

Conodonts from the Upper Ordovician – Lower Silurian carbonate platform of North Greenland

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GRØNLANDS GEOLOGISKE UNDERSØGELSE

Bulletin 159

1990

An outline map of Greenland, showing the island's irregular coastline and several smaller islands to the east. The map is oriented vertically, with the northern tip at the top.

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Abstract

Samples from Upper Ordovician and Lower Silurian strata of the North Greenland carbonate platform have yielded approximately 16 500 identifiable conodont elements referable to 25 multi-element genera and 71 species and subspecies. A single genus, *Pseudobelodella* and 17 species and subspecies are new. In addition, 8 informal groups of indeterminate species of *Oulodus* are described.

The Upper Ordovician conodont species can be referred to 'Fauna 12' of the American Midcontinent Province where the presence of *Rhipodognathus symmetricus* in the late Richmondian is typical of shallow water deposits. The Ordovician-Silurian boundary is difficult to place in this study using conodonts. New

conodont zonations are proposed for Lower Silurian shelf and slope biofacies; two new early Llandovery conodont zones are erected in the slope biofacies, the *Aspelundia expansa* Biozone (?earliest Rhuddanian to early Aeronian) and the *Aspelundia fluegeli* Biozone (early Aeronian to early Telychian). The *Pterospodus celloni* Biozone is shown to be particularly valuable in the correlation of strata of late Llandovery age throughout North Greenland.

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Dansk sammendrag

I øvre ordoviciske og nedre silure bjergarter i Nordgrønland er der fundet ca. 16 500 identificerbare conodont-elementer, som kan placeres i 25 multielement slægter og 71 arter eller underarter. Der opstilles og beskrives en ny slægt, *Pseudobelodella*, og 17 nye arter eller underarter. Herudover beskrives 8 taxonomisk uformelle grupper af ubestemmelige arter af slægten *Oulodus*.

De øvre ordoviciske conodonte kan stratigrafisk sammenlignes med 'Fauna 12' fra den 'Amerikanske Midtkontinent Provins'. Her er tilstedeværelsen af *Rhipodognathus symmetricus* i det øverste Richmondian typisk for lavvandsaflejringer og arten antages at vise

samme aflejringsmiljø for de nordgrønlandske faunaer og sedimente. Grænsen mellem Ordovicium og Silur i Nordgrønland er vanskelig af identificere præcist på grundlag af conodonte alene.

Der defineres to nye conodont-biozoner af nedre Llandovery alder: *Aspelundia expansa* Zone (?tidligste Rhuddanian til tidlig Aeronian) og *Aspelundia fluegeli* Zone (tidlig Aeronian til tidlig Telychian). De indgår i en ny conodont-biozonering opstillet for kontinental-sokkel og -skrænt facies i Nedre Silur. Det dokumenteres, at *Pterospodus celloni* Zonen kan følges over hele Nordgrønland i øvre Llandovery sedimente og derfor er specielt velegnet til korrelation af disse lag.

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Geological setting

The Franklinian Basin of North Greenland represents the continuation of a geological terrane extending from Alaska through the Canadian Arctic Archipelago and Ellesmere Island into North Greenland. During the late Ordovician and early Silurian the southern margin of the basin was rimmed by an extensive carbonate platform (fig. 1) with the platform margin forming a pronounced scarp-like feature. North of the scarp, slope and deep-water trough environments received clastic sediments (cf. Higgins *et al.*, in press). The trough expanded southwards during the late Llandovery, drowning most of the carbonate platform; only isolated mound complexes survived into the early Wenlock in

the Peary Land – Kronprins Christian Land area and into the late Silurian in western North Greenland.

Carbonate platform deposits of this period are assigned to the Morris Bugt and Washington Land Groups originally described in western North Greenland (Peel & Hurst, 1980; Hurst, 1980b) but recently extended to include formations outcropping in central and eastern North Greenland (Smith *et al.*, 1989; Sønderholm & Harland, unpublished) (fig. 2). Slope and deep-water trough deposits are placed within the Peary Land Group (Hurst, 1980b; Hurst & Surlyk, 1982; Larsen & Escher, 1985, 1987).

