 r.

Genus Cordylodus Pander 1856

1856 Cordylodus, Pander: 33

Type species. — By subsequent designation, Ulrich & Bassler (1926: 8), Cordylodus angulatus Pander, 1856: 33.

Remarks. — Miller (1980) reviewed the taxonomy of Cordylodus and proposed the terms rounded and compressed for the elements of its bimembrate apparatus, in reference to the cusp cross-section.

Cordylodus sp. nov. A

Fig. 15 a


Remarks. — The basal cavity of the compressed element is extremely shallow and extends posteriorly as a slit to the end of the posterior process; the basal margin, from the antero-basal corner to the end of the posterior process, is straight to gently convex; there is a noticeable increase in the inclination of the denticles posteriorly and the element is bowed. No rounded element was recovered.

The only previously figured specimens which closely resemble Cordylodus sp. nov. A are those of Landing & Barnes (1981) and Nowlan (1985), both from the Cape Clay Formation of the Canadian Arctic Islands. These elements also possess denticles which increase in inclination to the posterior and the cusp that is bowed slightly inwards. The species is also present in larger numbers in unpublished GGU collections from Warming Land, North Greenland, but there is again no associated element.
Remarks. – The species was found in a single sample 15 m up the Cape Weber Formation on Ella Ø.

Number of specimens. – 3.

Genus Cristodus Repetski 1982

1982 Cristodus, Repetski: 18

Type species. – By original designation, Cristodus loxoides Repetski, 1982: 18.

Remarks. – The apparatus is bimembrate, with a geniculate “monodenticulate” element and a gently recurved “multidenticulate” element (terminology of Repetski 1982).

Cristodus loxoides Repetski 1982

Fig. 15 b–d

1980 New genus, new species – Grether & Clark: 14, pl. 1: 44, 45
1980 New genus B – Kennedy: 49, pl. 2: 36, 37
1982 Cristodus loxoides, Repetski: 18–19, pl. 5: 6a–7c
1982 Gen. nov. A sp. nov. A – Stouge: pl. 4: 14, 15
1983 Loxodus? sp. aff. Loxodus bransoni Furnish – Stouge: pl. 3: 1, 2
1988 Cristodus loxoides Repetski – Stouge & Bagnoli: 114, pl. 1: 18, 19

Remarks. – The first description of the species was that of Barnes & Tuke (1970) from the St. George Group of Newfoundland and it has been recorded subsequently in open nomenclature. The illustrations of the monodenticulate element, together with Repetski’s (1982) description, indicate considerable variation in the length of the cusp and in the angle of the anterior edge relative to the base. The specimens from North Greenland correspond most closely to specimens from the El Paso Group (Repetski 1982) and the St. Peter Sandstone (Grether & Clark 1983). The multidenticulate elements conform exactly to Repetski’s description.

Range. – The species ranges from 20 m to 195 m in the Wandel Valley Formation in Kronprins Christian Land and was recorded from a sample 4 m up the same formation in Peary Land.

Number of specimens. – 4 monodenticulate, 4 multidenticulate.

Cristodus? sp. A

Fig. 15 e

Remarks. – A geniculate coniform element broadly similar to the monodenticulate element of C. loxoides. It differs in having a widely flared basal cavity open to the posterior. The tip of the cusp is albid.
Range. – Found at 306 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 1 monodenticulate.

Genus Diaphorodus Kennedy 1980

1980 Diaphorodus, Kennedy: 51

Type species. – By original designation, Acodus delicatus Branson & Mehl, 1933: 56.

Remarks. – Kennedy (1980) erected Diaphorodus to include some species previously assigned to Acodus. He decided that until the apparatus of A. erectus, the type species, was reconstructed, it was preferable to regard Acodus as a nomen dubium. The apparatus of Diaphorodus is quinquemembrate and consists of a laterally costate, pastinate, P element, a geniculate coniform M element and a symmetry transition series of Sa, Sc and Sd elements. The elements are albid and adenticulate.

Diaphorodus delicatus
(Branson & Mehl 1933)

Fig. 16 a–e

v * 1933 Acodus delicatus, Branson & Mehl: 56, pl. 4: 10
v 1933 Cordyodus simplex, Branson & Mehl: 64, pl. 4: 11
v 1933 Palitosus distortus, Branson & Mehl: 62, pl. 4: 12
v 1933 Oistodus expansus, Branson & Mehl: 60, pl. 4: 4
v 1933 Oistodus vulgaris, Branson & Mehl: 60–61, pl. 4: 5
1973 Acodus deltatus deltatus Lindström – McTavish: 39–40, pl. 1: 1–9, 12–14, fig. 3 p–t
v p 1977a Acodus brevis, Branson & Mehl – Lindström: 5–6, Acodus – pl. 2: 2, 3, 4 only
1982 Acodus delicatus Branson & Mehl – Repetski: 10–11, pl. 1: 5a–9c
non 1982 Acodus? sp. cf. A. delicatus Branson & Mehl – Stouge: 34, pl. 4: 1, 2, 5
1987 Diaphorodus delicatus (Branson & Mehl) – Ethington et al.: pl. 8:1: 1

Remarks. – The apparatus was reconstructed and thoroughly described by Kennedy (1980) and with the relatively small amount of material at hand little can be added to this description. Many of the elements, especially M, Sa and Sc, have morphologies which are common to several species and can only be assigned in the presence of the more diagnostic P elements.

Range. – From 976 m to 992 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 5 M, 2 Sa, 1 ?Sc, 1 Sd.

Diaphorodus? sp. nov. A

Fig. 16 h–l

Remarks. – This distinctive species has an apparatus which fits exactly the generic diagnosis of Diaphorodus given by Kennedy (1980), the elements being albid, adenate, and with poorly developed keels. The apparatus contains a pastinate P element, a geniculate coniform M element and a transition series of Sa, Sc and Sd elements. The elements are characteristic in having extremely long processes. Of previously described species, Diaphorodus sp. nov. A most closely resembles D. longibasis (McTavish) but differs in that all of the processes are sub-equal in length rather than only the posterior process being extended. It is distinguished from Diaphorodus? emanuelensis (McTavish) in having much longer processes on all elements and a P element that is pastinate.

Range. – At 20 m above the base of the Wandel Valley Formation in Kronprins Christian Land.

Number of specimens. – 15 P, 29 M, 2 Sa, 11 Sc, 14 Sd.
Diaphorodus? sp. B

Fig. 16 m–q

Remarks. – Ethington & Clark (1982) described a plexus of elements which they tentatively assigned to D? emanuelensis. They commented that the apparatus shows a total intergradation of element types, rendering grouping of morphologies very difficult. The same is true of the small number of specimens from Greenland. Only a few features are common to all element types; the rudimentary denticles mentioned by Ethington & Clark (1982) are often present. Most elements, with the exception of the Sd element, have a nick at the junction between the cusp and the upper edge of the base. The Sa element is similar to, but narrower than, the Sa element of D. delicatus.

Range. – From 848 m to 992 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 17 P, 17 M, 6 Sa, 20 Sc, 4 Sd.

Genus Drepanodus Pander 1856

1856 Drepanodus, Pander: 20

Type species. – By subsequent designation, Miller (1889: 313) Drepanodus arcuatius Pander, 1856: 20.
**Drepanodus arcuatus** Pander 1856

Fig. 17 p-r

* 1856 *Drepanodus arcuatus*, Pander: 20, pl. 1: 2, 4, 5, 17 (? pl. 1: 30, 31)

1856 *Drepanodus flexuosus*, Pander: 20, pl. 1: 6–8

1955 *Acontioides arcuatus* Lindström: 547, pl. 2: 1–4, fig. 3 A

1955 *Drepanodus arcuatus* Pander – Lindström: 558–560, pl. 2: 30–33, fig. 3 J

1955 *Drepanodus cf. arcuatus* Pander – Lindström: 560–561, pl. 2: 45, 46, fig. 4c


1955 *Drepanodus sculponea*, Lindström: 567, pl. 2: 40, fig. 3 L

1955 *Scandalodus pipa*, Lindström: 593, pl. 4: 38–42, fig. 3 P

1971 *Drepanodus arcuatus* Pander – Lindström: 41, figs 4, 8


1979 *Drepanodus arcuatus* Pander – Tipnis et al.: pl. 2: 1–3


1982 *Drepanodus arcuatus* Pander – Ethington & Clark: 36–37, pl. 3: 4–6, 12

1982 *Drepanodus arcuatus* Pander – Repetski: 19–20, pl. 6: 1a, b

1982 *Drepanodus cf. D. arcuatus* Lindström (sic) – Repetski: 20, pl. 6: 4a–c, fig. 4 Q

1982 *Drepanodus? gracilis* (Branson & Mehl) – Repetski: 20, pl. 6: 6a–c, fig. 4 S

1982 *Drepanodus sculponea* Lindström – Repetski: 22, pl. 7: 9a–c

1982 *Scandalodus cf. S. pipa* Lindström – Repetski: 44, pl. 20: 5a–c, fig. 7 G

1982 *Drepanodus arcuatus* Pander – Stouge: pl. 5: 18–19

1983 *Drepanodus? arcuatus* Pander – Stouge: pl. 4: 1; 2

1983 *Drepanodus arcuatus* Pander – Ni in Zeng et al.: pl. 10: 33, 35

1984 *Drepanodus cf. arcuatus* Pander – Dzik: 336–337, pl. 3: 5, 6, 77

1985 *Drepanodus arcuatus* Pander – An et al.: pl. 12: 10–13, 15

1988 *Drepanodus arcuatus* Pander – Stouge & Bagnoli: 115–116, pl. 2: 1–6

Remarks. – The apparatus of *D. arcuatus* was first reconstructed by Lindström (1971) who included two element types, drepanodiform and oistodiform. A more complex apparatus plan was proposed by van Wamel (1974) and supported by Löfgren (1978). In van Wamel’s interpretation, the apparatus is quadr imagemem and composed of elements termed arcuatiform, sculponeaform, pipaform, and graciliform, although Löfgren considered the first two to be variants of the drepanodiform and the last two to be oistodiform variants. A further variant within the apparatus is a posterolateral costate arcuatiform element (Löfgren 1978).

The Greenland specimens conform to previous descriptions with the major exception that graciliform elements were not recovered. In addition, some elements, particularly arcuatiform specimens, can be difficult to distinguish from those of *D. concavus* (Branson & Mehl). In such cases the distribution of white matter has been used to distinguish between species although this is a somewhat variable character (Kennedy 1980) and some specimens of *D. arcuatus* morphology are alb. Arcuatiform elements of *D. arcuatus* tend to have a less flared base and are generally smaller than those of *D. concavus*. Sculponeaform elements are closely similar to those of *D. concavus* but the pipaform and graciliform elements are quite characteristic and offer a more secure means for distinguishing the two species.

No costate arcuatiform elements were recovered from Greenland, an absence also noted in Utah (Ethington & Clark 1982) and Argentina (Serpagli 1974). This was tentatively explained as being due to the presence of a separate sub-species in these areas by Löfgren (1978). Further work is needed to clarify the relationship of Midcontinent Province *D. arcuatus* to North Atlantic Province *D. arcuatus* although for the present they are considered to be conspecific.

Range. – From 10 m to 95 m in the Wandel Valley Formation in Kronprins Christian Land and from 164 m up the Cape Weber Formation into the Narwhale Sound Formation on Ella Ø.

Number of specimens. – 44 arcuatiform, 0 graciliform, 41 pipaiform, 27 sculponeaform.

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**Drepanodus concavus** (Branson & Mehl 1933)

Fig. 17 a–j

* 1933 *Oistodus concavus*, Branson & Mehl: 59, pl. 4: 6

1933 *Oistodus gracilis*, Branson & Mehl: 60, pl. 4: 20

1933 *Oistodus pandus*, Branson & Mehl: 61, 110–111, pl. 4: 21, 22


1982 *Drepanodus sp. 1* – Ethington & Clark: 40, pl. 3: 13, fig. 11

1982 *Drepanodus? sp. 2* – Ethington & Clark: 40–41, pl. 3: 14, fig. 12

1982 *Drepanodus concavus* (Branson & Mehl) – Repetski: 20, pl. 6: 11a–c, fig. 4 R

1982 *Drepanodus pandus* (Branson & Mehl) – Repetski: 20, pl. 6: 7a–c

1982 *Oistodus gracilis* Branson & Mehl – Repetski: 32, pl. 9: 10a-c

1982 *Drepanodus? gracilis* (Branson & Mehl) – Stouge: 34, pl. 3: 2, 3

1982 *Oistodus concavus* Branson & Mehl – Stouge: 35, pl. 2: 23

1982 *Drepanodus pandus* (Branson & Mehl) – Moskalenko: 109, pl. 26: 8

1983 *Drepanodus? gracilis* (Branson & Mehl) – Stouge: pl. 2: 6, 7

Meddelelser om Grønland, Geoscience 26 · 1991
Remarks. – The elements included here were treated under form taxonomy until Kennedy (1980) grouped them together as a species of Drepanodus. As first revisor Kennedy chose D. concavus from the three available names used by Branson & Mehl (1933). The morphology of the component elements is very close to that of D. arcuatus but Kennedy cited the major differences as being the hyaline nature, the large size of elements and the profile of the arcuatiform element of D. concavus. The identification of specimens from Greenland has of necessity rested largely on their albid or hyaline nature. This may, however, prove untenable since some of the albid arcuatiform elements seem to have the compressed and extended antero-basal corner characteristic of D. concavus.

Other differences occur in the oistodiform elements (sensu Löfgren 1978). In D. arcuatus pipiform elements are common but graciliform rare with a ratio of approximately 5:5:1. The situation is reversed in D. concavus, with those elements interpreted as pipiform by Kennedy (1980) being the rarest components of the apparatus. These elements are highly characteristic with a basal margin turned through 110° and bearing a lip on the anterior part (Kennedy 1980: pl. 1: 31; Abaimova 1975: pl. 4: 11). In addition, the basal asymmetry of the graciliform element of D. arcuatus noted by Lindström (1955) is not seen in the graciliform of D. concavus and the cusp-base junction is acute in the latter species. The pipiform and graciliform elements of D. arcuatus and D. concavus may not be fully homologous and it is possible that the “graciliform” of D. concavus (sensu Kennedy 1980) is homologous with the pipiform of D. arcuatus. Kennedy (1980) noted that specimens transitional between arcuatiform and sculponeaform morphology occur. This is also the case in Greenland, where relatively few specimens corresponding closely to Kennedy’s figures have been found, the majority of arcuatiform elements being more similar to those figured by Abaimova (1975: pl. 4: 3–5). The specimens described herein as Drepanodus sp. C are closely similar to arcuatiform elements of D. concavus except for the presence of an antero-laterally directed antero-lateral costa. These elements may prove to be the equivalent element in D. concavus to those of the form taxon Acontiodus arcuatus Lindström included in the apparatus of D. arcuatus by van Wamel (1974) and Löfgren (1978).

Drepanoistodus lucidus of Stouge & Bagnoli (1988) is a hyaline species of very similar morphology to D. concavus, from which it differs principally in possessing a suberectiform element. If the suberectiform elements here described as ?Drepanoistodus suberec tus (Branson & Mehl) prove to be part of the apparatus of D. concavus it will necessitate both a change of genus for the latter species and a revision of ideas concerning the early evolution of Drepanoistodus.

Range. – D. concavus ranges from the base of the Wandel Valley Formation into the Westervig Elv Member in central Peary Land and up to 200 m in Kronprins Christian Land. The species has a range from 134 to 1086 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 183 arcuatiform, 82 graciliform, 16 pipiform, 48 sculponeaform.

Drepanodus? costatus Abaimova 1971

Remarks. – The specimens have costae which are most pronounced in the posterior part of the cusp at the point of greatest recurvature, although one or more of the costae may run subparallel to the posterior margin until near the cusp tip. The specimens illustrated by Moskalenko (1982) are more prominently costate than those from Greenland and those figured by Abaimova (1971, 1975).

In the absence of large collections, it is difficult to decide whether D? costatus represents a poorly known species of Drepanodus or is a unimembrate apparatus, possibly referable to Eucharodus.
“Drepanodus” sp. A
Fig. 17 l
Remarks. – A slender reclined coniform element of biconvex cusp cross-section. Albid above the basal cavity, which is deep and straight-sided.

“Drepanodus” sp. B
Fig. 17 m
Remarks. – Cusp rounded in cross-section, reclined. Posterior and anterior margins are straight. The base is widely flared and very shallow; unequally developed laterally with a faint ridge running antero-laterally. Hyaline except for a thin growth axis; surface smooth.

Drepanodus sp. C
Fig. 17 n, o
1982 “Scolopodus” inconstans Branson & Mehl – Stouge: 35, pl. 2: 24
Remarks. – The element is close in overall morphology to the arcuiform element of *Drepanodus concavus* but has a sharp, antero-lateral costa on the less-expanded inner face. The costa is present only on the base, starting near the anterior margin and diverging basally, and is directed antero-laterally. A second, sharp costa may be present on the outer face, very close to, and parallel with, the anterior margin. In such elements, there is a v-shaped groove between the costae.
Costate arcuiform elements are known to occur in the apparatus of *D. arcuatus* (van Wamel 1974; Löfgren 1978) but have not been described in the apparatus of *D. concavus*. The costate arcuiform elements of *D. arcuatus* ("Acontiodus arcuatus" Lindström, 1955") have the costae situated adjacent to the posterior margin and running the full length of the cusp. *Drepanodus* sp. C may be an homologous element in the *D. concavus* apparatus but larger collections are needed to ascertain whether this is definitely the case.

Genus *Drepanoistodus* Lindström 1971

1971 *Drepanoistodus*, Lindström: 42

Type species. – By original designation, *Oistodus forceps* Lindström 1955: 574.

*Drepanoistodus* aff. *forceps* (Lindström 1955)

Fig. 18 a–c

<table>
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<th>Year</th>
<th>Author</th>
<th>Reference</th>
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<td>1978</td>
<td>Drepanoistodus forceps (Lindström) – Löfgren: 53–54, pl. 1: 1–6 (synonymy to 1977)</td>
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<tr>
<td>1985</td>
<td>Drepanoistodus forceps (Lindström) – An et al.: pl. 8: 3, 7, 17</td>
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<td>1985</td>
<td><em>Oistodus forceps</em> (Lindström) – Ethington &amp; Clark: 43, pl. 3: 22–24, fig. 13</td>
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<tr>
<td>1985</td>
<td>Non 1985 <em>Drepanoistodus forceps</em> (Lindström) – An et al.: pl. 8: 3, 7, 17</td>
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</table>

Remarks. – Ethington & Clark (1982) considered specimens of *Drepanoistodus* from Utah, Nevada (Ethington & Clark 1971) and Alberta (Ethington & Clark 1965) to be closely related to *D. forceps* but possibly not conspecific. The specimens from Ella Ø closely resemble theirs in having a less acute, more rounded antero-basal corner to the r element than is normal in Baltic collections of *D. forceps* (Lindström 1955; Löfgren 1978).

Range. – From 848 m to 992 m in the Cape Weber Formation on Ella Ø.
Number of specimens. – 2 p, 17 q, 11 r.

?*Drepanoistodus suberectus* (Branson & Mehl 1933)

Fig. 18 d, e

<table>
<thead>
<tr>
<th>Year</th>
<th>Author</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1933</td>
<td>Oistodus suberectus, Branson &amp; Mehl: 111, pl. 9: 7</td>
<td></td>
</tr>
<tr>
<td>1933</td>
<td>Oistodus erectus, Branson &amp; Mehl: 110, pl. 9: 4, 10, 12</td>
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<tr>
<td>1970</td>
<td>Drepanodus homocurvatus Lindström – Lee: 320–322, pl. 7: 16, 17</td>
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Remarks. – From 4 m to 9 m in the Wandel Valley Formation in central Peary Land and at 404 m in the Cape Weber Formation on Ella Ø.
Number of specimens. – 3.

Genus *Drepanoistodus* Lindström 1971

1971 *Drepanoistodus*, Lindström: 42

Type species. – By original designation, *Oistodus forceps* Lindström 1955: 574.
Remarks. — Clark (1972) proposed that the apparatus of _D. suberectus_ lacked an oistodiform element in the Early and early Middle Ordovician and consisted simply of _p_ and _q_ elements. Repetski (1982) chose to retain Early Ordovician representatives in _D. suberectus_ but placed them in an un-named subspecies. It is unlikely that these elements can remain in _D. suberectus_ since even if a close relationship were established as suggested by Clark, the lack of an _r_ element is sufficient to warrant assignment of a separate binomen.

The _q_ elements of _?D. suberectus_ are very similar to the arcuatiform element of _Drepanodus concavus_ and are distinguished by the presence of white matter. Since the presence of white matter is variable, and its taxonomic significance in this group debatable (Kennedy 1980), this is not a totally reliable character and some of the more hyaline specimens of _?D. suberectus_ may have been included in _D. concavus_; the opposite may also be true.

The _p_ element differs from that of _D. suberectus_ in being less drawn out antero-basally and in having a basal cavity that is more widely flared posteriorly. The _q_ element differs in commonly having an anterior margin which is deflected inwards, flanked posteriorly by a shallow groove.

An alternative approach would be to include the suberectiform _p_ element in the apparatus of _D. concavus_. The respective morphologies are sufficiently similar to warrant this but would require removal of the species from _Drepanodus_. More substantial collections will be needed to test this possibility.

Range. — Up to 30 m in the Wandel Valley Formation in central Peary Land and from 35 m to 200 m in the Wandel Valley Formation in Kronprins Christian Land.

Number of specimens. — 24 _p_, 25 _q_.

_Drepanoistodus_ sp. A

Remarks. — Only the _r_ element of this species was recovered but it is very distinctive owing to its small size. The element has a long base, a convex basal margin and is acostate.

Range. — From 20 to 200 m in the Wandel Valley Formation in Kronprins Christian Land and at 868 m in the Cape Weber Formation on Ella Ø.

Number of specimens. — 10.

**Genus Eucharodus** Kennedy 1980

1980 _Eucharodus_, Kennedy: 57

Type species. — By original designation, _Drepanodus parallelus_ Branson & Mehl, 1933: 58–60.

_Eucharodus apion_ sp. nov.

Remarks. — _apion_ (Gr.), pear, with reference to the basal outline.
Type material. — The holotype is MGUH 18.764 from sample GGU 274945 collected at 195 m above the base of the Wandel Valley Formation, close to the top of the Amdrup Member, to the east of Danmark Fjord (section JSP 800702-1). The paratype is MGUH 18.765 from GGU 274944 at 200 m in the same section.

Diagnosis. — Apparatus unimembrate. A hyaline coniform element with a proclined to erect cusp, strongly deflected to the inner side and a characteristic, pear-shaped basal outline; the basal cavity is very shallow.

Description. — Cusp proclined to erect, upper edge of base very short, flat to broadly convex, curving round evenly into cusp. Posterior margin sharp, straight or very slightly curved, may continue across base as a costa. Anterior margin sharp, straight in lower half, gently curved at mid-height, straight distally. Cusp symmetrically biconvex, strongly deflected inwards. Basal margin straight anteriorly, curving up posteriorly so that cavity opens to posterior. Basal outline pear-shaped, narrow anteriorly, broadening rapidly at one third of the distance to the posterior. Base gently expanded laterally, anterior margin sharply rounded and a continuation of anterior keel. Cavity very shallow, apex posterior. Hyaline, thin growth axis runs from basal cavity apex to cusp tip parallel to posterior margin.

Remarks. — Kennedy (1980) included only two species in Eucharodus, E. parallelus and E. toomeyi, although he did note that new, undescribed species were present in Canadian and Early Whiterockian faunas. These are distinguished by elongation of the base, shape of the basal cavity, curvature, flattening and tapering of the cusp and white matter distribution. E. apion is a characteristic, mono-elemental species distinguished from E. parallelus and E. toomeyi, by the symmetrical, pear-shaped basal outline, the very shallow basal cavity and the strong, inward declination of the cusp. E. apion is also present in the communis Biozone of the El Paso Group (J. E. Repetski, pers. comm.).

Range. — From 195 m to 200 m in the Wandel Valley Formation in Kronprins Christian Land and at 868 m in the Cape Weber Formation on Ella Ø.

Number of specimens. — 13.

Eucharodus parallelus
(Branson & Mehl 1933)

Fig. 19 d–f

Remarks. — The type specimens of Eucharodus parallelus (Branson & Mehl) are hyaline elements from the Jefferson City Formation of Missouri (Kennedy 1980). Subsequent to Branson & Mehl's (1933) description, Furnish (1938) described similar specimens from the Prairie du Chien Beds of the Upper Mississippi Valley, and named them Drepanodus subarcuatus. Kennedy (1980) noted that Furnish's specimens from the older

Oneota Dolomite are albid whereas those from the Shakopee Dolomite are hyaline and differ in subtle morphological details; unfortunately no holotype was selected by Furnish (1938) but Kennedy (1980) chose to nominate one of the hyaline Shakopee specimens as lectotype, thus rendering D. subarcuatus a junior subjective synonym of D. paralle/us.

Mound (1968) was the first to suggest that D. arcuatus, D. paralle/us, D. simplex and D. subarcuatus are conspecific and, as first revisor, chose D. paralle/us as the name for the species; D. arcuatus is a primary homonym of D. arcuatus Pander, 1856. Mound's specimens do not, however, belong to the same species as those described by Branson & Mehl (1933). Independent studies by Barnes & Tuke (1970) led them to the same conclusion but they chose the name D. simplex. Druce & Jones (1971) considered D. simplex distinct from D. subarcuatus, but Kennedy (1980) noted that their specimens are albid and not related to the species under discussion.

Kennedy (1980) recognised that an apparatus containing D. paralle/us, D. simplex and D. arcuatus was essentially mono elemental and did not correspond to the apparatus plan of Drepanodus as established by Lindström (1971), van Wamel (1974) and Löfqren (1978). He therefore erected a new genus, Eucharodus, with E. paralle/us as the type species.

Dzik (1983) considered E. paralle/us to be a member of the same apparatus as Ulrichodina abnormalis (Branson & Mehl) and noted a similarity between this combination of elements and the apparatus of Scandodus furnishi Lindström. Such a reconstruction is not supported by the Greenland faunas since the two species are unrelated in terms of occurrence and abundance. The specimens from Greenland comply well with Kennedy's (1980) redescription of Branson & Mehl's types. The basal cavity outline varies from ovate to sub-circular and may be mildly asymmetrical. The antero-basal angle varies from 70° upwards, although a few specimens have angles as low as 60° (rather lower than in Kennedy's redescription). The postero-basal angle is 50–60°. The cusp varies from sub-erect to reclined and is of biconvex cross-section with sub-rounded to keeled margins. Most specimens have sharply rounded to sharp margins. The apparatus is unimembrate although variations in morphology do occur and are continuous, with only end members discernible.

Range. – E. paralle/us ranges from the base of the Pyramid plateau Member into the Vestervig Elv Member in Peary Land. In Kronprins Christian Land, it ranges from the base of the Danmarks Fjord Member into the Alexandrine Bjerre Member. The species has a
range of 64–1010 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 689.

**Eucharodus toomeyi** (Ethington & Clark 1964)

(Fig. 19 g)

**Remarks.** The specimens from Peary Land and Kronprins Christian Land are closely similar to the holotype of *Scolopodus filosus xyron* (Repetski 1982: pl. 22: 6a–c). The holotype has a rounded anterior margin, a sharp posterior edge, a weakly expanded base and is finely striate. The Greenland specimens differ only in having a more ovate basal outline and less inflated lateral faces on the base. The second specimen illustrated by Repetski (1982: pl. 22: 1a–c) is more coarsely striate, to the point of being finely costate, and is markedly asymmetrical. Elements of this morphology have not been recovered from Greenland and their assignment to the same species is queried.

**S. filosus xyron** of Repetski (1982) differs from "*Scolopodus* filosus" Ethington & Clark in having a cusp that is laterally compressed at the posterior margin, producing a sharp edge. The difference is considered sufficient to warrant a distinction at specific level. A second possibility, that the elements are members of the same apparatus, is ruled out by the lack of co-occurrence in Greenland and the very limited stratigraphic range of this taxon in relation to that of "S." filosus in the El Paso Group (Repetski 1982).

The apparatus appears to be unimembrate and does not correspond to the apparatus structure of *S. sublaevis* Pander, the type species of *Scolopodus* as reconstructed by Fähræus (1982). It does, however, fit the diagnosis of *Eucharodus* (Kennedy 1980) and the species is reasigned to that genus.

**Remarks.** – The specimens at hand conform well with the description given by Ethington & Clark (1964). The species was placed within *Eucharodus* by Kennedy (1980) since no associated elements of a *Drepanodus* apparatus had been reported; the hyaline elements were thought by Kennedy to be the components of a unimembrate apparatus. The Greenland material supports this interpretation.

**Range.** – From 10 m to 200 m in the Wandel Valley Formation in Kronprins Christian Land and in a single sample at 4 m in Børglum Elv. It ranges from 342 m up to 4 m in the Cape Weber Formation into the Narwhale Sound Formation on Ella Ø.

Number of specimens. – 20.

**Eucharodus xyron**? (Repetski 1982)

(Fig. 19 h, i)

**Remarks.** – *E. xyron*? occurs from the base of the Wandel Valley Formation into the Vestervig Elv and Alexandrine Bjerget Members in Børglum Elv and Kronprins Christian Land respectively.

Number of specimens. – 28.

**Genus Fahraeusodus** Stouge & Bagnoli 1988

1988 Fahraeusodus, Stouge & Bagnoli: 118–119

**Type species.** – By original designation, ?*Microzarkodina adentata* McTavish, 1973: 49–50.

**Remarks.** – In addition to the type species, Stouge & Bagnoli (1988) included two other species in *Fahraeusodus*: *F. marathonenensis* (Bradshaw) and *F. mirus* Stouge & Bagnoli. All three have apparatuses made up of a P element (dolabriform in *F. adentata* and *F. marathonensis*), an oistodiform M element and a tri- or quadrimembrate symmetry transition series wherein the sym-
Symmetry is expressed by subtle variation in costae/keels on the cusp, which may be extended as short adenticulate processes. The generic affinity and evolutionary origin of *F. adentata* and *F. marathoniensis* have been the subject of some debate and uncertainty. Although McTavish (1973) and Ethington & Clark (1982) tentatively assigned the species to *Microzarkodina* Lindström the apparatus are not closely comparable. The seximembrate apparatus of *Microzarkodina* comprises a carinate P element, an oistodiform M element with characteristic rounded anterior margin and arched posterior process, and a quadrimembrate symmetry transition series which includes a true alate Sa element and a digerate Sb. I concur with Ethington & Clark (1982) that a relationship with *Microzarkodina* is doubtful.

Ethington & Clark (1982) compared the general apparatus composition and white matter distribution of *F. adentata* and *F. marathoniensis* with *Protoprioniodus* McTavish. The style of symmetry transition is similar, as is the overall apparatus composition. Ethington & Clark drew attention to the presence of a flange parallel to the basal margin in both *F. marathoniensis* and *P. aranda*. There are, however, significant differences in the morphology of the P and M elements, and in the adenticulate nature of *Protoprioniodus* ramiform elements. The well-preserved material described from Cow Head by Stouge & Bagnoli (1988) reveals similarities to *Paracordylodus* Lindström, which are particularly close between *P. gracilis* Lindström, the type species, and *F. marathoniensis*. Both have dolabrate P elements, oistodiform M elements, and S elements with anticusp and a quadrimembrate symmetry transition series. All elements have a flange running parallel to the basal margin similar to that in *Protoprioniodus*. The denticles of *P. gracilis* elements have a characteristic narrow, striate costa in the centre of the lateral face, a micro-morphological feature also possessed by *F. marathoniensis* (cf. Stouge & Bagnoli 1988: pls 4: 16, 17, 8: 18). It is quite likely that *Fahraeusodus* and *Paracordylodus* are sister groups, although the precise species relationships are not yet clear. *Protoprioniodus* may constitute a third member of the lineage.

### Fahraeusodus marathoniensis
*(Bradshaw 1969)*

*Description.* - P element

Cusps and denticles erect to reclined, sharp-edged. Anterior margin keeled, may be deflected forwards. Antero-basal angle 70° and sharply curved. Posterior process may be slightly twisted. Ridge may run parallel to basal margin a short distance above it. Basal margin below cusp slightly convex but more or less a straight line from antero-basal corner to posterior end of process. Basal cavity shallow, anterior margin short, posterior margin extended under process; apex below posterior margin of cusp.

M element

Coniform, geniculate. Anterior margin curves evenly into antero-basal corner; anticusp short. Posterior process may bear keel on upper edge. Basal cavity weakly expanded, does not affect straight line of basal margin from anticusp to posterior process.

Ramiform elements

Sc element generally similar to P but has long anticusp which may be longer than cusp. Denticles more reclined distally. Posterior process curves around evenly through approximately 90° into posterior margin of anticusp. Anterior margin keeled, may be deflected inwards.

Sb element has costa along one lateral face of cusp crossing basal cavity apex, curving posteriorly to meet basal margin at point of maximum basal cavity width. Anterior keel may be deflected to opposite lateral face. There is a very smooth transition from Sb to Sa, with a flat or broadly rounded anterior face developing. One antero-lateral costa is then directed slightly anteriorly, the opposite antero-lateral costa slightly posteriorly. In Sa end-members the costae are normal to the plane of the posterior process. Subdivision of intermediate elements between Sb and Sa is necessarily subjective. Sc elements may show development of an incipient lateral costa but there is more of a morphological jump from Sc to Sa than from Sa to Sb.

White matter occupies all of the denticles and all but the basal part of the cusp.

**Remarks.** - Although undoubtedly conspecific, there are small differences between Greenland *F. marathoniensis* and those from Ibex (Ethington & Clark 1982), the El Paso Group (Repetski 1982) and the St. George Group (Stouge 1982). The P elements in the Greenland

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36 Meddelelser om Grønland, Geoscience 26 · 1991
collections are close to those figured by Ethington & Clark (1982) and Repetski (1982) but those of Stouge (1982) differ in having a low carina which extends down the cusp to the basal margin where it interrupts the usually straight line of the basal margin. The M elements of Repetski are similar to the Greenland ones but those included by Ethington & Clark differ markedly by having a costa on the cusp, a longer anticusp and an almost right-angled junction between posterior process and cusp. The ramiform elements of Ethington & Clark and Stouge are within the range of variation shown by the Greenland specimens as, in general, are those of Repetski. However, Repetski also included an “oepikoidiform” element which bears two lateral costae and an anterior keel, hence adding an Sd member to the transition series. Although fragmentary, the figured specimen is consistent in morphology with the other ramiform elements but Ethington & Clark specifically state that they did not recover an element of this morphology and it is not present in Greenland. The reason does not lie in collection size, since those from Greenland and El Paso are of similar magnitude and that from Ibex is substantially larger. The problem must remain unresolved for the present.

Range. – From 95 m in the Wandel Valley Formation into the Alexandrine Bjarne Member, Kronprins Christian Land and 848–1010 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 59 P, 52 M, 26 Sa, 38 Sb, 46 Sc.

Genus Fryxelodontus Miller 1969

1969 Fryxelodontus, Miller: 426

Type species. – By original designation, Fryxelodontus inornatus Miller, 1969: 426–429.

“Fryxelodontus” sp. A

Fig. 21 a–c

Remarks. – A single specimen of each of three element types was recovered from the Cape Weber Formation. All elements have nodose denticleation on at least one process and are very thin walled. The number of processes varies from one to three. The single-processed form has a larger, proclined node (“cusp”) at the ante-
rior. The basal cavity extends the full length of the element but is deepest below the anterior node. The element with two processes has them directed at 90° and the basal cavity occupies the entire lower surface. The element with three processes has them in anterior, lateral and posterior positions, the anterior and posterior ones being sinuous; a larger node is situated centrally and the nodes on the processes are less well-developed than on the other two elements.

The only comparable elements in the Lower Ordovician are Fryxellodonus? corbatoi Serpagli and F? ruedemanni Landing. These two species are similar in their apparatus plan but elements of F? ruedemanni have only one nodose process, the others being smooth (Landing 1976). These two species were not included in Fryxellodonus by Miller (1980), who considered them to be members of a new genus. Stouge & Bagnoli (1988) synonymised the two species and tentatively assigned them to Polonodus Dzik, together with a new species P? lofgreni. The differences between these species and Polonodus is sufficient to suggest that a new genus is still necessary and further material is needed to fully assess the relationships between "F". sp. A, P? corbatoi, P? lofgreni, early Polonodus and Nericodus Lindström.

Range. – At 976 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 3.

Genus Glyptoconus Kennedy 1980

1980 Glyptoconus, Kennedy: 61

Type species. – By original designation, Scolopodus quadraplicatus Branson & Mehl, 1933: 63.

Glyptoconus quadraplicatus (Branson & Mehl 1933)

Fig. 22 a–d

1933 Scolopodus quadraplicatus, Branson & Mehl: 63, pl. 4: 14, 15


1964 Scolopodus robustus, Ethington & Clark: 700, pls 113: 7, 115: 18, 21, fig 2 A

1964 Scolopodus quadraplicatus, Ethington & Clark: 700–701, pl. 115: 20, 22–24, fig. 2 C

1964 Scolopodus variabilis, Ethington & Clark: 701, pl. 115: 14–16, 19

1979 Scolopodus quadraplicatus Branson & Mehl – An: 106–107, pl. 1: 5

1980 Scolopodus quadraplicatus Branson & Mehl – Grether & Clark: pl. 1: 18, 19

1980 Scolopodus triplicatus Ethington & Clark – Grether & Clark: pl. 1: 34, 35


1981 Scolopodus quadraplicatus Branson & Mehl sic – An: pl. 2: 1, 8


1982 Scolopodus quadraplicatus Branson & Mehl – Repetski: 50, pl. 23: 4a–5c

1982 Scolopodus triplicatus Ethington & Clark – Repetski: 52, pl. 24: 1a–c, 4a–c

1982 Scolopodus variabilis Ethington & Clark – Repetski: 52, pl. 24: 5a–c, fig. 8 U


1982 Scolopodus quadraplicatus Branson & Mehl – Moskalenko: 138–139, pl. 27: 12, 16, 17


1983 Glyptoconus quadraplicatus (Branson et Mehl) – Ni in Zeng et al.: pl. 10: 21, 22

1983 Glyptoconus quadraplicatus (Branson et Mehl) – Ni et al.: pl. 1: 28

1983 Scolopodus quadraplicatus Branson et Mehl – An et al.: 146–147, pl. 12: 8, 9

1985 Scolopodus quadraplicatus Branson et Mehl – An et al.: pl. 2: 6–9

1986 Glyptoconus quadraplicatus (Branson & Mehl) – Smith & Peel: fig. 3 A

1987 Glyptoconus quadraplicatus (Branson & Mehl) – Ethington et al.: pl. 8: 1: 3

1988 Glyptoconus quadraplicatus (Branson & Mehl) – Stouge & Bagnoli: 120, pl. 3: 18, 19

Fig. 21. "Fryxellodonus" sp. A: a: lateral view, × 100, MGUH 18.771, GGU 240014. b: upper view, × 100, MGUH 18.772, GGU 240014. c: upper view, × 100, MGUH 18.773, GGU 240014.
Remarks. – Elements with similar morphologies to Scolopodus quadraplicatus Branson & Mehl were described by Ethington & Clark (1964) and given the names S. robustus, S. triplicatus and S. variabilis. Specimens with the morphologies of S. quadraplicatus and S. triplicatus from Greenland, like those from Missouri (Kennedy 1980) and Utah (Ethington & Clark 1982), show a complete intergradation between forms with two lateral grooves (S. quadraplicatus) and those with only one lateral groove (S. triplicatus). It is clear that they belong in the same apparatus, as concluded by Kennedy (1980) and Ethington & Clark (1982). An additional type of element is present in the Greenland faunas with no groove on one lateral face and only an extremely faint lateral groove on the opposite face. This is effectively a continuation of the transition from S. quadraplicatus to S. triplicatus to a form which has only the posterior groove well-developed.