Previous research

Conodont studies in the Arctic are as yet in their infancy. Scattered data are available, mainly from Ordovician to Devonian collections, but many reports are of a biostratigraphical nature with few taxonomic studies. A series of publications dealing with Ordovician conodont biostratigraphy has appeared as a result of regional mapping programmes in the Canadian Arctic (e.g. Barnes, 1974, 1977; Barnes *et al.*, 1974; Brideaux *et al.*, 1975; McGill, 1974; Mayr *et al.*, 1978, 1980; Morrow, 1973; Tipnis & Cecile, 1980) while an unpublished study by Mirza (1976) dealt taxonomically and biostratigraphically with sections of late Ordovician to late Silurian age from Ellesmere Island. Overshine & Webster (1970), Savage (1985) have recorded Silurian conodonts from Alaska.

Ordovician faunas have been described from the Northwest territories, Canada by Tipnis *et al.* 1978 and McCracken & Nowlan (1984). An Ordovician–Silurian boundary correlation using graptolites and conodonts for the northern Yukon was published by Lenz & McCracken (1982); Norford & Orchard (1983) and Over & Chatterton (1987) described Llandovery conodonts and graptolites from the Mackenzie Mountains, Northwest Territories, Canada.

Records of conodonts from the Ordovician in Greenland include Aldridge (1982) who described a new ge-

nus, *Besselodus arcticus*, from the Aleqatsiaq Fjord Formation of the Morris Bugt Group in Washington Land. The conodont biostratigraphy of the Morris Bugt Group is described by Smith *et al.* (1989). Stouge (1977, 1978) and Stouge *et al.* (1985) recorded faunas from the Lower Ordovician of Washington Land and East Greenland, while Stouge & Peel (1979) described Ordovician conodonts from southern West Greenland. Miller & Kurtz (1979) and Kurtz & Miller (1981) noted the occurrence of early Ordovician faunas in East Greenland. Smith (1985) has monographed Ordovician conodont faunas from North and East Greenland. Smith & Peel (1986), Ineson *et al.* (1986), Peel & Smith (1988) and Fortey & Peel (1989, in press) documented small Ordovician faunas from eastern North Greenland.

Aldridge (1979) and Stouge & Stouge (1985) described small conodont faunas from the Silurian of Peary Land and Hall Land respectively. Stratigraphic reports by Hurst (1980b, 1984) include unpublished conodont records supplied by R. J. Aldridge and H. A. Armstrong (University of Nottingham) largely summarised in Aldridge & Armstrong (1982).

The present monograph is based on a study of late Ordovician and early Silurian conodonts from throughout North Greenland contained in an unpublished Ph.D. thesis (Armstrong, 1983). The concentration of