The relationship of S. robustus and S. variabilis to this apparatus has been a matter of some debate. Repetski (1975) included them in the apparatus of S. quadraplicatus, considering S. robustus to be an extreme variant of S. variabilis. Although reverting essentially to form taxonomy, Repetski (1982) still treated S. robustus as a junior synonym of S. variabilis. In his thorough review of G. quadraplicatus, Kennedy (1980) included S. variabilis as a possible morphological variant within the apparatus in which the two postero-lateral costae are more developed than the antero-lateral ones. However, Kennedy omitted S. robustus from synonymy with G. quadraplicatus on the grounds that it had not been found in the Jefferson City Formation. S. variabilis is a common component of faunas containing G. quadraplicatus in Greenland although S. robustus is much rarer. I include both S. variabilis and S. robustus as junior subjective synonyms of G. quadraplicatus.

The gargantuan element of Kennedy (1980: pl. 1: 45) is also present in my collections. This is a large, robust element which has deep grooves and, frequently, secondary costa. Kennedy suggested that these elements are not simply oversized versions of normal elements but reflect responses to environmental stress.

The apparatus of G. quadraplicatus thus contains a wide range of forms, particularly with respect to the distribution of costae and grooves. The most common elements have two lateral grooves and a posterior groove bounded by antero-lateral and postero-lateral costae. In some specimens one lateral groove may be very faint or absent and in a few specimens the opposite lateral groove is correspondingly reduced. The postero-lateral costae may be closely spaced and in a few extreme specimens they are very close, with a much reduced posterior groove. The elements may show the development of bifid postero-lateral costae and some specimens have secondary costae running along the lateral grooves. Elements may be striae, the striae not showing preferential development on any one particular type of element.

This apparatus style does not correspond to that of Scolopodus sublaevis, the type species of Scolopodus, as determined by Fähræus (1982) since, in particular, it lacks a “scandodontiform” element. Additionally, the elements are not multicostate. To accommodate these differences, Kennedy (1980) erected Glyptoconus. The smooth transitions between elements makes it very difficult to subdivide the apparatus into discrete element types. Kennedy described it as bimembrate, consisting of symmetrical and asymmetrical types and similarly Barnes et al. (1979) classified it as a Type 1B apparatus. If elements of the types referred to S. variabilis and S. robustus are included, a transfer to the Type IA category may be warranted. In such an apparatus, “Scolopodus quadraplicatus” would be the s element, “Scolopodus triplicatus” the t and “S. variabilis” and “S. robustus” the u element. If such a plan is adopted, smooth transition does not take place from s through to u but from s to t and s to u.

Eucharodus parallelus very commonly occurs in association with G. quadraplicatus and has been mentioned by Kennedy (1980) and Ethington & Clark (1982) as a possible member of the apparatus. Kennedy (1980) dismissed this on the basis of differing ranges, the lack of transitional forms and the absence of any similar Canadian apparatuses. I concur with this view and would add that the abundance peaks of the two species in Greenland are often substantially different.

Acontiodus staufferi Furnish and Ulrichodina deflexa Furnish were included as part of the apparatus of G.
quadraplicatus by Landing & Barnes (1981: 1615) but this is not supported by the collections from Greenland. U. deflexa does have a similar cross-section to quadri-costate elements of G. quadraplicatus but has not been recovered from Greenland to date, whilst A. staufferi is a very rare component of Greenland faunas and has a much shorter range.

Range. – G. quadraplicatus ranges from the base of the Pyramid plateau Member into the Vestervig Elv Member in Peary Land. It was been recovered from the Danmarks Fjord Member at Kap Holbæk and occurs from the base to 140 m in the Wandel Valley Formation in Kronprins Christian Land. On Ella Ø the species ranges from 64 m above the base of the Cape Weber Formation into the Narwhale Sound Formation.

Number of specimens. – 732.

Genus Histiodella Harris 1962

1962 Histiodella, Harris: 207

Type species. – By original designation, Histiodella altifrons Harris, 1962: 208–209.

Histiodella donnae Repetski 1982

Fig. 23 a

v 1982 ?Histiodella sp. – Ethington & Clark: 50, pl. 5: 18
* 1982 Histiodella donnae, Repetski: 25–26, pl. 8: 6a–7c, fig. 51

Remarks. – The element is palmate with a convex anterior face and a concave posterior face with median costa. Incipient denticles are visible along the edges, which are convex in outline. The basal cavity is shallow and limited to the area directly below the posterior costa. The element is albid in all but the basal region. The element is a typical Histiodella Sa as figured by McHargue (1982). The only species of Histiodella reported from the Lower Ordovician is H. donnae Repetski from the El Paso Group (Repetski 1982). An Sa element of this species was mentioned, but not illustrated, by Repetski (1982). The Sa element from the Cape Weber Formation does, however, correspond to that in H. donnae (R. L. Ethington, pers. comm.).

Range. – H. donnae was recovered 880 m up the Cape Weber Formation on Ella Ø.

Number of specimens. – 1.

Histiodella? sp. A

Fig. 23 b

Remarks. – A single specimen of a bladed element was recovered from the Amdrup Member of the Wandel Valley Formation in Kronprins Christian Land. The element is triangular in lateral profile with the cusp situated toward the anterior. The anterior margin is adenticulate and the posterior margin bears four denticles. The basal margin is straight and the basal cavity is a flat plate, widest anteriorly. The element is comparable to the bryantodontiform element of Histiodella figured by McHargue (1982: pl. 1: 1–21).
Genus *Juanognathus* Serpagli 1974

1974 *Juanognathus*, Serpagli: 49

Type species. – By original designation, *Juanognathus variabilis* Serpagli, 1974: 49–50.

Remarks. – The apparatus was classified by Barnes et al. (1979) as Type IA but a particularly smooth transition between the s, t and u elements was noted.

*Juanognathus variabilis* Serpagli 1974

Fig. 23 c, d

\[ v \quad 1974 \quad *Juanognathus variabilis*, Serpagli: 49–50, pls 11: 1a–7c, 22: 6–17, fig. 8 \]

\[ v \quad 1982 \quad *Juanognathus variabilis* Serpagli – Ethington & Clark: 50–51, pl. 5: 8–10, 17 (synonymy to 1974) \]

\[ v \quad 1982 \quad *Juanognathus variabilis* Serpagli – Repetski: 27, pls 8: 9a–c, 9: 1a–2c, fig. 5 L \]

\[ non \quad 1985 \quad *Juanognathus variabilis* Serpagli – An et al.: pls 5: 1, 8, 6: 1 \]

\[ 1988 \quad *Juanognathus variabilis* Serpagli – Stouge & Bagnoli: 120, pl. 3: 20, 21 \]

Remarks. – Only a very small number of elements were recovered. Some specimens have sharp posterior carinae.

Range. – Found at 185 m in the Wandel Valley Formation in Kronprins Christian Land. From 935 m to 1060 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 4.

*Juanognathus* sp. nov. A

Fig. 23 e

Description. – Only u elements have been recovered. Upper edge of base long, curving evenly into proclined cusp. Anterior face broad, evenly rounded, terminated by lateral costae. Costae directed postero-laterally, sharply rounded, posterior faces flat, dying out towards basal margin. Posterior face semi-circular in cross-section. Element usually symmetrical but costae may be asymmetrically placed. Basal margin straight, basal outline circular to sub-triangular with apex posterior. Basal cavity deep, apex anterior. Albid in all except basal area.

Remarks. – The element is generally similar to the u element of *J. variabilis*, but differs in that none of the specimens have short adenticulate processes, nor is the cusp twisted. Although Serpagli (1974) included specimens in *J. variabilis* whose costae did not reach the basal margin, the absence of any of the characteristic element morphologies or symmetry transitions of *J. variabilis* preclude inclusion of the Greenland specimens. *J. sp. nov. A* seems to be a closely related but distinct species.

The species also bears some similarity to large specimens of *Protopanderodus leonardii* but differs in being antero-posteriorly, rather than laterally, compressed and in having more prominent costae.

Range. – From 848 to 880 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 16.

Genus *Jumudontus* Cooper 1981

1971 New Genus B, Sweet, Ethington & Barnes: pl. 1: 34

1981 *Jumudontus*, Cooper: 169


*Jumudontus gananda* Cooper 1981

Fig. 23 f

\[ 1971 \quad *Jumudontus gananda*, Cooper: 170–172, pl. 31: 13 \]

\[ 1982 \quad *Jumudontus gananda* Cooper – Ethington & Clark: 51–52, pl. 2: 9, 10 (synonymy to 1981) \]

\[ 1982 \quad "*Spathognathodus*" sp. Ethington & Clark – Repetski: 53, pl. 25: 8a–10c \]

Remarks. – This characteristic species is a potentially important zonal taxon in the Canadian and has been used in the provisional zonal schemes of Ethington & Clark (1982) and Harris & Repetski (pers. comm). Only a single specimen was recovered but it falls well within the range of morphology of previously figured specimens.

Range. – At 848 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 1.

Genus *Oepikodus* Lindström 1955

1955 *Oepikodus*, Lindström: 570
Type species. – By original designation, **Oepikodus smithensis** Lindström, 1955, 571–572.

Remarks. – The taxonomic status and apparatus structure of **Oepikodus** have been the subjects of much discussion in the literature. The genus was erected by Lindström (1955) for elements with a denticulate posterior process, a suberect cusp and antero-lateral costae which may be developed as short adenticulate processes. The multielement composition was first ascertained by Lindström (1971) who included pastinate, quadriminate and geniculate coniform elements and assigned the species to **Prioniodus**.

The trimembrate concept for the apparatus of **Oepikodus** was maintained by most authors (e.g. Bergström & Cooper 1973; van Wamelen 1974; Serpagli 1974; Fährus & Nowlan 1978) and was used as the principal means of distinguishing the genus from the generally similar elements of **Prioniodus** and **Baltoniodus** which are sexi- and septimembrate respectively (Bergström 1981). However, a symmetry transition series within the oepikodiform element of previous authors was recognised by Ethington & Clark (1982) with element positions distinguished by lateral costae rather than true processes. Repetski (1982) included four members (belodiform, tetraprioniodiform, hibbardelliform and cordyloform) in the transition series and revised the diagnosis of the genus to distinguish it from **Prioniodus** and **Baltoniodus**.

The Greenland collections contain only three elements in the transition series in contrast to the four of Repetski (1982). The Sa element is bicostate, the Sb unicostate and the Sc acostate. Repetski included this Sa as a “tetraprioniodiform” Sd element and recognised a different “cordyloform” Sa with no anticusp. The reason for these differences is unclear but is not due to collection size since both are substantial.

The apparatus was classified as Type IVD by Barnes (1965). However, a symmetry transition series within the **Oepikodus** quadratus (Graves & Ellison) – Ethington & Clark: 193–194, pl. 2: 9
1965 **Subcordylodus** sp. – Ethington & Clark: 201–202, pl. 2: 6
1972 **Gothodus communis** Ethington & Clark – Ethington: 24, pl. 1: 20
1972 **Oepikodus quadratus** (Graves & Ellison) – Ethington: 24, pl. 1: 24–26, ?27
1972 **Oistiodus longiramos** Lindström – Ethington: 23, pl. 1: 3
1973 **Prioniodus evae communis** (Ethington & Clark) – McTavish: 45–46, pl. 3: 27, 29–32, 37, fig. 6a–e
1974 **Prioniodus** (**Oepikodus**) intermedius, Serpagli: 69–73, pls 15: 1a–4b, 27: 1–7, 31: 2a–6, fig. 15 D–F
1980 **Oepikodus communis** (Ethington & Clark) – Kennedy: pl. 2: 33, 34
1982 **Prioniodus evae** Lindström – Teraoka et al.: pl. 2: 3–6, 8
1982 **Prioniodus** n. sp. C McTavash (sic) – Teraoka et al.: pl. 2: 7, 10
1981 **Prioniodus navis** Lindström – Teraoka et al.: pl. 2: 9
1982 **Oepikodus communis** (Ethington & Clark) – Repetski: 30–31, pl. 11: 5a–8b, 10a–b, 12a–c
1982 **Oepikodus communis** (Ethington & Clark) – Stouge: 38–39, pl. 4: 9–12
1982 **Oepikodus** sp. cf. **O. communis** (Ethington & Clark) – Stouge: 40, pl. 6: 17–20
1983 **Oepikodus communis** (Ethington & Clark) – Stouge: pl. 3: 4–6
1983 **Oepikodus** sp. cf. **O. communis** (Ethington & Clark) – Stouge: pl. 4: 10
1985 **Baltoniodus intermedius** (Serpagli) – An et al.: pl. 7: 13, 14, 16, 17
1988 **Oepikodus communis** (Ethington & Clark) – Stouge & Bagnoli: 121, pl. 5: 8–12

Remarks. – Graves & Ellison (1941) described **Cordylodus quadratus** from the Marathon Limestone of Texas. This was considered to be a senior synonym of **Oepikodus equidentatus** Ethington & Clark, 1964, by Ethington & Clark (1971) and Ethington (1972) and hence of **Oepikodus communis** (Ethington & Clark). In their description of the Ibex fauna, Ethington & Clark (1982) preferred, however, not to formalise a revision until a restudy of the Marathon Limestone conodonts had confirmed synonymy. Should such a study show that the two taxa are conspecific, **O. quadratus** will have priority.

**O. communis** was considered to be a subspecies of **Prioniodus evae** by McTavish (1973) because of the similarity of the pastinate elements. Subsequent workers have considered the absence of denticles on the anterior and lateral processes of **O. communis** sufficient to warrant a distinction at specific level.

**Oepikodus communis**

(Ethington & Clark 1964)

Figs 24 a–f, i. j. 25, 26
Serpagli (1974) erected a species, *Prioniodus* (*O.*) *intermedius* for specimens he considered to be intermediate between *O. smithensis* and *O. communis*. This was distinguished from *P. (O.) communis* mainly on details of the processes, with the pastinate element having a more posteriorly deflected anterior process and a less arched posterior process that curved up distally. The ramiform elements differed in possessing hindeodellid denticles and the coniform had a longer anterior process. All of these characters are seen as variations of *O. communis* in the Greenland faunas and *O. intermedius* is treated as a junior subjective synonym of *O. communis* following the practice of Ethington & Clark (1982) and Repetski (1982). *O. communis* was recovered from the St. George Group of Newfoundland by Stouge (1982) together with specimens he described as *O. sp. cf. O. communis*, which he considered to be allied to *O. intermedius*. All of his figured specimens are within the range of variation of *O. communis*.

As noted above, Repetski (1982) included a sixth member in the apparatus of *O. communis* but did not figure it. The extra element would be the Sa of the transition series with the element here interpreted as Sa reassigned to an Sd position. This Sa is distinguished by the lack of anticusp. Such an element was figured and questionably included in *O. quadratus* by Ethington (1972) but is not present in the Greenland collections nor in the large collection described by Ethington & Clark (1982). Both of these collections are smaller than that described by Repetski, but given that over 400 S elements have been recovered from Greenland it is highly unlikely that, if present in the species, it was possessed by all individuals.

Natural assemblages. — Two fused clusters of *O. communis* were recovered from the Cape Weber Formation. The smaller (GGU 240006) probably comprises five ramiform elements although very poor preservation does not enable a precise evaluation. Three of the elements bear prominent costae on the lateral face and are probably Sb or Sa elements. All elements have the same orientation.

The larger cluster comprises at least twelve elements (Figs 25 a–c, 26; GGU 239755) all in the same plane. In the centre of the cluster are two P elements, distinguished by the posteriorly inclined denticles and trian-
gular basal cavity outline (elements 8 and 9 on Fig. 26). The posterior processes are orientated at 90° with respect to each other and both elements are sinistral. Elements 1–7 and 10–12 are S elements, but the costae used to differentiate between element types are mainly obscured and subdivision is not possible. No M elements are present.

Three features distinguish the cluster from later Palaeozoic ramiform-pectiniform natural assemblages such as those of Ozarkodina (Mashkova 1972; Nicoll & Rexroad 1987) or polynathacean species (Aldridge et al. 1987). 1) All of the elements are rotated with respect to each other. 2) The P elements are surrounded by S elements rather than occurring to the posterior or, more usually in the case of fused clusters, as a discrete assemblage (Nicoll & Rexroad 1987). 3) The two P elements are both sinistral whereas in later ramiform-pectiniform apparatuses only a single pair of each morphology would be expected. These differences may be sufficient to dismiss the cluster as a coprolite or other artefact but recent evidence suggests that they may be in keeping with the architecture of Early Ordovician ramiform-pectiniform apparatuses. Promissum pulchrum was described from the latest Ordovician of South Africa as the earliest vascular plant macrofossil (Theron & Kovács-Endrődy 1986; Kovács-Endrődy 1987). In-
stead, it is a well-preserved prioniodontid bedding-plane assemblage (Aldridge et al. 1988; Theron et al. 1990), although of unusual morphology and architecture in comparison with younger assemblages. The P elements are intimately associated with the ramiform basket and there are three pairs, two of which are of similar morphology. It would be possible to produce the element distribution seen in the O. communis cluster from an apparatus composition and architecture of this type. It is more difficult to explain the element rotation from a compactional/collapse process and for this reason the authenticity of the assemblage must be considered equivocal.

Range. - O. communis occurs from 55 to 200 m in the Wandel Valley Formation in Kronprins Christian Land. The species has a range 514–1161 m in the Cape Weber Formation on Ella Ø.

Number of specimens. - 186 P, 128 M, 94 Sa, 92 Sb, 210 Sc.

Oepikodus sp. A
Fig. 24 h
Remarks. - The single Sa element recovered has a slightly proclined cusp, a posterior process bearing twelve denticles, a very constricted basal cavity and two, long, adenticulate, postero-laterally directed processes subtending an angle of about 30° with the posterior process. White matter is present in the cusp and along the growth axes of the denticle. The denticulation of the posterior process is similar to that of Fahraeusodus marathonensis but the element does not occur in abundant samples with that species and cannot be considered a member of the apparatus.

Range. - Found at 976 m in the Cape Weber Formation on Ella Ø.

Number of specimens. - 1.

Oepikodus sp. B
Fig. 24 g
Remarks. - The element compares with Sa elements of Oepikodus in having symmetrically disposed lateral costae and an erect cusp with anticusp, but differs in that the anticusp and proximal anterior margin are denticulate. The denticles are small, serrate, directed anteriorly, or of equal size to those on the posterior process and end at approximately the same level on the cusp. The general shape is also similar to that of Stolodus stola (Lindström 1955), a species which occasionally develops denticle-like serrations on the costae and keels (van Wamel 1974).
Range. – Found 115 m up the Wandel Valley Formation in Kronprins Christian Land.

Number of specimens. – 1.

Genus *Oistodus* Pander 1856

1856 *Oistodus*, Pander: 27

Type species. – By subsequent designation, Ulrich & Bassler (1926: 7), *Oistodus lanceolatus* Pander, 1856: 27.

Remarks. – The apparatus of the type species is trimembrate (Lindström 1973; van Wamel 1974; Löfgren 1978), comprising non-geniculate tertiopedate and alate elements and a geniculate element. No species with this apparatus was recovered from Greenland but "Oistodus" is here used in the form taxonomic sense for geniculate elements with an as yet unknown apparatus.

"*Oistodus* ectyphus* sp. nov.

Fig. 27 a

Derivation of name. – Ektyphos (Gr.), puffed up, with reference to the cusp tip.

Type material. – The holotype is MGUH 18.801 from sample GGU 240014 collected at 976 m above the base of the Cape Weber Formation on Ella Ø.

Description. – Geniculate. Upper edge of base short to very short, convex, sharp. Posterior margin sharp proximally, antero-basal angle 90°. Anterior margin curves evenly through 90° or less, narrowly rounded proximally. Cusp strongly laterally compressed near base, width decreases very slowly, distally inflated and of circular cross-section, twisted and deflected inwards in large specimens.

Basal margin slightly concave; basal outline symmetrical, widest anteriorly, narrows rapidly to posterior. Basal cavity small, conical, situated anteriorly, apex near anterior margin.

Hyaline; thickened cusp tip causes characteristic darkening in this region. Keeled upper edge of base albid.

Remarks. – Although the apparatus is unknown, the swollen cusp tip of this geniculate element is highly characteristic. Consequently, it may be of some biostratigraphic utility and is named as a sciothaxon (sensu Bengtson 1985). "*O.* ectyphus" was recovered only from the Cape Weber Formation on Ella Ø.

**Range.** – 848–976 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 7.

Genus *Oneotodus* Lindström 1955

1955 *Oneotodus*, Lindström: 581


1984 Leneaodus, Abaimova: 29–30

Type species. – By original designation, *Distacodus? simplex* Furnish, 1938: 328.

Remarks. – The apparatus structure of *Oneotodus* has been the subject of some debate. Barnes et al. (1979) considered it to be Type 1B or IC, that is, bimembrate with cusp symmetry defining element types or unimembrate. Miller (1981) thought it to be an apparatus of acostate to multicostate non-geniculate elements forming a symmetry transition series. Ethington & Brand (1981), in their review of the genus, concluded that the apparatus consisted of elements which varied in cusp cross-section, curvature and costal development. The Greenland material supports this latter hypothesis but more work on larger collections is needed to determine the exact nature of transition between elements within species of the genus.

An (in An et al. 1983) proposed the genus *Paraserratognathus* for a group of newly described species from North China. The majority of these species have a characteristic morphology and probably should be referred to a new genus. However, the taxon selected as the type species, *P. obesus* Yang (in An et al. 1983) is apparently unimembrate and is broadly similar in morphology to *O. costatus* Ethington & Brand. *Paraserratognathus* An may thus be a junior synonym of *Oneotodus* Lindström. Abaimova (1984) proposed *Leneaodus* for a squat acostate but striate conform element of very similar morphology to *Oneotodus*.

**Oneotodus costatus** Ethington & Brand 1981

Fig. 27 b–j

v p 1944 Sculopodus n. sp. – Mehl & Ryan in Branson: 45, pl. 6: 41–45, (non pl. 6: 46, 47)


v 1982 Oneotodus aff. *simples* (Furnish) – Ethington & Clark: 73–74, pl. 8: 7

1982 Sculopodus abruptus, Repetski, 45–46, pl. 21: 1a–c, 3a–c, fig. 7 K

1982 Oneotodus costatus Ethington & Brand – Stouge: 41, pl. 2: 18, 19, 25


1988 Paraserratognathus cf. *P. abruptus* (Repetski) – Stouge & Bagnoli: 127, pl. 4: 10

Meddelelser om Grønland, Geoscience 26 · 1991
Fig. 27. "Oistodus" ectypus sp. nov. a: inner lateral view (holotype) ×60, MGUH 18.801, GGU 240014. Oneotodus costatus Ethington & Brand. b: lateral view, ×40, MGUH 18.802, GGU 274958. c: lateral view, ×60, MGUH 18.803, GGU 274959. d: lateral view, ×60, MGUH 18.804, GGU 274958. e: lateral view, ×60, MGUH 18.805, GGU 274958. f: lateral view, ×60, MGUH 18.806, GGU 239968. g: lateral view, ×100, MGUH 18.807, GGU 274944. h: upper view, ×100, same specimen. i: lateral view, ×100, MGUH 18.808, GGU 274944. j: basal view, ×60, same specimen as (d), GGU 274958. "Oneotodus" mitra Abaimova. k: posterior view, ×60, MGUH 18.709, GGU 226394. Oneotodus sp. A. l: lateral view, ×60, MGUH 18.810, GGU 239985. m: upper view, ×40, same specimen.

Remarks. - For several years, O. costatus was commonly misidentified as Scolopodus cornutiformis Brandon & Mehl until the mistake was noted by Ethington & Brand (1981). O. costatus differs from S. cornutiformis in being albid and circular in cross-section. A considerable variation in morphology is present within the species. The costae from which the species takes its name vary from being closely spaced, low and rounded to widely spaced and prominent, with the anterior face of each costa aligned at a low angle to the cusp and the posterior face almost normal to the cusp. Costae are present only on lateral and posterior faces of strongly costate forms but may be present, though faint, on the anterior face of specimens with costae of low relief.

The curvature of the cusp is also variable although the majority of specimens are reclined at approximately 30–40° to the plane of the basal margin. The basal cavity is of more consistent morphology, having a short, steep anterior margin and a long gently sloping posterior margin. Both of these margins are straight. The apex of the cavity is situated anteriorly, beneath the main part of the cusp. The basal outline is more or less ovate.

Ethington & Clark (1982) mentioned that some of their elements had "rejuvenated" cusps and Stouge & Bagnoli (1988) figured a similar specimen as Paraserratognathus aff. P. abruptus (Repetski). The morphological consistency of these specimens suggests that they are not of regenerative origin. Such specimens are more
recurved, have short cusps, often of reduced diameter, and were interpreted by Ethington & Brand (1981) as normal elemental variations. The extreme variants of this type from Greenland come close to the morphology of Wandella guyi gen. et sp. nov. of which O. costatus may be the ancestor.

The specimen figured by Stouge & Bagnoli (1988) as O. costatus is striate around the base and has finer costae than is normal in this species. Although Stouge & Bagnoli noted that their few specimens were small, which could account for these differences, they may not be conspecific with O. costatus.

Range. – From the base of the Wandel Valley Formation into the Vestervig Elv Member of Peary Land and into the Alexandrine Bjerge Member of Kronprins Christian Land. O. costatus has a range of 150–880 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 2.

"Oneotodus" mitra Abaimova 1971

Fig. 27 k

* 1971 Oneotodus mitra, Abaimova: 80–81, pl. 10: 12
1975 Oneotodus mitra Abaimova – Abaimova: 82–83, pl. 7: 4, 7, fig. 7: 16–18, 21–24

Remarks. – The specimens are comparable with the figured specimens of Abaimova (1971, 1975) in having a very flared base surmounted by an extremely small cusp. One specimen has a lower, wider base than those figured by Abaimova.

Range. – Found 4 m up the Wandel Valley Formation in Borglum Elv, Peary Land, and at 306 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 2.

Oneotodus sp. A

Fig. 27 l, m

Remarks. – The upper edge of the base is short and rounded, curving sharply around into the erect to rec­lined cusp, which is slightly compressed antero-posteriorly. The anterior face is rounded and faintly costate. The posterior face is broadly rounded with multiple, low, rounded costae. The basal margin is straight, the basal outline is sub-triangular to circular. The base is very flared and the basal cavity is fairly shallow and conical with an apex close to the anterior margin. The cusp is albid. The element is grossly similar to O. costa­tus but differs in having an antero-posteriorly compressed cusp and a more flared base.

Genus Parapanderodus Stouge 1984

1984 Parapanderodus, Stouge: 65

Type species. – By original designation, Parapanderod­us arcuatus Stouge, 1984: 65–66.

Revised diagnosis. – Apparatus trimembrate; s element with rounded or laterally compressed cross-section, posterior furrow or v-shaped groove; t element asym­metrical, antero-posteriorly compressed but twisted, furrows on either side of posterior carina, u element symmetrical, antero-posteriorly compressed, furrows on either side of posterior carina. All elements striate, proclined – erect. Albid or hyaline.

Remarks. – Stouge (1984) erected the genus Parapande­rodus for a group of striate, proclined – erect conform elements with posterior grooves and unflared bases. P. arcuatus Stouge was selected as the type species and other species from the Table Head Formation were also included in the genus: P. cf. con­similis (Moskalenko), P. elegans Stouge, P. striatus (Graves & Ellison) and P? aff. triangularis (Ethington & Clark). The apparatus was considered to consist of a transition from simple, slender slightly rounded elements to laterally compressed or heart-shaped costate forms. A group of spe­cies referred to Semiaccontiodus Miller was considered by Stouge (1984) to be closely related to Parapanderod­us based on the presence of a posterior furrow and striation.

The evidence from Greenland indicates that elements with morphologies corresponding to all of Stouge’s Pa­rapanderodus species occur in single collections so that all may be considered as variants of a single species. Furthermore, evidence from fused clusters, distribu­tional data (both areal and temporal) and morphology indicates that elements of the forms assigned to Semi­accontiodus asymmetricus and S. presymmetricalus by Stouge constitute the t and u elements of the apparatus (see P. striatus – Remarks for details). The s position is occupied by the rounded – grooved transition noted by Stouge. A similar apparatus reconstruction was arrived at by both Dzik (1983) and Lofgren (1985). The closely inter-related distributions and almost identical mor­phology within each apparatus position make it prob­able that only a single species is present in the Table Head Formation and includes specimens described by Stouge as P. arcuatus, P. cf. consimilis, P. elegans, P. striatus, P? aff. triangularis, Semiaccontiodus asymmetricus and S. presymmetricalus. Within this group of spe­
cies the oldest applicable name is *Drepanodus striatus* Graves & Ellison, 1941. Subsequent descriptions of this species referred it to *Scolopodus* Pander, wherein it is a junior secondary homonym of *Scolopodus striatus* Pander, 1856. In consequence, the element has traditionally been described under the synonym *Scolopodus gracilis* Ethington & Clark, 1964. When transferred to *Parapanderodus* the senior synonym can be reinstated.

A question remains, however, as to whether *P. striatus*, of which the holotype is Canadian, is conspecific with the Middle Whiterockian species described by Barnes & Poplawski (1973) and Stouge (1984). In terms of their apparatus composition and external morphology, the two are indistinguishable but Whiterockian representatives tend to be albid (Sweet et al. 1971; Barnes 1977; Stouge 1984; R. L. Ethington & J. E. Repetski, pers. comm.). Unfortunately, no systematic observations of white matter variation through the lineage have been published to date. Until this has been tested, I consider it preferable not to split the lineage into species on this basis and, consequently, only a single species, *P. striatus*, is recognised.

A further problem is an apparent discrepancy between the range of the s element and that of the t and u elements. Numerous authors (Nowlan 1976; Ethington & Clark, 1982; Repetski, 1982) have noted that the s element apparently extends further into the Whiterockian than do the other two. Stouge’s (1984) collections from the Table Head Formation demonstrate however that all three elements are present in the *holodentata* Biozone of Sweet (1984). The discrepancy may possibly be due to the generally small size of Whiterockian collections which would give an artificially longer range for the more abundant s element.

*Parapanderodus striatus* (Graves & Ellison 1941)

Figs 28 a–f, 29 a–d, 30

<table>
<thead>
<tr>
<th>Year</th>
<th>Reference</th>
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<td>1964</td>
<td><em>Scolopodus gracilis</em>, Ethington &amp; Clark: 699, pl. 115: 2–4, 8, 9</td>
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<td><em>Scolopodus triangularis</em>, Ethington &amp; Clark: 700, pl. 115: 6, 11, 13, 17, fig. 21</td>
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<td>1978</td>
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<tr>
<td>1979</td>
<td><em>Juuagnathus assimetricus</em> (Barnes &amp; Poplawski) – Bergström: 303, fig. 4 E</td>
</tr>
<tr>
<td>1980</td>
<td><em>Scolopodus triangularis</em> Ethington &amp; Clark – Grether &amp; Clark: pl. 1: 41</td>
</tr>
<tr>
<td>1980</td>
<td>“<em>Scolopodus</em>” gracilis Ethington &amp; Clark – Mayr et al.: 211, pl. 32: 1: 2</td>
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<td>1981</td>
<td><em>Scolopodus gracilis</em> Ethington &amp; Clark – Repetski &amp; Perry: pl. 2: 1, 2</td>
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<td>1982</td>
<td><em>Protoapanderodus? assimetricus</em> Barnes &amp; Poplawski – Ethington &amp; Clark: 83–84, pl. 9: 11, 12, 14, 19</td>
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<td>1982</td>
<td><em>Scolopodus pararcorniformis</em>, Ethington &amp; Clark: 102, pl. 11: 21, fig. 25</td>
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<td>1982</td>
<td><em>Protoapanderodus assimetricus</em> Barnes &amp; Poplawski – Repetski: 39, pl. 15: 1a–c</td>
</tr>
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<td>1982</td>
<td><em>Scolopodus gracilis</em> Ethington &amp; Clark – Repetski: 48, pl. 22: 5a–b, 8a–10b (722: 11a–b, fig. 7 S)</td>
</tr>
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<td>1982</td>
<td><em>Scolopodus?</em> sp. A – Stouge: 43–44, ?pl. 2: 2, 3, 4, 11, (non pl. 2: 1, 5, 6, 10)</td>
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<td><em>Semiacontiodus assimetricus</em> (Barnes &amp; Poplawski) – Stouge: pl. 5: 14–16</td>
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<td>1983</td>
<td><em>Scolopodus? gracilis</em> Ethington &amp; Clark – Stouge: pl. 1: 2, 3, 8, 9</td>
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<td>1983</td>
<td><em>Semiacontiodus</em> sp. cf. <em>asymmetricus</em> (Barnes &amp; Poplawski) – Stouge: pl. 4: 3, 4, 7</td>
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<td>1984</td>
<td><em>Parapanderodus cf. consimilis</em> (Moskalenko) – Stouge: 66, pl. 9: 16–19</td>
</tr>
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<td>1984</td>
<td><em>Parapanderodus striatus</em> (Graves &amp; Ellison) – Stouge: 67, pl. 10: 1–3</td>
</tr>
<tr>
<td>1984</td>
<td><em>Semiacontiodus assimetricus</em> (Barnes &amp; Poplawski) – Stouge: 68, pl. 10: 5–10, 15</td>
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<td>1984</td>
<td><em>Semiacontiodus preasymmetricus</em>, Stouge: 68–69, pl. 10: 16–19</td>
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<td>1985</td>
<td><em>&quot;Scolopodus gracilis&quot;</em> Ethington &amp; Clark – Löfgren: fig. 4 AG–AI</td>
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<td>1985</td>
<td><em>Scolopodus gracilis</em> Ethington &amp; Clark – An et al.: pl. 6: 6</td>
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</table>

Meddelelser om Grønland, Geoscience 26 · 1991
Parapanderodus emarginatus (Barnes & Tuke) – Stouge & Bagnoli: 126–127, pl. 7: 1 only (non pl. 7: 2, 3)

Parapanderodus paracornutiformis (Ethington & Clark) – Stouge & Bagnoli: 127, pl. 7: 6, 8, ?, ?, ?

Remarks. – The distribution and morphology of elements described in form taxonomy as Scolopodus gracilis, Scolopodus triangularis, Protopanderodus asymmetricus and Scolopodus paracornuformis strongly support inclusion in the same apparatus as s, t and u elements respectively. The elements show related abundance peaks and maintain a relatively constant ratio of approximately 6:1:1 (s:t:u). As noted above, Drepanodus striatus Graves & Ellison is the senior available synonym. Supplementary evidence for the apparatus composition comes from three fused clusters which also provide some constraints on the apparatus architecture.

Two of the clusters contain only s elements, of morphologies previously referred in form taxonomy to Scolopodus gracilis and Scolopodus triangularis. The smallest contains three elements. The tip and posterior margin of one element is fused to the base and anterior margin of the opposing elements (Fig. 29b). The former fractured during mounting for SEM and only the cusp tip remains in situ. The third element is fused to the side of the opposing pair but is twisted so that it lies obliquely across them. The second cluster (Fig. 29a) comprises at least nine elements but is poorly preserved and somewhat disorganised. The elements occur in nested sets, a feature better demonstrated by the third cluster, and some of the sets are opposed. It is not possible to rule out a faecal or other artefactual origin, although the element nesting may be an original feature which has survived this process.

The third cluster is the most significant, both taxonomically and palaeobiologically (Fig. 29c, d). It contains five s elements, four of which occur as a nested set with the sub-triangular anterior margins located in the v-shaped posterior margin of the adjacent element (Fig. 30). Element size decreases towards the posterior (in conventional element terminology) and the posteriormost element has a narrow, rather than v-shaped, posterior groove. The largest, anterior most element became detached during handling. Elements with a v-shaped posterior groove were referred in form taxonomy to S. triangularis and those with a narrow groove to S. gracilis. The posterior face of a t element is fused to the side of the four nested s elements. The edge of the widest postero-lateral face is sub-parallel to the curvature of the nested s elements and the margin of the narrower face hence runs obliquely across their lateral faces. The t element is of P. asymmetricus morphology and supports the inclusion of this element in the apparatus. The fifth s element is attached to the anterior face of the t element.

The anterior-posterior nesting of the s elements, with the close relationship to element morphology, is a feature not previously observed in coniform natural assemblages. In contrast, those of Belodina (Nowlan, 1979), Besselodus (Aldridge, 1982) and Panderodus (Dzik & Drygant, 1986; Smith et al. 1987) show a lateral juxtaposition of laterally compressed elements. This difference may reflect a significant division, both systematically and functionally, between apparatuses with laterally compressed elements and Panderodus-like architecture (Smith et al. 1987) and those with P. striatus-like morphology of which G. quadraplicatus may be another example. To some extent this division would correspond to the Type I and Type III apparatuses of Barnes et al. (1979).

Range. – P. striatus occurs from 10 m above the base of the Wandel Valley Formation into the Alexandrine Bjerge Member in Kronprins Christian Land and from 71 m above the base into the Vestervig Elv Member in Børglum Elv. It occurs from 150 m above the base of

Fig. 28. Parapanderodus striatus (Graves & Ellison). a: lateral view of s element, × 40, MGUH 18.811, GGU 274944. b: lateral view of s element, × 40, MGUH 18.812, GGU 274944. c: oblique postero-lateral view of t element, × 60, MGUH 18.813, GGU 274944. d: posterior view of t element, × 60, MGUH 18.814, GGU 240006. e: posterior view of u element, × 40, MGUH 18.815, GGU 240007. f: lateral view of u element, same specimen.
Fig. 29. Parapanderodus striatus (Graves & Ellison).
a: lateral view of fused cluster of s elements (stereo-pair), × 120, MGUH 18.816, GGU 240024. b: lateral view of fused cluster with nested s elements (stereo-pair), × 60, MGUH 18.817, GGU 239743. c: postero-lateral view of fused cluster with nested s elements and a t element (stereo-pair), × 60, MGUH 18.818, GGU 239753. d: posterior view, same specimen (stereo-pair). Stereo-pairs photographed with 6° separation. Samples GGU 239743 and 239753 are from section PF 770709-1 on Albert Heim Bjerge and were recovered respectively from 516 m and 630 m above the base of the Cape Weber Formation.
the Cape Weber Formation on Ella Ø into the Narwhale Sound Formation.

Number of specimens. – 1408 s, 228 t, 228 u.

**Genus Protopanderodus** Lindström 1971

1971 Protopanderodus, Lindström: 50

Type species. – By original designation: *Acontiodus rec­flalls* Lindstrom, 1955: 549.

**Protopanderodus elongatus** Serpagli 1974

Fig. 31 a–c


v ? 1982 *Protopanderodus elongatus* Serpagli – Eth­ington & Clark: 84, pl. 9: 15

v ? 1982 *Protopanderodus elongatus* Serpagli – Rep­etski: 39, pl. 16: 4a–c, 5a–c, 7a–c, 9a–b, 11a–c, 12a–c, fig. 6 T


Remarks. – The specimens at hand conform to Ser­pagli’s (1974) description and all of the element types (acostate, unicostate and bicostate) are present. The Greenland specimens are, however, very small, albid in all but the basal region and strongly laterally compressed. The anterior margin is blunt on the base, becoming sharper distally. The element types are intergradatory and the costae vary in position on the lateral faces, being symmetrical, placed anteriorly or post­eriorly, or asymmetrical. The specimens differ from those subsequently described by Ethington & Clark (1982) and Repetski (1982) which are less albid, less compressed and larger. It will only be possible to decide whether these specimens are conspecific when the full range of morphological variation within *P. elongatus* is known.

Range. – 438–992 m in the Cape Weber Formation on Ella Ø and at 200 m above the base of the Wandel Valley Formation in Kronprins Christian Land.

Number of specimens. – 44.