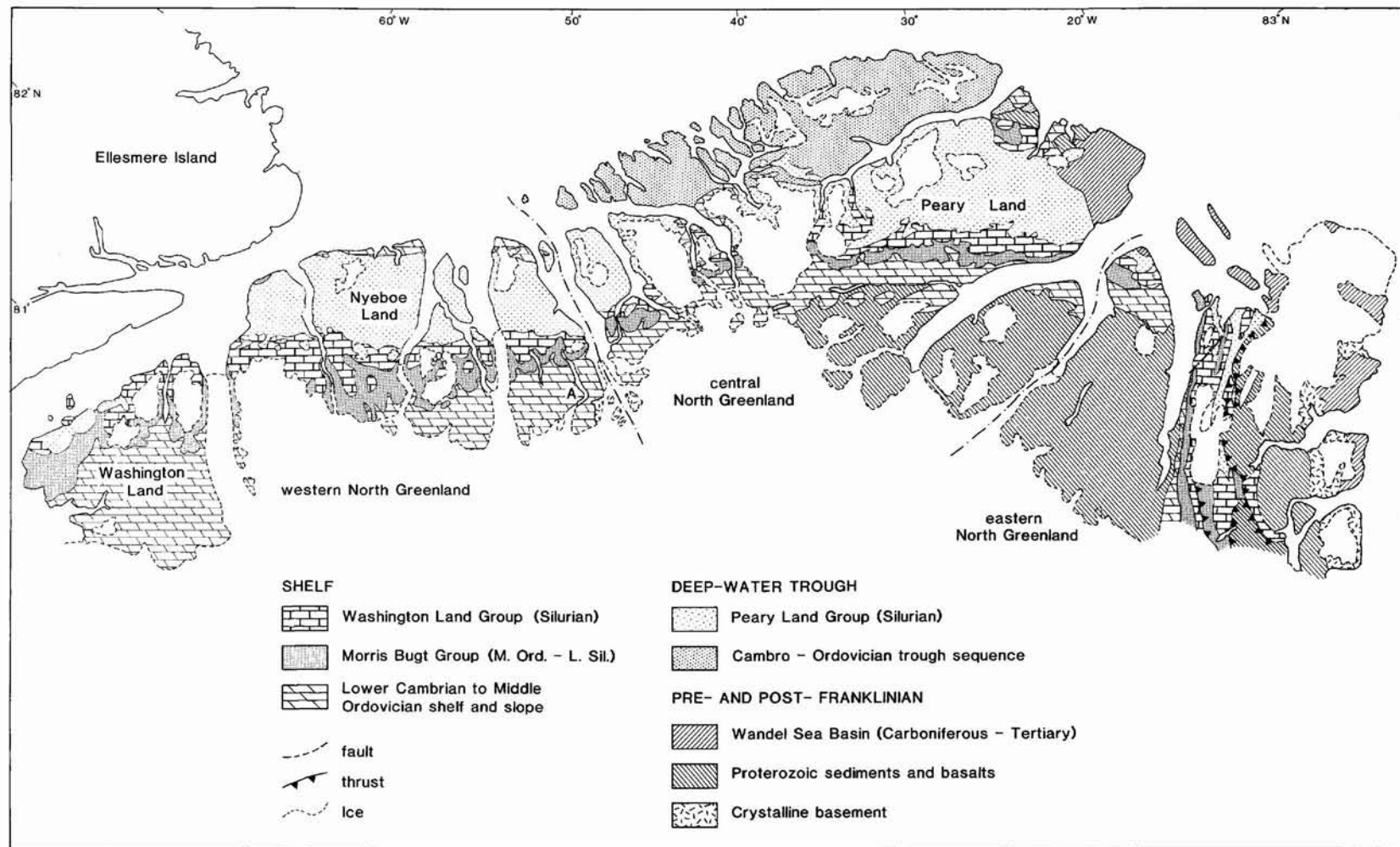


Fig. 1. Simplified geological map of Franklinian Basin sediments in North Greenland. A, 'Apollo SØ' (adapted from Smith *et al.*, 1989).