**Protopanderodus gradatus** Serpagli 1974

Fig. 31 d–l

v ? 1967 *Palodus variabilis* Furnish – Higgins: fig. 2.7

v * 1974 *Protopanderodus gradatus*, Serpagli: 75–77, pls 15: 5a–8b, 26: 11–15, 30: 1a, b, fig. 17

v 1976 *Protopanderodus gradatus* Serpagli – Land­ing: 639, pl. 4: 8, 9, 11, 13


1982 *Protopanderodus gradatus* Serpagli – Rep­etski: 39, pl. 17: 1a–5c, fig. 6 U, Z, AA

? 1982 *Protopanderodus* cf. *P. gradatus* Serpagli – Repetski: 39, pl. 17: 6a–7c, fig. 6 W

1985 *Protopanderodus gradatus* Serpagli – An et­ al.: pl. 5: 2, 3, 15


Remarks. – *P. gradatus* from Greenland is closely simi­lar to the San Juan material of Serpagli (1974), who mentioned that the transition from “Scmulodus”-like specimens to “Scolopodus”-like specimens is incom­plete. Elements described by Ethington & Clark (1982) are transitional between the two end members and similar elements have been found in the Cape Weber For­mation. They are similar to the element figured third from the left in Serpagli’s fig. 17 but have a lateral groove on the opposite face to the antero-lateral groove. This lateral groove is very close to the posterior margin.

A rare component of the apparatus is a short-based, erect element which has an untwisted laterally-grooved cusp of lenticular cross-section. Repetski (1982) in­cluded some acostate, laterally compressed elements within *P. gradatus*. These were not found in the Cape Weber Formation although Repetski’s collection is larger than that from Greenland.

Range. – From 438 to 992 m in the Cape Weber For­mation on Ella Ø and from 95 to 155 m in the Wandel Valley Formation in Kronprins Christian Land.

Number of specimens. – 110.

52

Meddelelser om Grønland, Geoscience 26 · 1991
Fig. 31. Protopanderodus elongatus Serpagli. a: lateral view, $\times 60$, MGUH 18.819, GGU 240015. b: lateral view, $\times 100$, MGUH 18.820, GGU 240015. c: opposite lateral view, same specimen. Protopanderodus gradatus Serpagli. d: outer lateral view of scolopodiform element, $\times 40$, MGUH 18.821, GGU 240014. e: inner lateral view of intermediate element, $\times 40$, MGUH 18.822, GGU 240014. f: outer lateral view, same specimen. g: inner lateral view of intermediate element, $\times 40$, MGUH 18.823, GGU 240014. h: outer lateral view, same specimen. i: inner lateral view of scandodiform element, $\times 60$, MGUH 18.824, GGU 240015. j: outer lateral view, same specimen. k: inner lateral view of short-based element, $\times 60$, MGUH 18.825, GGU 240014. l: outer lateral view, same specimen. Protopanderodus leonardi Serpagli. m: lateral view, $\times 60$, MGUH 18.826, GGU 240014. n: lateral view, $\times 60$, MGUH 18.827, GGU 240015. Protopanderodus cf. gradatus Serpagli. o: inner lateral view, $\times 60$, MGUH 18.828, GGU 226397.

**Protopanderodus cf. gradatus Serpagli 1974**

Fig. 31 o

Remarks. – A few specimens from the Wandel Valley Formation in Peary Land are very similar in morphology to the scandodiform element of *P. gradatus*. However, since the characteristic, and usually more abundant, intermediate and scolopodiform elements have not been recovered from Peary Land these elements are only questionably included in *P. gradatus*.

Range. – 30–46 m above the base of the Wandel Valley Formation in central Peary Land.

Number of specimens. – 4.

**Protopanderodus leonardi Serpagli 1974**

Fig. 31 m–n

1974 Protopanderodus leonardi, Serpagli: 77–79, pls 16: 1a–4c, 27: 12–16, fig. 18
1982 *Protopanderodus* leonardi Serpagli – Eth­ington & Clark: 85, pl. 9: 18, 22, 23 (syn­onymy to 1981)
1982 Protopanderodus leonardi Serpagli – Rep­etski: 40, pl. 17: 8a–c, 10a–b, fig. 6 X

Remarks. – Nearly all of the Greenland specimens are of the bilaterally symmetrical element. No associated “scandodiforms” were found and hence part of the Pro­topanderodus apparatus is missing. The overall mor-
The basal cavity, curvature, general size and white matter distribution are comparable and Ethington & Clark (1982) suggested that the two are conspecific, with *P. leonardii* being the truly symmetrical member of the apparatus. This would result in an apparatus more closely similar to that of *P. rectus*, the type species, consisting of twisted asymmetrical elements, grooved sub-symmetrical elements and symmetrical elements (van Wamel 1974). Ethington & Clark (1982) noted, however, a discrepancy in the two ranges in the Ibex area and refrained from combining the two species until further studies resolved the problem. *P. leonardii* does occur below *P. gradatus* on Ella 0 although only a few specimens are involved. Additionally, in Kronprins Christian Land, *P. leonardii* occurs with no associated *P. gradatus*. The relatively small amount of material from Greenland precludes, however, a conclusive solution.

Range. – From 342 to 1140 m in the Cape Weber Formation on Ella 0 and from 95 to 200 m above the base of the Wandel Valley Formation in Kronprins Christian Land.

Number of specimens. – 52.

**Genus Protoprioniodus** McTavish 1973

1965 New genus and species, Ethington & Clark: 203
1971 New genus A, Sweet et al.: pl. 1: 19, 22
1972 *Mehlodus*, Ethington & Clark: 393 (nomen nudum)
1973 *Protoprioniodus*, McTavish: 47-48
1974 Gen. nov. B, Serpagli: 93

Type species. – By original designation, *Protoprioniodus simplicissimus* McTavish, 1973: 47-49.

Remarks. – The apparatus of *Protoprioniodus* was included within Type IIB by Barnes et al. (1979), who interpreted it as a simple transition series with no other associated elements. The geniculate conform element (*oistodiform*) was included in the transition series. Bergström (1981: W147) reached a similar conclusion and placed the genus within the Oistodontidae. The recognition that the apparatus includes adenticulate platform elements (Cooper 1981; Ethington & Clark 1982) means that it is more like a typical prioniodontid apparatus, with a ramiform transition series Sa–Sc, an oistodiform M and an adenticulate, platform-like P element, the latter occurring in low numbers.

**Protoprioniodus papiliosus** (van Wamel 1974)

Fig. 32 a–g

p* 1974 *Oistodus papiliosus*, van Wamel: 76–77, pl. 1: 19a, b only (non pl. 19: 18a, b, 20a, b)

v 1974 Gen. nov. B n. sp. 1, Serpagli: 93, pl. 19: 4a, b, 29: 4, 5, fig. 26

Description. – M element

Geniculate conform, cusp reclined, one-third longer than base. Posterior margin sharp. Anterior margin sharp with keel deflected by up to 90° above the basal flange. Lateral faces flat. Antero-basal angle 20°, postero-basal angle approximately 20°. Upper edge of base short.

Basal cavity very narrow, very shallow, low apex situated anteriorly. Basal margin straight or very slightly concave anteriorly. Basal flange absent or weakly developed in some specimens.

Ramiform elements

Cusp erect with posterior keel and antero-lateral costae. Symmetry transition defined by relative positions of the bladelike costae extended as adenticulate processes. On Sa, costae directed slightly posteriorly giving rounded anterior face on which low median costa is developed. Sb with one costa in or near plane of posterior process, other roughly at right angles, directed antero-laterally; cusp slightly twisted relative to posterior process. Sc with costae directed antero-laterally creating an anterior face with median furrow, cusp again slightly twisted.

Posterior process bears high, thin blade, triangular in profile. Posterior edge slopes down evenly, or may be slightly concave, until it meets a flange at 90°. Flange, characteristic of *Protoprioniodus*, running parallel to basal margin, present on all processes and continued across anterior face. Angle between posterior process and antero-lateral processes varies from almost 90° to approximately 30° (in Sa). Basal cavity shallow and very constricted.

All elements entirely albid with sharp junction parallel to basal margin, at level of flange if present.

Remarks. – The adenticulate platform element included in species of *Protoprioniodus* by Cooper (1981) and Ethington & Clark (1982) has not been recovered from Greenland. This is perhaps not surprising considering the approximately 8:1 ratio of ramiforms:platforms (Ethington & Clark 1982) and the small collection at hand.

*P. papiliosus* was originally placed in *Oistodus* by van Wamel (1974) but is albid, unlike true species of *Oistodus*. The “deltaform” and geniculate elements figured by van Wamel (1974: pl. 1: 18, 20) were not recovered by Ethington & Clark (1982) and do not occur in the Greenland collections. The apparatus does not conform to that of *Oistodus* but since the holotype of the species is the “triangulariform” element of van Wamel, his specific name is available. Ethington & Clark (1982) considered that their specimens comparable with the holo-
type should be placed in *Protoprioniodus* and speculated that they may be rare components of the *P. aranda* Cooper apparatus. The discovery of an associated oistodiform of different morphology to that in *P. aranda* indicates that *P. papiliosus* is a distinct species. The elements have a typical *Protoprioniodus* morphology: they possess a flange parallel to the basal margin, are albid above the flange and have a blade-like keel on the posterior process. The narrow, shallow basal cavity is also consistent with this genus. The species differs from *P. aranda* in having a more slender, unflexed geniculate coniform with no lateral carina but a characteristic laterally deflected anterior margin to the cusp and a straight basal margin. The ramiforms have a characteristic triangular keel on the posterior process.

*Protoprioniodus cowheadensis*, described by Stouge & Bagnoli (1988: 137, pl. 14: 1–5) from the *communis* Biozone of the Cow Head Group, Newfoundland, has ramiform elements similar to those of *P. papiliosus*, but is distinguished by the oistodiform elements which bear a closer resemblance to those of *P. aranda*.

**Remarks.** – The species ranges from 55 m to 200 m in the Wandel Valley Formation of Kronprins Christian Land and from 848 m to 992 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 8 M, 10 ramiform.

**Genus Pteracontiodus** Harris & Harris 1965

1965 *Pteracontiodus*, Harris & Harris: 41
1965a *Eoneoprioniodus*, Mound: 195

**Type species.** – By original designation, *Pteracontiodus aquilatus* Harris & Harris, 1965: 41–42.

**Remarks.** – Mound (1965a) erected *Eoneoprioniodus cryptodens* as a form taxon for cordyloiod elements from the Joins Formation and selected it as the type species of *Eoneoprioniodus*. The first full reconstruction was made by Ethington & Clark (1982) who concluded that the apparatus was quinquemembrate with a symmetry transition series comprising cordyloiodiform, acodiform, trichonodelliform and distacoidiform elements together with an oistodiform element. They also reached the conclusion that the elements of Mound’s species were sufficiently similar to the type species of *Pteracontiodus, P. aquilatus*, to warrant inclusion in that genus, which has seniority over *Eoneoprioniodus* by nine months.

*Pteracontiodus* is one of several closely related genera in the late Canadian and Early Whiterockian with a very complex nomenclatural history. Bergström (1981: W138–40), for example, considered *Trigonodus* Nieper and *Triangulodus* van Wamel to be junior synonyms of *Eoneoprioniodus*, and *Pteracontiodus* to be a closely related genus with an unknown apparatus. *Triangulodus* was erected by van Wamel (1974) to include species differentiation from *Scandodus* Lindström on the basis of their seximembrate apparatus, in contrast to the trimembrate apparatus of *Scandodus*. van Wamel agreed with Lindström’s (1971) reconstruction of *Scandodus brevibasis* (Sergeeva) and selected *Paloiodus volchoven­sis* Sergeeva as the type species of *Triangulodus*. Subsequently, Lögren (1978) concurred with Lindström’s (1971) generic assignment and reassigned *Triangulodus brevibasis* to *Scandodus* although Lindström (1977a: 19) placed it in *Pteracontiodus*. Cooper (1981) reconstructed *Trigonodus larapintinensis* (Crespin) and amended the diagnosis to include hyaline elements forming a seximembrate apparatus comprising a coniform P element, a geniculate coniform M element and an Sa–Sd transition series with the symmetry marked by the varying distribution of costae. Cooper considered this genus to be a senior synonym of *Triangulodus*. In contrast, Ethington & Clark (1982) concluded that the type species of *Trigonodus, T. triangularis* Nieper, had an unknown apparatus, having been erected by Nieper as a form taxon for an acontiodiform element. They, therefore, assigned *T. larapintinensis* to *Scandodus*, on the basis of its similarity to *S. brevibasis*, pending further work. Additional uncertainty regarding the taxonomy of *Oisiodus brevibasis* Sergeeva is expressed by the inclusion of *Triangulodus* as a junior...
synonym of *Tripodus* Bradshaw by Ethington & Clark (1982) who thus, by implication, assigned *O. brevibasis* to two genera.

In this study, *Pteracontiodus* is considered to be a genus with an apparatus structure and/or element morphology distinct from *Scandodus*, *Triangulodus*, *Trigonodus* and *Tripodus*. Further resolution of the taxonomic status of these latter genera will require the examination of toptype material of the respective type species. Representatives of *Pteracontiodus* are hyaline, or predominantly so, with costae on the cusp produced basally as short, adenticate processes. The apparatus is quinquemembrate and consists of a geniculate conform M element, and an Sa–Sd symmetry transition series containing trichonodelliform (Sa), acodiform (Sb), cordylodiform (Sc) and distacodiform (Sd) elements. The apparatus is very similar to that of *Multivositodus* but lacks the single denticle on each process seen in members of that genus.

**Pteracontiodus bransoni** (Ethington & Clark 1982)

Fig. 33 a–n

<table>
<thead>
<tr>
<th>Year</th>
<th>Reference</th>
</tr>
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<tbody>
<tr>
<td>1933</td>
<td><em>Paltodus jeffersonensis</em>, Branson &amp; Mehl: pl. 4: 18</td>
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<td>1944</td>
<td><em>Distacodus</em>? sp. – Mehl &amp; Ryan in Branson: pl. 6: 25, 26</td>
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<td>1964</td>
<td><em>Oistodus</em> sp. – Ethington &amp; Clark: 694, pl. 114: 21</td>
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<td>“Oistodus”? sp. – Serpagli: 57, pls 12: 4a, b, 24: 11, 30: 9a, b</td>
</tr>
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<td>“<em>Paltodus jeffersonensis</em>” Branson &amp; Mehl, nomen nudum – Kennedy: 63, pl. 2: 1</td>
</tr>
<tr>
<td>1982</td>
<td><em>Oistodus bransoni</em>, Ethington &amp; Clark: 65–66, pl. 7: 1–3, 5, 6, fig. 17</td>
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<tr>
<td>1982</td>
<td><em>Oistodus</em> n. sp. – Repetski: 32–33, pl. 11: 3a–4c, 9a–c, 11a–c, fig. 5 X, Y, Z, AA</td>
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Description. – M element

Upper edge of base short, keeled, meeting cusp at angular junction, usually acute. Posterior margin sharp, evenly curved throughout length. Anterior margin sharp, gently curved throughout length. Cusp tapers rapidly to fine point. Inner and outer faces gently convex, inner face with median carina. Antero-basal angle 30°, postero-basal angle 30°. Basal margin straight except at base of carinae where it is convex. Basal cavity inflated at base of carinae, flares more inwards, narrow and slit-like at anterior and posterior. Element grades into Sc element morphology to some extent.

Sa element

Upper edge of base sharp, short, curving evenly into erect cusp. Posterior margin sharp, gently curved throughout length. Anterior face broadly rounded, tapering evenly, may be depressed centrally at antero-basal corner. Antero-lateral costae sharp, evenly curved throughout length. Postero-lateral faces concave. Posterior margin a broad carina, may bear a keel. Basal outline triangular. Basal margin straight to arched anteriorly, concave postero-laterally. Cavity moderately deep, opens to posterior, apex anterior.

Sb element

Upper edge of base short, keeled, meets reclined to recurved cusp at angular junction, usually acute. Posterior margin sharp, gently curved for most of length, straight distally. Anterior margin bears low, narrow, sharp keel, gently curved throughout length. Inner face flat anteriorly, curving round to meet posterior margin. Outer face bears sharp costa, produced as adenticate process basally, directed antero-basally. Antero-lateral outer face concave. Postero-lateral outer face flat or slightly convex, a groove may be present adjacent to cusp-base junction. Cusp cross-section triangular in all but very mature specimens. Basal margin markedly convex. Basal outline approximately triangular. Basal cavity shallow, opens to posterior; apex central or just anterior.

Sc element

Upper edge of base very short, keeled, meeting recurved cusp at an angular junction, usually acute. Posterior margin sharp, convex proximally, straight distally. Anterior margin regularly curved proximally, straight distally. Cusp strongly laterally compressed. Outer face convex, may bear a very low median carina. Inner face broadly convex, may bear a carina; if so, there is a groove between carina and anterior margin. Cusp may be deflected inwards. Basal margin strongly medi ally and posteriorly convex, anteriorly concave. Basal outline lenticular, compressed anteriorly, swollen medi ally, open to posterior. Apex situated at maximum cavity width or just anterior.

Sd element

Upper edge of base short, keeled, meeting rec curved cusp at angular junction, usually acute. Posterior margin sharp, gently curved proximally, straight distally. Anterior margin sharply rounded, curved in proximal two-thirds, straight in distal one-third, produced basally as adenticate anticusp deflected inwards, anterior margin of process at 70° to upper edge of base. Inner face bears low carina. Outer face bears two prominent costae, directed antero-laterally and posterolaterally, produced basally as adenticate processes. Basal outline quadrate, basal cavity directed posteriorly, apex anterior.

All elements finely striate, hyaline with a thin growth axis, and have a nicked margin at junction between posterior margin and upper edge of base. On larger specimens a low, rounded ridge runs parallel to basal margin a short distance above it.

Remarks. – Ethington & Clark (1982) erected *P. bransoni* as a replacement name for *Paltodus jeffersonensis* which was figured but not described by Branson & Mehl.
(1933) and subsequently declared a nomen nudum by Kennedy (1980). The apparatus of *P. bransoni* reconstructed by Ethington & Clark (1982) from the Ibex area is identical to that from Greenland and the quintemembrate composition is incompatible with an assignment to *Oistodus* Pander, as made by Ethington & Clark (1982), since the type species has a trimembrate apparatus (Lindström 1973; van Wamel 1974; Löfgren 1978). The apparatus is, however, very similar to that of *Pteracontiodus cryptodens* (Harris & Harris) as reconstructed by Ethington & Clark (1982) and the species is hence reassigned to *Pteracontiodus*.

Large specimens of *P. bransoni* from Greenland are characterised by having a rounded ridge or band on the base which runs parallel to the basal margin. Specimens which have a similar, though lesser, development of this feature were illustrated by Ethington & Clark (1982: pl. 7: 2, 5).

**Range.** - From 114 to 128 m in the Wandel Valley Formation of Børglum Elv and from 10 to 200 m in Kronprins Christian Land. From 848 to 1010 m in the Cape Weber Formation on Ella Ø.

**Number of specimens.** - 44 M, 24 Sa, 30 Sb, 30 Sc, 7 Sd.

**Genus Reutterodus Serpagli 1974**

1974 *Reutterodus*, Serpagli: 79

**Type species.** - By original designation, *Reutterodus andinus* Serpagli, 1974: 79–81.

**Remarks.** - Serpagli (1974) described a trimembrate apparatus comprising a coniform element, a digyrate element with denticulate lateral processes. These elements were said to form a continuous symmetry transition series and the digyrate ("unibranched") element was selected as the holotype.

Ethington & Clark (1982) subsequently recovered only the coniform element in quite large collections (53 specimens) from the Pogonip Group and suggested that this element was not part of the *Reutterodus* apparatus. Stouge & Bagnoli (1988) also failed to recover digyrate and alate elements in their collection of nine elements from a single sample. Both specimens recovered in this study are of conform elements.

The digyrate element was recovered by Repetski (1982) but only in small numbers and the assignment to *Reutterodus andinus* was again queried.

An (1979) figured and named a closely similar conform element, *Reutterodus? depressus*. It differs from the conform element of *R. andinus* in having a rather longer lateral process and more prominent inturned anterior margin. It may well, however, prove to be conspecific with the conform element discussed here.

**Range.** - From 992 m in the Cape Weber Formation into the Narwhale Sound Formation on Ella Ø.

**Number of specimens.** - 2.

**Fig. 34.** *Reutterodus andinus* Serpagli. a: inner lateral view, ×40, MGUH 18.843, GGU 240018. b: outer lateral view, same specimen.

Fig. 33. *Pteracontiodus bransoni* (Ethington & Clark). a: posterior view of Sa element, ×40, MGUH 18.834, GGU 274945. b: posterior view of Sa element, ×40, MGUH 18.835, GGU 274959. c: inner lateral view of Sb element, ×40, MGUH 18.836, GGU 274959. d: inner lateral view of Sb element, ×40, MGUH 18.837, GGU 227806. e: outer lateral view, same specimen. f: inner lateral view of Sd element, ×40, MGUH 18.838, GGU 274959. g: outer lateral view, same specimen. h: inner lateral view of Sc element, ×40, MGUH 18.839, GGU 227847. i: outer lateral view, same specimen. j: inner lateral view of M element showing basal band, MGUH 18.840, GGU 274945. k: outer lateral view of M element, ×40, MGUH 18.841, GGU 274945. l: inner lateral view, same specimen. m: outer lateral view of juvenile M element, ×60, MGUH 18.842, GGU 274945. n: inner lateral view, same specimen.
Genus *Scalpellodus* Dzik 1976

1976 *Scalpellodus* Dzik: 421

Type species. – By original designation, *Protopandero­

**Scalpellodus? narhvalensis** sp. nov.

Fig. 35 a–i

? 1982 "*Scolopodus*" aff. "*S.* filosus* Ethington &
Clark – Ethington & Clark: 100, pl. 11: 23, 25, 29
? 1982 *Protopandero­
dus longibasis* (Lindström) –
Repetto: 40, pl. 17: 11, 12
? 1988 "*Scolopodus*" aff. "*S.* filosus* Ethington &
Clark – Stouge & Bagnoli: 138–139, pl. 15: 1, 2

Derivation of name. – After Narhval Sund, a fjord
bounding one side of Ella Ø.

Type material. – The holotype is MGUH 18.849, an r
element. Paratypes are MGUH 18.844 (p element),
MGUH 18.845 (p/q element), MGUH 18.846 (p/q ele­
ment), MGUH 18.847 (q element) and MGUH 18.848
(r element). All type material is from sample GGU
240014 collected at 976 m above the base of the Cape
Weber Formation on Ella Ø (section PF 770824–1).

Diagnosis. – Apparatus trimembrate, comprising a
squat recurved r element, a short-based proclined to
erect q element and a long-based proclined p element.
The p and q intergrade in morphology and have better
developed striae than the r element. All elements albid;
p, q and most r elements striate, but with a smooth basa­
band.

Description. – p element

Since p and q elements intergrade, only the end mem­
bers of the series are described. p element slender; cusp
one third to one half total length. Upper edge of base
long, usually approximately one half the total element
length. Element sharply curved at cusp – base junction,
then straight, proclined and evenly tapering. Anterior
margin rounded, curving evenly into lateral faces; ter­
minated by postero-lateral shoulders which fade out
wards basal margin. Posterior face narrow, flat and
with central low, sharply rounded keel. Base unex­
panded, antero-basal angle 90°, postero-basal angle 90°
although antero-basal angle may be slightly more and
postero-basal angle correspondingly less. Basal margin
straight; basal outline ovate; basal cavity very deep with
straight anterior margin parallel to anterior margin of
cusp, posterior margin straight, slopes anteriorly so that
apex is close to anterior margin just before point of
maximum recurvature. Base and cusp finely striate but
striae do not reach basal margin, leaving a smooth basal
band.

q element

Base one third total length of element; upper edge of
base straight, curves round sharply into proclined cusp.
Cusp straight or very slightly curved, antero-posteriorly
compressed and may be asymmetrical with respect to
base. Anterior margin rounded, curves evenly as far as
postero-lateral costae. Posterior face convex. Base
moderately expanded posteriorly, antero-basal angle
90°, postero-basal angle 60°. Basal outline ovate; basal
margin straight; basal cavity more shallow than that of p
element, anterior margin parallel to anterior margin of
base, posterior margin parallel to upper edge of base,
apex near anterior margin just before point of maxi­
num recurvature.

The transition from p to q is most easily seen in the
change of cusp cross-section and the length of the base.
From p to q the element becomes more antero-post­
ieriorly compressed, the posterior keel is lost and the
postero-lateral costae become more pronounced. The
cusp becomes more recurved, and the maximum point
of recurvature is situated progressively lower down the
element. As a result the basal cavity becomes more
shallow. The base becomes more expanded posteriorly
and as a consequence the postero-basal angle decreases
from 90° to about 60°.

r element

Upper edge of base about one third the total element
length, straight, very strongly recurved into cusp. An­
terior margin straight in basal part then curves round
rapidly through 90° or more into cusp. Cusp very short,
straight, tapers rapidly, laterally compressed in cross­
section, sharply rounded anteriorly and posteriorly,
may be twisted with respect to base. Base laterally
compressed, antero-basal angle 70°, postero-basal angle
30–45°. Anterior margin of base sharply rounded, up­
per edge of base rounded; inner lateral face, to which
cusp is deflected, is flat, may bear a very low, rounded,
antero-lateral costa which may have oblique striae.
Basal outline roughly ovate but widest posteriorly; basal
cavity shallow with anterior margin parallel to anterior
margin of cusp but slightly convex (towards the cavity),
posterior margin parallel to upper edge of base and
straight, apex near anterior margin.

Surface frosting on many specimens prevents obser­
vation of the micro-sculpture. The few good speci­
mens suggest that striae are not as well developed as on the p
and q elements; striae of lower relief and wider spacing
are seen on the inner lateral faces but the outer face is
smooth. Other specimens may be entirely smooth. The
smooth basal band is again present on striate specimens.
Fig. 35. Scalpellodus? narhvalensis sp. nov.
a: lateral view of p element (paratype), MGUH 18.844.
b: opposite lateral view, same specimen. c: lateral view of p/q element (paratype), MGUH 18.845. 
d: lateral view of p/q element (paratype), MGUH 18.846. e: lateral view of q element (paratype), MGUH 18.847. f: opposite lateral view, same specimen. 
g: inner lateral view of r element (paratype), MGUH 18.848. h: outer lateral view of r element (holotype), MGUH 18.849. i: inner lateral view, same specimen. 
All specimens from GGU 240014 and × 60.
Remarks. – The apparatus of Scalpellodus? narhvalensis with its short- and long-based elements, showing full transition, together with a squat recurved element is assignable to the Type IIIA category of Barnes et al. (1979).
Scalpellodus was erected by Dzik (1976) but amended by Löfgren (1978) who described its species in detail. She interpreted the apparatus as consisting of three elements, a short-based drepanodiform, a long-based drepanodiform and a scandodiform. In S. gracilis at least, transitional specimens were found between short- and long-based drepanodiform elements (Löfgren 1978: pl. 5: 3a–b); the third, scandodiform, element has a laterally compressed, strongly twisted cusp and an inwardly flaring base. All elements are striate with a smooth basal band. Cooper (1981) ratified the apparatus structure in his description of a conodont fauna from the Horn Valley Siltstone and homologised the short- and long-based drepanodiform elements of Löfgren (1978) with Sc and Sa element positions respectively. He classified the scandodiform as a transitional Sb.
The p and q elements of S? narhvalensis are very similar to the short- and long-based drepanodiform elements of S. gracilis, showing similar development of short and long bases, striae and white matter. They differ only in the possession of postero-lateral shoulders or costae and seem to have lesser differentiation into the symmetrical and asymmetrical forms mentioned by Löfgren (1978) although this may be a function of the small collections.
The principal difference between S? narhvalensis and other species of Scalpellodus, and the reason for the questioned generic assignment, is the profound difference between the r element of S? narhvalensis and the “scandodiform” of other species of Scalpellodus. In the r element, the cusp is much reduced in size, the base is enlarged, particularly posteriorly, and there may be a reduction in the development of striae. One of the few similarities is the asymmetrical development of the base with a greater expansion of the outer face and a flat inner face.
The genera most closely related to Scalpellodus are Cornuodus Fähræus and Protopanderodus Lindström. Löfgren (1978) considered that Cornuodus could be distinguished on the basis of microsculpture alone, with Scalpellodus being conspicuously striate. Elements belonging to Protopanderodus are distinctly costate and poorly striate. On these characters, S? narhvalensis cannot be placed in either Cornuodus or Protopanderodus.
An apparatus similar to that of S? narhvalensis was figured by Ethington & Clark (1982) who described it as ?“Scolopodus” aff. “S.” filosus, although they admitted that the similarity to “S.” filosus might be superficial. The apparatus contains short- and long-based elements together with a squat element; all are conspicuously striate and albid. The p and q elements differ from S?
**Genus Scalpellodus** Lindström 1955

1955 *Scalpellodus* Lindström: 592

Type species. – By original designation – *Scalpellodus furnishi* Lindström, 1955: 592.

Remarks. – The apparatus of the type species is triradiate, comprising a geniculate coniform element, a nongeniculate coniform element with suberect cusp and short base and a recurved coniform element with a longer base. The elements are hyaline and form a transition series (Bergström 1981: W144). The relationship of *Scalpellodus* to other, similar, genera is discussed under *Pteracontiodus* – Remarks.

“*Scalpellodus*” *ethingtonii* sp. nov.

Fig. 36 a, b

1938 *Oistodus inclinatus* Branson & Mehl – Furnish: 330, pl. 42: 18

1944 *Oistodus* sp. – Mehl & Ryan in Branson: pl. 7: 5, 6


1965 *Oistodus inaequalis* Pander – Ethington & Clark: 195, pl. 1: 11

1965 *Oistodus* sp. A – Ethington & Clark: 196, pl. 2: 18

1970 *Oistodus inaequalis* Pander – Barnes & Tuke: 89, pl. 20: 2, 3, 7

1980 *Oistodus* sp. aff. *O. inaequalis* Pander – Grether & Clark: pl. 1: 14 only

1982 *Oistodus inclinatus* & Clark: 75, pl. 8: 10, fig. 19

1982 *Oistodus inaequalis* Pander – Stouge: pl. 4: 16

1983 *Oistodus inaequalis* Pander – Stouge, pl. 2, fig. 2

1986 “*Scalpellodus*” *furnishi* Lindström sensu Ethington & Clark, 1964 – Smith & Peel: fig. 3 B

Derivation of name. – After Professor R. L. Ethington.

Type material. – The holotype is MGUH 18.851 from sample GGU 274959 collected 10 m above the base of the Wandel Valley Formation in Kronprins Christian Land (section JSP 800702-1). The paratype is MGUH 18.852 from GGU 274958 collected 20 m above the base of the formation in the same section.

Diagnosis. – As for description.

Description. – Geniculate, reclined at up to 45°. Upper edge of base short, sharp; angular junction with posterior margin of cusp. Posterior margin sharp, straight. Anterior margin sharp to keeled, straight; keel may be deflected inwards. Outer face flat, gently rounded anteriorly; inner face more convex, sometimes with low
carina. Basal outline asymmetrical, anterior pinched, widest at posterior, outer side flat to slightly convex, inner side highly convex. Outer face of base continuous with cusp or slightly expanded. Inner face highly expanded, sharp angular junction with cusp, greatest expansion at base of carina. Cavity opens inwards; apex shallow, below carina. Cusp entirely albid or with inverted v of white matter leading from growth axis; some specimens just have a very thick growth axis.

Remarks. – “S.” ethingtoni was first described by Ethington & Clark (1964) who included the element in Scandodus furnishi Lindström, the type species of the genus. The element differs from the holotype in having a shorter cusp and more triangular outline. In the subsequent 25 years the element has been described many times but the associated members of the apparatus, if any, remain unknown. As a consequence, the element has been assigned to a variety of taxa with the outcome that its identity is shrouded by erroneous placements and open nomenclature. In order to provide a stable basis for future taxonomic work, I have decided to formally name the species as a sciotaxon.

“S.” ethingtoni is similar in general terms to the r element in Chionoconus avangna sp. nov., but the profile is more triangular due to the shorter cusp, the carina is less well-developed, the antero-basal angle is larger and the basal cavity opens inwards to a greater degree. In addition, white matter is of a more variable, and usually lesser, development than in C. avangna, which is entirely albid. However, morphological extremes do overlap somewhat and there is evidence for related distribution. Further work is necessary to test whether the relationship between the two species is ecological or systematic.

Range. – “S.” ethingtoni occurs in the lower 30 m of the Wandel Valley Formation in Borgan Elv and from the base up to 200 m in Kronprins Christian Land. It ranges from 164–495 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 77.

Genus Sco/opodus Pander 1856

1856 Sco/opodus Pander: 25

Type species. – By subsequent designation, Ulrich & Bassler (1926: 7), Sco/opodus sublaevis Pander: 25.

Remarks. – The apparatus of Sco/opodus was first reconstructed by Lindström (1971) who, in the absence of information regarding Pander’s species, provisionally based the description of the genus on S. rex Lindström. The apparatus was diagnosed as including costate, hyaline, conform elements of rounded, symmetrical and asymmetrical cross-section.

Using material from Öland, Fähræus (1982) was able to assemble Pander’s (1856) relevant form species into two apparatuses: S. sublaevis, the type species, and S. quadratus. Fähræus considered S. rex Lindström to be a junior synonym of S. quadratus and he amended the diagnosis of Sco/opodus to include apparatuses of hyaline, slender, costate conform elements with a transition series of symmetrical to asymmetrical cusp cross-section.

In the past, it has been traditional to assign many Midcontinent Realm coniform elements to Sco/olodus simply on the basis of their costate morphology and regardless of apparatus composition, white matter content or basal cavity characteristics. As the apparatuses of these elements are becoming known, many are being assigned to other genera. For example, Glyptoconus quadruplicatus, Oneododus costatus, Parapanderodus striatus and Tropodus comptus previously had some or all of their elements assigned to Sco/olodus. Two elements described here are still from apparatuses of un-
certain structure and consequently uncertain generic affinity. These species are retained for the time being in “Scolopodus”.

“Scolopodus” emarginatus
Barnes & Tuke 1970

Fig. 36 c

v 1944 Paldus n. sp. - Mehl & Ryan in Branson: 52, pl. 7: 17, 18 only (non pl. 7: 7, 8, 13, 14, 19—24)
* 1970 Scolopodus emarginatus, Barnes & Tuke: 91—92, pl. 18: 2, 6—8, fig. 6 C
v 1982 “Scolopodus” emarginatus Barnes & Tuke – Ethington & Clark: 99—100, pl. 11: 15, 16
1982 Scolopodus emarginatus Barnes & Tuke – Repetski: 47, pl. 22: 3a—c
1982 Scolopodus emarginatus Barnes & Tuke – Stouge: pl. 5: 8, 9
p 1988 Parapanderodus emarginatus (Barnes & Tuke) – Stouge & Bagnoli: 126—127, pl. 7: 3 only (non pl. 7: 1, 2)

Remarks. – The specimens at hand conform closely to the detailed description by Barnes & Tuke (1970) who noted that their specimens of “S.” emarginatus were smooth. Ethington & Clark (1982) widened the diagnosis to include specimens which had low, widely-spaced costae on the lateral faces. The Greenland material is, on the whole, smooth although some specimens are faintly striate and a few have coarse striae around the basal margin that rapidly fade out.

Barnes & Tuke (1970) commented that some of their specimens were mildly asymmetrical. Those from Greenland are commonly asymmetrical and some specimens from the Cape Weber Formation, have one lateral face which is much reduced in size.

Stouge & Bagnoli (1988) included an additional two elements within the apparatus of S. emarginatus. One, a “symmetrical slender” element, is indistinguishable from the s elements of Parapanderodus striatus and the other, “symmetrical squat”, element is described here as Alloxocomus sp. A. The latter element is extremely scarce in Greenland samples, and there is no evidence for an apparatus of this composition.

Range. – “S.” emarginatus occurs in the lowest samples in the Wandel Valley Formation of central Peary Land and Kronprins Christian Land and ranges into the Vestervig Elv and Alexandrine Bjerge Members respectively. It ranges from 178 m up the Cape Weber Formation into the Narwhale Sound Formation on Ella Ø.

Number of specimens. – 51.

“Scolopodus” filosus
Ethington & Clark 1964

Fig. 36 d

v * 1964 Scolopodus filosus, Ethington & Clark: 699, pl. 114: 12, 17, 18, 19, fig. 2 E
non 1975 Scolopodus cf. S. filosus Ethington & Clark – Cooper & Druce: 576, pl. 1: 32
1982 Scolopodus filosus Ethington & Clark – Ethington & Clark: 100, pl. 11: 22 (synonymy to 1978)
1982 Scolopodus filosus Ethington & Clark – Repetski: 47, pl. 22: 2a—c
non 1982 Scolopodus filosus xyon, Repetski: 47, pl. 22: 1a—6c, fig. 7 M
? 1982 Semiacontiodus sp. cf. S. cordis (Hamar) – Stouge: pl. 5: 12, 13
? 1983 Semiacontiodus sp. cf. S. cordis (Hamar) – Stouge: pl. 4: 11

Remarks. – “S.” filosus was thoroughly described by Ethington & Clark (1964) and the Greenland material conforms well with their description. Ethington & Clark (1982) thought it possible that elements of this morphology may be rare variants of the Parapanderodus striatus apparatus in which elements lack the characteristic posterior groove. The morphologies of the two taxa are certainly very similar and the samples in the Wandel Valley Formation which contain extremely large numbers of P. striatus elements also have the greatest recorded abundances of “S.” filosus. I consider it highly likely that “S.” filosus is conspecific with P. striatus, but decline to formalise this pending further confirmation.

A subspecies of “S.” filosus, S. filosus xyon, was erected by Repetski (1982). The two taxa are here considered to be distinct species and Repetski’s subspecies is reassigned to Eucharodus (q.v.).

Range. – “S.” filosus occurs from the base of the Wandel Valley Formation to a height of 200 m in Kronprins Christian Land and at 384 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 42.

Scolopodus quadratus Pander 1856?

Fig. 36 e

?* 1856 Scolopodus quadratus, Pander: 26, pls 2: 6a—d, A: 5d
? 1856 Scolopodus costatus, Pander: 26, pls 2: 7a—d, A: 5e
? 1856 Scolopodus striatus, Pander: 26, pls 2: 8a—d, A: 5f
? 1955 Scolopodus rex paltodiformis, Lindström: 596, pl. 3: 33, 34
Remarks. – Fähraeus (1982) included S. rex Lindström as a junior synonym of S. quadratus Pander. Ethington & Clark (1982) and Repetski (1982) have given thorough descriptions of possible representatives of S. quadratus from the Midcontinent Province. The Greenland material is similar but is too sparse to assess whether it is truly conspecific with S. quadratus.

Range. – From 20 to 115 m in the Wandel Valley Formation in Kronprins Christian Land and from 976 to 992 in the Cape Weber Formation on Ella Ø.

Number of specimens. – 9.

Scolopodus sp. A
Fig. 36 f

Range. – Found 164 m above the base of the Cape Weber Formation on Ella Ø.

Number of specimens. – 1.

Genus Semiacontiodus Miller 1969

1969 Semiacontiodus Miller: 420

Type species. – By original designation, Acontiodus (Semiacontiodus) nogamii Miller, 1969: 421.

Semiacontiodus sp. A
Fig. 36 g

Remarks. – The specimens from Ella Ø are albid, the anterior margin is rounded, the lateral faces meeting these at an acute angle. The postero-lateral costae are sharp to sharply rounded and the posterior face enclosed by them is deep and v-shaped. On large specimens the lateral faces may bear longitudinal, rounded ridges and grooves of low relief.

Landing & Barnes (1981) thought these elements might belong in an undescribed apparatus of Juanognathus but the range of morphologies seen in apparatuses of Juanognathus is not evident in the small collections from Devon Island or Ella Ø. The asymmetrical and symmetrical element-types reported by Landing & Barnes do, however, agree with the emended diagnosis of Semiacontiodus (Miller 1980). The symmetrical element of Semiacontiodus is somewhat antero-posteriorly compressed and has postero-lateral costae, a description which Semiacontiodus sp. A fits well.

Range. – Semiacontiodus sp. A occurs from 15–46 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 7.

Genus Toxotodus nov.

Type species. – Scolopodus carlæ Repetski, 1982: 49–50

Derivation of name. – toxotes (Gr.), archer, bowman; odous (Gr.) tooth; with reference to the arrow-headed outline of the elements.

Diagnosis. – Apparatus unimembrate. Elements antero-posteriorly compressed, striate, albid. Basal cavity very shallow or reduced, symmetrical or asymmetrical with respect to cusp.

Remarks. – In addition to the specimens of the type species described by Repetski (1982), specimens figured as Juanognathus? sp. A by Stouge (1982: pl. 1: 10, 11) may represent a species of Toxotodus, but are very poorly preserved. A second, new, species of Toxotodus, T. amphigyus is described below.

Toxotodus amphigyus sp. nov.
Fig. 37 a–d

Derivation of name. – amphigyos (Gr.), double-pointed, pointed at both ends.

Type material. – The holotype is MGUH 18.858. Paratypes are MGUH 18.859 and 18.860. All type material is from sample GGU 274944 collected 200 m above the base of the Wandel Valley Formation in Kronprins Christian Land (section JSP 800702–1).

Diagnosis. – A species of Toxotodus with prominent, narrow costae on the posterior face. Basal cavity reduced to an extremely small pit or sub-circular disc with pit.

Description. – Cusp antero-posteriorly compressed, bi-convex in cross-section; posterior face more rounded, anterior face almost flat, lanceolate in posterior profile, maximum width at one third height, narrows gradually...
to distal tip, tapers more rapidly proximally to point. Lateral edges strongly convex as far as maximum width then gently convex. Anterior face striate. Posterior face coarsely striate, may bear low, median carina. Basal regions atriaste.

Basal cavity reduced to extremely small, shallow pit at proximal tip of cusp; alternatively, cusp may terminate proximally at subcircular basal disc. Disc projects from cusp, has rounded edges, commonly located oblique to main axis; facing latero-basally, basal pit on disc always situated at proximal tip of cusp.

Remarks. — *T. amphigyus* is distinguished from *T. carlae* in having a more coarsely striate posterior face, a cusp which tapers proximally to a point and a basal cavity of rather different character. Those elements of *T. amphigyus* with a basal pit are clearly distinct and those with a basal disc differ in that the disc lacks a rim and has rounded edges, whereas *T. carlae* has a definite, though shallow, cavity. The basal pit of *T. amphigyus* may be homologous with the basal cavity apex of *T. carlae*.

*T. amphigyus* has been reported from the Canadian Arctic Islands by Nowlan (1976) in an unpublished Ph. D. thesis and from Washington Land (Kurtz & Miller, GGU int. rept.). It occurs in a stratigraphically older sample than those containing *T. carlae* in section PF 770824-1 on Ella Ø.

Range. — From 20 m to 200 m in the Wandel Valley Formation in Kronprins Christian Land and at 848 m in the Cape Weber Formation on Ella Ø.

Number of specimens. — 37.

*Toxotodus carlae* (Repetski 1982)

Fig. 37 e, f

- 1982 *Scolopodus carlae*, Repetski: 49–50, pl. 23: 1a–2d
- 1988 *Parapanderodus carlae* (Repetski) — Stouge & Bagnoli: 126, pl. 7: 4 only (non pl. 7: 5)

Remarks. — Repetski (1982) included this species in *Scolopodus* Pander. The apparatus type and element morphology do not, however, compare with the type species as described by Fähnreus (1982), nor do they conform with the diagnoses of any other available genus.

The specimens of *T. carlae* from Greenland are closely similar to those described by Repetski (1982). The basal cavity is very shallowly conical with a very small apex. The rim surrounding the basal cavity is not always perfectly symmetrical and may be extended unequally to one side. The cavity itself may be offset from the midline. The cusp is antero-posteriorly compressed with evenly curved anterior and posterior faces.

Stouge & Bagnoli (1988) also included a slender costate conform element within the apparatus, although the only two specimens recovered, one of each morphology, came from different samples.

Range. — From 868 to 976 m in the Cape Weber Formation on Ella Ø.

Number of specimens. — 6.

**Genus *Tropodus* Kennedy 1980**

1980 *Tropodus* Kennedy: 65

Type species. — By original designation, *Paltodus compactus* Branson & Mehl, 1933: 61.

Remarks. — The apparatus, as reconstructed here, is quadrimembrate or quinquemembrate and consists of a fluid transition series of tricostate, quadricostate, symmetrical and asymmetrical quinquecostate (comptiform) elements. Barnes et al. (1979) considered *Wallisicodus* to have a Type 1B apparatus, but Kennedy (1980) subsequently removed Early Ordovician species previously assigned to that genus into *Tropodus*. The apparatus conforms most closely to Type 1A but due to the fluid transition intermediate element types are seen, as in *Juanognathus*. Indeed, the similarities in the transition series, costal morphology and white matter distri-
bution may indicate a relationship between these two genera. Within a Type IA apparatus the tricostate forms would be \( s_1 \) elements, the quadricostate forms \( s_2 \), the asymmetrical quinquecostate forms \( t \) and the symmetrical quinquecostate forms \( u \) elements.

Bagnoli et al. (1988) and Stouge & Bagnoli (1988) introduced a radically different interpretation of the Tropodus apparatus. They reconstructed a prioniododontid apparatus similar to that of Diaphorodus Kennedy in which the elements here included in Tropodus represented the \( S \) elements and those of Chionoconus avangna constituted the \( P \) and \( M \) elements. The two widely recognised species of Tropodus, T. australis and T. comptus, were considered to be subspecies of T. comptus, sharing identical \( P \) and \( M \) elements and differentiated using the \( S \) elements (Stouge & Bagnoli 1988). Although a reconstruction of this type cannot be ruled out, the synonymy lists of the two species indicate differences in their respective occurrences which need to be accounted for if they are synonymous.

A second species, T. sweeti (Serpagli), was also included in the genus, although in contrast to T. comptus the \( P \) elements were considered to be diagnostic whilst the \( S \) elements were similar to T. comptus. Many of the specimens figured by Serpagli (1974) as Walliserodus australis were placed in the synonymy list of T. sweeti, although the morphological basis for this division was not made clear. The distinguishing characters were further obscured by a taxonomic error in which the holotype of Walliserodus australis (Serpagli 1974: pl. 19: 10, pl. 29: 8) was included in the synonymy list of both T. australis and T. sweeti. There does not appear to be any basis for dividing the apparatus in either Serpagli’s collection or that from Greenland, and the original species concepts are retained here.

**Tropodus australis** (Serpagli 1974)

Fig. 38 a–c

\[ \text{v} \] 1972 *Paltodus volchovenensis* Sergeeva – Ethington: 22, pl. 1: 14


\[ \text{v} \] 1976 *Walliserodus australis* Serpagli – Landing: 641–642, pl. 4: 16, 19, 22, 23

\[ \text{v} \] 1988 *Tropodus comptus australis* (Serpagli) – Stouge & Bagnoli: 141–142, pl. 16: 3, 74, 75

\[ \text{p} \] 1988 *Tropodus sweeti* (Serpagli) – Stouge & Bagnoli: 142, pl. 16: 11–14 (non pl. 16: 10, 15)

Remarks. – The small collection of elements referred to this species was recovered from samples immediately above the highest occurrence of T. comptus (Branson & Mehl) in the Cape Weber Formation. The most distinctive element is the quinquecostate form which has very strongly developed, basally projecting costae. The postero-lateral costae of this element may bear small, serrate denticles at the proximal end. Similar serrate elements have been figured by Serpagli (1974: pls 19: 7, 29: 15) and Landing (1976: pl. 4: 19); one specimen of this type was found in the Cape Weber Formation (Fig. 38c).

The tricostate elements are usually asymmetrical in cusp cross-section and also have basally projecting costae. They outnumber the quinquecostate elements by 2:1 in the San Juan Limestone (Serpagli 1974) and by 3:1 in the Cape Weber Formation.

The apparatus is completed by laterally compressed quadricostate elements, with anterior, posterior and asymmetrically disposed lateral costae, and comptiform elements. The comptiform elements figured by Serpagli (1974) included both laterally expanded and compressed forms. The single specimen recovered from the Cape Weber Formation is of the latter type.

Range. – 992–1010 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – tricostate 6, laterally compressed quadricostate 2, quinquecostate 2, comptiform 1.

**Tropodus comptus** (Branson & Mehl 1933)

Fig. 38 d–n

\[ \text{v} \] * 1933 *Paltodus comptus*, Branson & Mehl: 61, pl. 4: 9

\[ \text{v} \] * 1933 *Scolopodus pseudquadrate*, Branson & Mehl: 63, pl. 4: 19

\[ \text{non} \] 1975 *Scolopodus pseudquadrate* Branson & Mehl – Abaimova: 97–98, pl. 9: 8–10, fig. 8: 5, 7–11

\[ ? \] 1975 *Scolopodus sexpliactus* Jones – Cooper & Druce: 578–579, pl. 1: 29

\[ \text{v} \] * 1971 *Paltodus sp.* A. – Ethington & Clark: pl. 2: 12


\[ \text{v} \] 1982 *Walliserodus comptus* (Branson & Mehl) – Ethington & Clark: 114–116, pl. 13: 6, 7, 11–13, fig. 34

\[ \text{v} \] 1982 *Paltodus comptus* Branson & Mehl – Repetski: 37, pl. 14: 10a–c

\[ \text{v} \] 1982 *Scolopodus pseudquadrate* (Branson & Mehl) – Repetski: 50, pl. 23: 7a–c

\[ \text{v} \] 1982 *Scolopodus aff. S. pseudquadrate* (Branson & Mehl) – Repetski: 50, pl. 23: 9a–c, fig. 7 Q

\[ \text{v} \] * 1982 *Tropodus comptus* (Branson & Mehl) – Stouge: 45, pl. 4: 3, 4, 6–8

\[ \text{v} \] 1983 *Tropodus comptus* (Branson & Mehl) – Stouge: pl. 3: 13, 14

\[ \text{p} \] 1988 *Tropodus comptus* (Branson & Mehl) – Bagnoli et al.: 215–216, pl. 41: 9, 10 only (non pl. 41: 8, 11)

\[ \text{non} \] 1988 *Tropodus comptus* (Branson & Mehl) – Stouge & Bagnoli: 141–142, pl. 16: 1, 2

\[ \text{p} \] 1988 *Tropodus comptus* (Branson & Mehl) – Stouge & Bagnoli: 141–142, pl. 16: 6–8, 79
Diagnosis. — A quadrimembrate apparatus composed of tricostate quadricostate, symmetrical quinquecostate and comptiform elements. All elements have long bases and are albid. The costae are lower in relief than those on T. australis and are never denticulate. Antero-lateral costae may bifurcate basally.

Description. — Tricostate element
Upper edge of base straight, curves round evenly into posterior margin. Upper edge and posterior margin marked by sharp, well-defined costa, offset from midline towards outer face. Inner lateral face convex, maximum point of curvature near posterior costa. Outer lateral face flat. Antero-lateral costae symmetrically disposed, deflected postero-laterally. Anterior face broadly rounded but depressed in the centre basally.

Quadricostate element
Upper edge of base straight, curving evenly into posterior margin of proclined cusp. Element bowed. Posterior margin marked by two sharp, well-defined costae; one posterior, the other postero-lateral, spacing varies and may become posterior and lateral in position. Outer lateral face flat, inner lateral face convex. Antero-lateral costae symmetrically disposed, deflected postero-laterally. Anterior face broadly rounded, depressed centrally at antero-basal corner.

Comptiform element
Upper edge of base straight, curving round very gradually into posterior margin of cusp. Cusp more proclined than other elements. Posterior margin marked by costa; narrow, well-defined, flat-sided, may be extended postero-basally. Element bowed. Outer lateral face bears three strongly developed, sharp costae positioned at upper outer edge, centre and lower outer edge of outer lateral face, directed posteriorly, laterally and antero-laterally respectively. Central, or more rarely upper, costa may be bifid. Anteriormost costa marks outer antero-lateral corner. Fifth costa marks inner antero-lateral corner; costa directed laterally. Thus, five costae situated in inner antero-lateral, posterior and upper, central and lower outer antero-lateral positions. Anterior face narrow, rounded and twisted with cusp.

Symmetrical quinquecostate element
Upper edge of base straight, curves evenly into posterior margin of proclined cusp. Element not bowed. Upper edge of base and posterior margin marked by narrow, well-defined costa, situated on midline. Posterior face delimited by postero-lateral costae; narrow and sharp. Deep, v-shaped grooves between posterior and postero-lateral costae. Lateral faces flat. Antero-lateral costae symmetrically disposed, deflected towards posterior. Anterior face broadly rounded except for depression at antero-basal corner. Anterior face narrower or wider than posterior face.

Remarks. — Ethington & Clark (1982) described a fifth element, termed "asymmetrical multicostate", with anterior and posterior keels and asymmetrical lateral costae. Upon examination, the element illustrated by Ethington & Clark (1982, pl. 13: 6, fig. 34) was seen to be a tricostate element with a bifid outer antero-lateral costa. This element type is present, although rare, in Greenland and is included within the tricostate category.

The quadrimembrate apparatus of T. comptus described here does not agree with the interpretation of Kennedy (1980) who considered it to be bimembrate, possessing only symmetrical and asymmetrical quinquecostate elements. Ethington & Clark (1982) and Repetski (1982) subsequently figured the tricostate and quadricostate elements. Kennedy (1980) distinguished between T. comptus and T. australis on the basis of apparatus structure, T. australis having numerous, variably costate forms and T. comptus being bimembrate. Other criteria must now be used; one major distinction is that the costae of T. australis are much more strongly developed and occasionally bear small, serrate denticles. A further difference is the presence of both laterally expanded and compressed asymmetrical quinquecostate elements in T. australis, but only compressed versions in T. comptus. The symmetrical quinquecostate element of T. comptus has a sub-quadrate basal outline whereas that of T. australis is more pentagonal. White matter is more extensive in T. australis, only the basal cavity is hyaline, whereas in T. comptus the proclined part of the base is hyaline. A possible distinction may also lie in the ratio of tricostate to quinquecostate elements. T. australis specimens from the Cape Weber Formation show a ratio of 3:1 and Serpagli (1974) recorded a ratio of 2:1 in the San Juan Limestone. In T. comptus, the ratio is reversed with tricostate elements outnumbered by quadricostate elements in collections from the Ibex area (Ethington & Clark 1982) and Greenland.

Several specimens have been erroneously identified as T. comptus by previous authors. These were discussed by Kennedy (1980) who also tentatively included some specimens described as A codus deltatus longi basis and A codus transi tans by McTavish (1973: pl. 1: 17, 23). The morphology of the former is not consistent with other elements of the apparatus and the inclusion of A. transi tans must remain questionable. A baimova (1975) illustrated and described a number of elements as Sco lopodus pseudo quadratus. These belong to a variety of taxa, none of which is T. comptus.

Ethington & Clark (1982) considered Sco lopodus sex plicatus Jones and S. aff. S. cornutiformis (Branson &
Mehl) of Cooper & Druce (1975) to be synonymous with *T. comptus*. The figured specimen of *S. sexplicatus* may be an asymmetrical quinquecostate element but that of *S. aff. S. cornutiformis* is too recurved and does not belong in *T. comptus*.
Range. – *T. comptus* ranges from the base to 114 m in the Wandel Valley Formation in Peary Land and from the base to 200 m in the same formation in Kronprins Christian Land. The species has a range of 164 to 976 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 45 tricostate, 35 quadricostate, 49 symmetrical quinquecostate, 51 comptiform.

**Tropodus? sp. A**

Fig. 39 a–g

1974 “*Scolopodus*” sp. 1 – Serpagli: 87, pls 18: 8a–d, 28: 11


? 1985 *Scolopodus asperus* An, Du et al. – An et al.: pl. 5: 11, 18

Remarks. – Only t and u elements were recovered, tricostate or quadricostate s elements were absent from the collection. An erect quinquecostate element occupies the u position and differs from its counterpart in *T. comptus* in being more antero-posteriorly compressed and having narrower lateral faces. The t element is proclined and has a broadly rounded anterior face which curves evenly into the gently convex outer lateral face. The postero-lateral face is convex with multiple costae. The transition between the two elements is smooth, with transitional specimens having the general morphology of a t element but with one or two prominent costae on the outer face. The elements recovered conform with the diagnosis of *Tropodus* (Kennedy 1980) but the inclusion is questioned due to the lack of s elements. The collection is, however, largely from a single sample.

Range. – From 130 to 200 m above the base of the Wandel Valley Formation in Kronprins Christian Land and at 128 m above the base in Børglum Elv.

Number of specimens. – 47.

**Tropodus sp. B**

Fig. 39 h, i

Description. – Upper edge of base long, sharp, may be produced as short, adenticulate posterior process, curves very gently into posterior margin of proclined cusp. Posterior margin keeled. Anterior margin keeled, turned inwards, produced basally as adenticulate anticusp. Outer face broadly convex, one or two medial costae running full length or dying out distally. Inner face concave, median carina, often a sharp, low costa posterior of midline and carina directed postero-laterally, decreasing in height distally; lateral costae produced as short adenticulate processes. Element bowed inwards.

Basal outline roughly quadrilateral, narrowest antero-laterally. Basal cavity moderately deep, conical, occupies carinate part of cusp, anterior parallel to anterior margin of carina, posterior concave to cavity, apex near anterior margin of carina. Albid in all but basal area.

Remarks. – The elements agree with the diagnosis of *Tropodus* (Kennedy 1980) in being keeled, with elongate bases and slightly arcuate cusps. Only two distinct element types were recovered, one bearing a single median costa on the outer face and the other with two outer lateral costae. The principal variation from element to element is in the prominence of the costa on the inner carina, the degree of convexity of the outer face and the prominence and persistence of the outer lateral costa in unicostate elements.

Range. – From 130 to 200 m above the base of the Wandel Valley Formation in Kronprins Christian Land and 992 m above the base of the Cape Weber Formation on Ella Ø.

Number of specimens. – 22.

**Genus Ulrichodina Furnish 1938**

1933 *Ulrichodina* Furnish: 334

Type species. – *Acontiodus abnormalis* Branson & Mehl, 1933: 57, a senior subjective synonym of the originally designated type species *Ulrichodina prima* Furnish, 1938: 335.

Remarks. – Sweet & Bergström (1972) were the first to interpret the apparatus of *Ulrichodina* and considered it to be unimembrate; this is supported by the Greenland faunas. Bergström (1981: W148) placed *Ulrichodina* within the monotypic *Ulrichodinidae*.

**Ulrichodina abnormalis** (Branson & Mehl 1933)

Fig. 40 a–c

v 1933 *Acontiodus abnormalis*, Branson & Mehl: 57, pl. 4: 25 only (non pl. 4: 24)

1938 *Ulrichodina prima*, Furnish: 335, pl. 41: 21, 22, fig. 1 A

v 1944 *Ulrichodina abnormalis* (Branson & Mehl) – Mehl & Ryan in Branson: 45, pl. 6: 4–8

1965 *Ulrichodina cristata*, Harris & Harris: 40–41, pl. 1: 5a–d

1971 *Ulrichodina prima* Furnish – Greggs & Bond: 1469–1470, pl. 2: 11

v 1971 *Ulrichodina* spp. – Ethington & Clark: pl. 2: 18, 25

1977 *Ulrichodina prima* Furnish – Barnes: 104, pl. 1: 9, 10
Fig. 39. *Tropodus*? sp. A. a: posterior view of symmetrical u element, ×40, MGUH 18.871. b: posterior view of symmetrical u element, ×40, MGUH 18.872. c: lateral view, same specimen. d: inner lateral view of symmetrical u element, ×60, MGUH 18.873. e: inner lateral view of asymmetrical t element, ×40, MGUH 18.874. f: inner lateral view of asymmetrical t element, ×60, MGUH 18.875. g: outer lateral view, same specimen. All specimens from GGU 274945. *Tropodus* sp. B. h: inner lateral view, ×60, MGUH 18.876, GGU 274945. i: outer lateral view, same specimen.

1980  *Ulrichodina prima* Furnish – Grether & Clark: pl. 1: 4, 5
1982  *Ulrichodina cristata* Harris & Harris – Ethington & Clark: 112–113, pl. 12: 22, 30
1982  *Ulrichodina abnormalis* (Branson & Mehl) – Repetski: 53–54, pl. 26: 9a–c
1982  *Ulrichodina* sp. – Stouge: pl. 3: 1
1983  *Ulrichodina* sp. – Stouge: pl. 3: 12
1986  *Ulrichodina abnormalis* (Branson & Mehl) – Smith & Peel: fig. 3: D, E

1988  *Ulrichodina abnormalis* (Branson & Mehl) – Stouge & Bagnoli: 142–143, pl. 16: 16

Remarks. – Despite the observation by Lindström (1964) that *U. prima* is a junior synonym of *U. abnormalis*, most occurrences, until recently, have been reported as *U. prima*. The possible inclusion of the anteriorly keeled *U. cristata* was first noted by Barnes & Tuke (1970) and it was first treated as a junior synonym by Greggs & Bond (1971). After studying the types, Repetski (1982) also considered them synonymous. The Greenland material contains both anteriorly...
rounded and keeled forms. The keel takes the form of a narrow, sharply rounded costa flanked by longitudinal, shallow grooves. Upon reaching the basal deflection the keel dies out or, in a few large specimens, is deflected to one side and fades out on one of the projecting antero-lateral corners. The presence of this keel in some specimens supports the inclusion of *U. cristata* as a junior synonym.

Very large specimens tend to have muted costae and grooves, although they retain the characteristic cross-section. The postero-lateral faces of some specimens are striate.

The largest collection of *U. abnormalis* (GGU 226394, 33 specimens) contains specimens typical of the species but also some which are shorter and have a more triangular outline. In all other features including cusp cross-section and basal outline these elements are the same as the more common form. Further work with large collections may establish this as a second element in the *U. abnormalis* apparatus.

As noted under *E. parallelus* – Remarks, Dzik (1983) considered *U. abnormalis* to be a member of the same apparatus as *E. parallelus*; this is not supported by the Greenland faunas.

Range. – *U. abnormalis* occurs from 164 to 868 m in the Cape Weber Formation on Ella Ø; from the base to 140 m in the Wandel Valley Formation in Kronprins Christian Land and from the base to 30 m in the Wandel Valley Formation in Børglum Elv.

Number of specimens. – 58.

**Ulrichodina? simplex**

Ethington & Clark 1982

Description. – Upper edge of base short, curving evenly round into posterior margin; angle between posterior margin and base approximately 135°. Posterior and anterior margins straight, keeled. Cusp biconvex, strongly laterally compressed. Base short, flared, particularly at the antero-lateral corners. Anterior edge of base depressed, anterior keel runs down depression. Basal cavity widely open to posterior. Basal margin convex, basal outline sub-rectangular. Lateral edges plicate. Apex situated immediately posterior to antero-basal deflection. Posterior margin of cavity convex (to cavity). Posterior-most parts of cavity higher than apex. White matter fills all but edges of basal cavity and all of anterior keel.

Remarks. – The species is unusual for *Ulrichodina* in being entirely albid, but is tentatively placed in this genus owing to the characteristic antero-basal deflection. *Ulrichodina* n. sp. 3 of Repetski (1982) has a similar lanceolate cusp cross-section and antero-basal depression but the posterior basal margin is not open and no mention is made of white matter. Nowlan (1976) described a species of *Ulrichodina* from the Canadian Arctic which is very similar to *U? simplex* in white matter distribution but has a different cusp cross-section, being rounded anteriorly.

Range. – From 195 to 200 m above the base of the Wandel Valley Formation in Kronprins Christian Land.

Number of specimens. – 2.

*Ulrichodina wisconsinensis* Furnish 1938

Fig. 40 e, f

<table>
<thead>
<tr>
<th>Year</th>
<th>Publisher</th>
<th>Page Numbers</th>
</tr>
</thead>
<tbody>
<tr>
<td>1938</td>
<td>Furnish</td>
<td>335, pl. 41: 19, 20, fig. 1 B</td>
</tr>
<tr>
<td>1967</td>
<td>Furnish</td>
<td>26: pl. 3: 14, fig. 5 B</td>
</tr>
<tr>
<td>1968</td>
<td>Furnish</td>
<td>421: pl. 6: 71, 74, 75</td>
</tr>
<tr>
<td>1971</td>
<td>Jones</td>
<td>71, pl. 7: 11, 12</td>
</tr>
<tr>
<td>1980</td>
<td>Furnish</td>
<td>55: pl. 26: 8a–c, fig. 8 T</td>
</tr>
<tr>
<td>1982</td>
<td>Furnish</td>
<td>143–144, pl. 28: 2</td>
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<tr>
<td>1987</td>
<td>Furnish</td>
<td>81: 2</td>
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Remarks. – The specimens closely fit the description of the type material, having evenly convex lateral faces, widest just behind the rounded anterior margin and narrowing to a posterior keel. Repetski (1982) noted a slightly inflated anterior margin in some specimens with a shallow groove on the lateral faces just anterior to the midline. This feature is seen on some of the Greenland specimens.

The antero-basal deflection may be a true depression or may be a downward extension of the anterior margin which is folded back underneath the basal cavity.

Range. – From the base up to 200 m in the Wandel Valley Formation in Kronprins Christian Land and in one sample 128 m up the Wandel Valley Formation in Peary Land.

Number of specimens. – 11.
Ulrichodina sp. nov. A

Fig. 40 g

Description. – Upper edge of base very short, meeting posterior margin of cusp at 160°. Posterior margin straight and keeled. Anterior margin straight, anterior face flat with central, narrow groove. One third of the way towards the posterior, each lateral face bears a narrow, rounded costa. Anterior face separated from lateral costae by a shallow groove. Antero-basal angle 60°. Base short, flared. Basal margin straight, indented at base of anterior face. Basal outline sub-circular, pinched posteriorly near keel. Cavity shallow, slightly concave; very small apex centrally situated just anterior to lateral costae.

Remarks. – The species differs from U. abnormalis in having a flat anterior face with a narrow central groove and narrow lateral costae.

Range. – The single specimen was recovered 167 m from the base of the Wandel Valley Formation in Kronprins Christian Land.

Number of specimens. – 1.

Ulrichodina sp. B

Fig. 40 h

1980 Ulrichodina wisconsinensis Furnish – Grether & Clark: pl. 1: 13

Remarks. – The element is generally similar in its morphology to U. wisconsinensis but it lacks the antero-basal depression and, more significantly, the posterior margin bears a single, laterally compressed denticle which is of greater reclination than the cusp. The specimen illustrated by Grether & Clark (1980) has the denticle at a greater angle to the posterior margin than the single specimen from the Wandel Valley Formation.

Range. – U. sp. B was found 3 m above the base of the Wandel Valley Formation in Kronprins Christian Land.

Number of specimens. – 1.

Genus Variabiloconus Landing, Barnes & Stevens 1986

1986 Variabiloconus Landing et al.: 1944, 1946

Type species. – By original designation, Paltodus bassleri Furnish, 1938: 325.
Remarks. — Sweet & Bergström (1972) were the first to note that *A. oneotensis*, *O7 triangularis* and *P. bassleri* were likely to be members of a single apparatus for which no generic name was available. Many authors continued, however, to treat the constituents as form taxa in the absence of large collections to lend supporting evidence. Another factor, no doubt, was that when the morphological variability of each element type was taken into account, the resulting apparatus was of unprecedented complexity for a coniform species. Landing & Barnes (1981) came to essentially the same conclusion as Sweet & Bergström (1972) but also included *S. sulcatus* of Furnish. They did not, however, include an oistodiform element, in contrast to Lindström (1977b: 430) who included *O. inclinatus* Branson & Mehl. The apparatus reconstruction of Landing & Barnes (1981) comprised a completely intergradational series of coniform elements in which variation occurs in the number of costae and their strength of development, in symmetry and in curvature. The species was placed, with qualification, in *Utahconus* Miller. The reconstruction of Landing & Barnes (1981) was ratified by Landing et al. (1986) who erected the genus *Variabiloconus* for the species. The principal element types of *V. bassleri* in the reconstruction of Landing et al. are: symmetrical tricostate (“*P. bassleri*”), asymmetrical tricostate (“*P. variabilis*”), asymmetrical tricostate with sharp costae (“*A. oneotensis*”), symmetrical quadricostate, symmetrical quinquecostate and asymmetrical costate (“*S. sulcatus*”) (Landing et al. 1986).

The collection of *V. bassleri* from the Cape Weber Formation is too small to test the apparatus reconstruction of Landing et al. (1986) and in the absence of contrary data their concept is used here. The elements are almost entirely of the symmetrical and asymmetrical tricostate types.

Range. — *V. bassleri* occurs up to 46 m in the Cape Weber Formation on Ella Ø.

Number of specimens. — 25.

Genus *Wandelia* nov.

Type species. — *Wandelia guyi* sp. nov.

Derivation of name. — After the Wandel Valley Formation of North Greenland.

Diagnosis. — The apparatus is mono elemental comprising a squat coniform with a cusp which is very reduced or absent. All species are transversely costate. Basal cavity very shallow and may be reduced to a narrow, shallow slit.

Remarks. — The genus is a very rare component of late Canadian faunas. Only *Wandelia guyi* has previously been figured (as *Scolopodus?* n. sp. C Stouge, 1982). *Wandelia* superficially resembles species of *Clavohamulus* Furnish but is distinguished by being costate or striate rather than having a surface sculpture of fine, granular nodes. Additionally, the elements of *Wandelia* are not always bilaterally symmetrical. The two genera are interpreted here as structural homoeomorphs.

Some specimens of *Oneotodus costatus* Ethington & Brand from Kronprins Christian Land are partly transitional to *W. guyi*. However, a substantial morphological gap is still present and the ranges are significantly different. It is likely that *W. guyi* is a branch of the *O. costatus* lineage which evolved during early *communis* Biozone time. The emended diagnosis of Ethington & Brand (1981) for *Oneotodus* includes coniforms with stout albid cusps of subcircular or ellipsoidal cross-section, circular to ovoid basal outline and a basal cavity of asymmetrical triangular shape in lateral profile. Without substantial further amendment, *W. guyi* and *W. candidisphaera* cannot be included in *Oneotodus* or *Paraserratognathus*, a probable junior synonym of *Oneotodus*.
**Wandelia guyi** sp. nov.

Fig. 41 a–c

1982 *Scolopodus? n. sp. C* – Stouge: 44, pl. 3: 16–18

1983 *Scolopodus? sp. C* – Stouge: pl. 3: 3

Derivation of name. – In memory of the late Peter J. Guy.

Type material. – The holotype is MGUH 18.888 and the paratype MGUH 18.887. Both specimens from sample GGU 240006 collected 848 m above the base of the Cape Weber Formation on Ella Ø (section PF 770824–1).

Diagnosis. – Cusp much reduced in size or almost absent, element strongly costate. Furrow between lateral, transverse costae runs down midline of element or obliquely across it. Anterior margin recurved through up to 90°, so that it may be parallel to basal margin. Basal cavity small and shallow, with a very small apex situated anteriorly.

Description. – Cusp very short, and poorly developed in relation to rest of element. Anterior of element rounded. Antero-basal angle 90°, anterior margin recurved through up to 90°. Lateral faces bear up to eight (usually three to four) costae which have steep posterior facets and gently sloping anterior facets. Costae continue across anterior face where a furrow separates the two sets; costae deflected to posterior near the furrow. Furrow may run down midline or obliquely across it. Costae die out before reaching basal margin and may slope towards anterior on lateral faces. Posterior face defined by two posteriormost costae, recessed between them, posterior surface flat or slightly convex. Basal margin straight to mildly convex. Basal outline ovate. Basal cavity is a longitudinal trough, open at posterior, parallel-sided or narrowing towards anterior; deepest at anterior with very small apex. Anterior margin of cavity rounded.

All but the most basal part of the element albid.

Remarks. – The species has been figured previously by Stouge (1982, 1983) who reported it as a species of *Scolopodus?*, but it does not conform to the apparatus plan or element morphology of the type species. The specimen figured by Stouge has rather more costae than the Greenland specimens. *W. guyi* is also present in my unpublished collections from the Croisaphuil Formation of the Durness Group, northwest Scotland.

Range. – *W. guyi* occurs in a single sample 9 m up the Wandel Valley Formation in Peary Land but occurs between 20 and 103 m in Kronprins Christian Land. The species has a range of 737–868 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 31.
**Wandelia candidisphaera** sp. nov.

Fig. 41 d–g

Derivation of name. – candidus, white (L); sphaera, globe (L).

Type material. – The holotype is MGUH 18.892. Para­
types are MGUH 18.889, 18.890 and 18.891. All type
material is from sample GGU 240014 collected 976 m
above the base of the Cape Weber Formation on Ella Ø.

Diagnosis. – The element consists of an albid, spherical
body and a base which slopes inwards from the base of
the sphere. The basal cavity is small, shallow and sub­
ovate. The spherical body is transversely costate with
numerous, thin serrate costae.

Description. – Spherical body bears multiple rows of
thin, serrate costae, directed posteriorly and increasing
in length towards posterior. Small posterior face may
take the form of either a flat area or a furrow. Base
slopes inwards from spherical body, anterior margin
slopes towards posterior. Basal cavity small, shallow,
sub-ovate, deepest anteriorly then shallowing rapidly
wards posterior. Base hyaline, spherical body entirely
albid.

Remarks. – *W. candidisphaera* differs from *W. guyi*
in having a more spherical overall shape together with
finer costae which are far more numerous, lower in
relief and serrate. The basal cavity is small and sub­
ovate whereas that in *W. guyi* the cavity is a very shal­
low, longitudinal trough.

The single occurrence of *W. candidisphaera* is above
the range of *W. guyi* on Ella Ø and it may represent a
continuation of the morphological trend observed be­
tween *O. costatus* and *W. guyi*, leading to a reduction in
the dimensions of the basal cavity and an entirely absent
cusp.

Range. – The specimens were found in a single sample
976 m up the Cape Weber Formation.

Number of specimens. – 11.

**Wandelia** sp. A

Fig. 41 h

Description. – Anterior and lateral areas of element
costate with thin, serrate costae of moderate relief run­
ing transversely across element. There is no median
furrow. Posterior face recessed and concave. There is
no cusp. Basal cavity approximately one third width of
element, parallel-sided; tiny apex situated anteriorly,
cavity shallows to posterior. A rim surrounds anterior
part of basal margin.

Remarks. – The morphology of *Wandelia* sp. A is inter­
mediate between that of *W. guyi* and *W. candidis­
phaera*. The overall shape is that of *W. guyi* but the
costae and lack of cusp are more akin to *W. candidis­
phaera*. The basal cavity is of intermediate width.

Range. – The single sample containing *W. sp. A* was
collected 103 m above the base of the Wandel Valley
Formation in Kronprins Christian Land.

Number of specimens. – 1.

**Genus novum A**

1982 New Genus 2, Ethington & Clark

**Gen. nov. A sp. nov. A**

Fig. 42 a–d

Description. – Coniform element A

Upper edge of base not discernible from posterior mar­
gin. Posterior margin sharp, evenly and gently curved.
Anterior margin flat to very broadly rounded, termi­
nated by low antero-lateral costae. Lateral faces slightly
convex. Basal margin straight. Basal outline triangular,
apex posterior. Basal cavity shallow.

Coniform element B

Upper edge of base of medium length, convex, sharp.
Posterior margin straight, sharp. Anterior margin flat to
very broadly rounded, terminated by antero-lateral ca­
rinae. Lateral faces flat. Base unexpanded, basal mar­
gin straight. Basal outline sub-triangular, modified an­
teriorly, apex of triangle posterior.

Pastinate element A

Anterior margin rounded. Anterior process high, sharp,
tapering gradually to posterior, one-third total length of
element. Cusp short, inner face flat, outer face convex,
convexity continued across base as sharp, prominent
lateral process. Posterior process commences lower
than anterior process/cusp junction, sharp, tapering to
posterior. Posterior margin sharply rounded. Processes
have fused, incipient denticles one quarter the process
height. Element twisted along its length. Basal cavity
very shallow and broad below anterior process, narrow
and slit-like below lateral and posterior processes.

Pastinate element B

Anterior process bears single, rounded denticle almost
as high as cusp, inner side of denticle bears small, sub­
sidiary denticle just below apex. Cusp short, biconvex,
lateral process very small and limited to basal margin.

**Meddelelser om Grønland, Geoscience** 26 · 1991
Posterior process tapers rapidly, upper edge almost meeting basal margin. Basal cavity shallow, broad below anterior process and cusp, narrow under lateral process, absent under posterior process.

All elements albid.

Remarks. – These elements are generally similar to those recorded as New Genus 2 by Ethington & Clark (1982) but they have not been reported with certainty elsewhere in the literature. Specifically, one specimen figured by Ethington & Clark (1982: pl. 13: 18) is closely similar to pastinate element A, although the other elements recorded by Ethington & Clark (1982) were not recovered from Greenland and, similarly, those from the Cape Weber Formation are not recorded from Utah. Ethington & Clark had a very small number of specimens and were not sure if they represented a single species, so declined to erect a new genus. This problem and the lack of specimens again prevents the erection of a new genus.

Stouge & Bagnoli (1988) figured an element of generally similar morphology to pastinate element A, but which differed in having three, or possibly four, central denticles. The Cow Head specimen is probably congeneric but more material is needed to establish the possible conspecificity. The overall morphology and denticulate nature of Stouge & Bagnoli’s specimen may indicate a relationship between Gen. nov. A and Jumudontus Cooper.

Range. – From 190 to 992 m in the Cape Weber Formation on Ella Ø.

Number of specimens. – 2 coniform A, 2 coniform B, 2 pastinate A, 1 pastinate B.

Gen. nov. A sp. nov. B

Fig. 42 e, f

Remarks. – Only pastinate A and B elements were recovered. They differ from those of Gen. nov. A sp. nov. A in having a greater height: length ratio, a stouter cusp, much shorter process and a more prominent lateral process on the pastinate A element which extends to the full height of the element. Gen. nov. A sp. nov. B was only recovered from central Peary Land.

Range. – Up to 9 m in the Wandel Valley Formation in Børglum Elv.

Number of specimens. – 5 pastinate A, 1 pastinate B.

Acknowledgements

My thanks are due foremost to Drs R. J. Aldridge (University of Nottingham) and J. S. Peel (GGU) for their advice, help and encouragement throughout. The project was initiated at the University of Nottingham as a Natural Environment Research Council studentship, the receipt of which is gratefully acknowledged, and is part of a continuing programme of research with GGU, who are also acknowledged for financial support. The project would not have been possible without the efforts of P. Frykman (DGU), Dr J. R. Ineson (DGU), Dr J. E. Mabillard (KSEPL) and J. S. Peel who collected the samples and deserve especial thanks.

Professor R. L. Ethington (University of Missouri – Columbia), Drs A. G. Harris (U.S. Geological Survey), G. S. Nowlan (Geological Survey of Canada) and J. E. Repetski (USGS) are thanked for their hospitality and access to their collections and type material. Professor E. Serpagli (University of Modena) kindly loaned type and figured material from the San Juan Formation. The manuscript was typed by J. Angell and J. Hodkinson and my thanks are due also to J. Wilkinson, S. Ripper and B. Thomas for drafting assistance and advice, and to K. Harvey for photographic assistance. Helpful comments
References


- & Rickards, R. B. & Aldridge, R. J. 1990. Bedding plane assemblages of Promissium pulcherum, 1986, a new giant Ash-
gill conodont from the Table Mountain Group, South Africa. – Palaeontology 33: 577–594.


Appendix 2: Abundance tables for sections JSP 800630-5 and JSP 800630-6, Danmarks Fjord Member, Kap Holbæk, eastern North Greenland.

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### Appendix 3: Abundance Table for Section JSP 800702-1, Danmarks Fjord and Amdrup Members, East Side of Danmark Fjord, Eastern North Greenland

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#### Appendix 3: Abundance table for section JSP 800702-1, Danmarks Fjord and Amdrup Members, east side of Danmark Fjord, eastern North Greenland.
## Appendix 4: Abundance Table for Section JEM 790627-1, Pyramideplateau Member, Børglum Elv, Peary Land, central North Greenland.

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