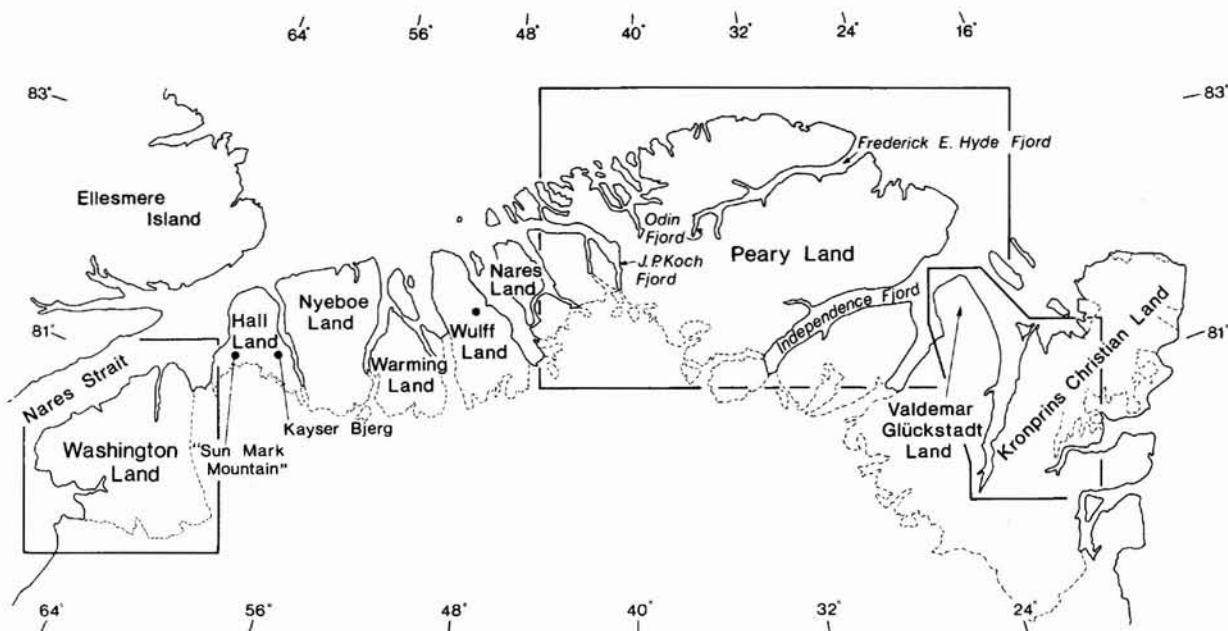


Fig. 2. General locality map. Detailed locality maps of Peary Land, Kronprins Christian Land and Washington Land are given in figs 3, 4, 14.

sampling localities in more easterly areas (Peary Land, Kronprins Christian Land) and the extreme west of the region (Washington Land) reflects the distribution of field work carried out in North Greenland by the Geological Survey of Greenland (GGU) from 1974 to 1980. The intervening area (Hall Land – Freuchen Land) was visited only sporadically during this period, but Silurian

strata were subsequently studied in detail by GGU during 1984 and 1985 (Larsen & Escher, 1985, 1987; Sønderholm *et al.*, 1987). The present monograph is based on samples collected during the first phase of GGU field work and does not include material collected in 1984 and 1985. Preliminary examination of this later material is summarised by Armstrong (1986a-c).

Samples and techniques

Samples intended for processing for conodonts were collected by a number of geologists (see acknowledgements), mainly in the course of compilation of sedimentary section logs. Generalised section logs are presented here, but full details are held by the Geological Survey of Greenland in Copenhagen.

Standard techniques of digestion in 10% acetic acid and separation of residues in bromoform were employed to recover conodonts from calcareous rock sam-

ples. Indurated shale samples from the Wulff Land Formation (Thors Fjord Member) of Peary Land were crushed, dry sieved at 75 μm and separated in bromoform. Scanning electron photomicrographs were taken on a Cambridge MK II stereoscan, using Ilford FP4 35 mm film. Specimens were coated with aluminium which was subsequently removed with a 5% solution of sodium hydroxide.

Lithostratigraphy and conodont biostratigraphy

Formations are briefly described in ascending order within each geographical area. More detailed descriptions are given by Hurst (1979, 1980a,b, 1984; Hurst & Surlyk, 1982), but see also Higgins *et al.* (in press), Larsen & Escher (1985, 1987), S nderholm *et al.* (1987), Smith *et al.* (1989).

Peary Land – Kronprins Christian Land

This area stretches from central Peary Land in the west to Kronprins Christian Land in the east (figs 2–4). Six formations and four members with a combined thickness approaching 800 m extend from the latest Ordovician (Richmondian) to the early Wenlock (Silurian).

Tures  Formation

The Tures  Formation (figs 5–10) is between 115 m and 150 m thick in Peary Land increasing to some 200 m in Kronprins Christian Land (Hurst, 1984; Peel *et al.*, 1981). It is characterised by medium to thick-bedded dolomite and limy dolomite with a distinctive alternation of light and dark grey beds. The beds are commonly strongly bioturbated as reflected by conspicuous mottling of the sediments. Rounded to irregular, calcite filled vugs are common; intraformational, flat-pebble conglomerates are found in the lower half of the formation (Armstrong & Lane, 1981). The sediments of the Tures  Formation suggest deposition in shallow subtidal to peritidal environments (Hurst, 1984).

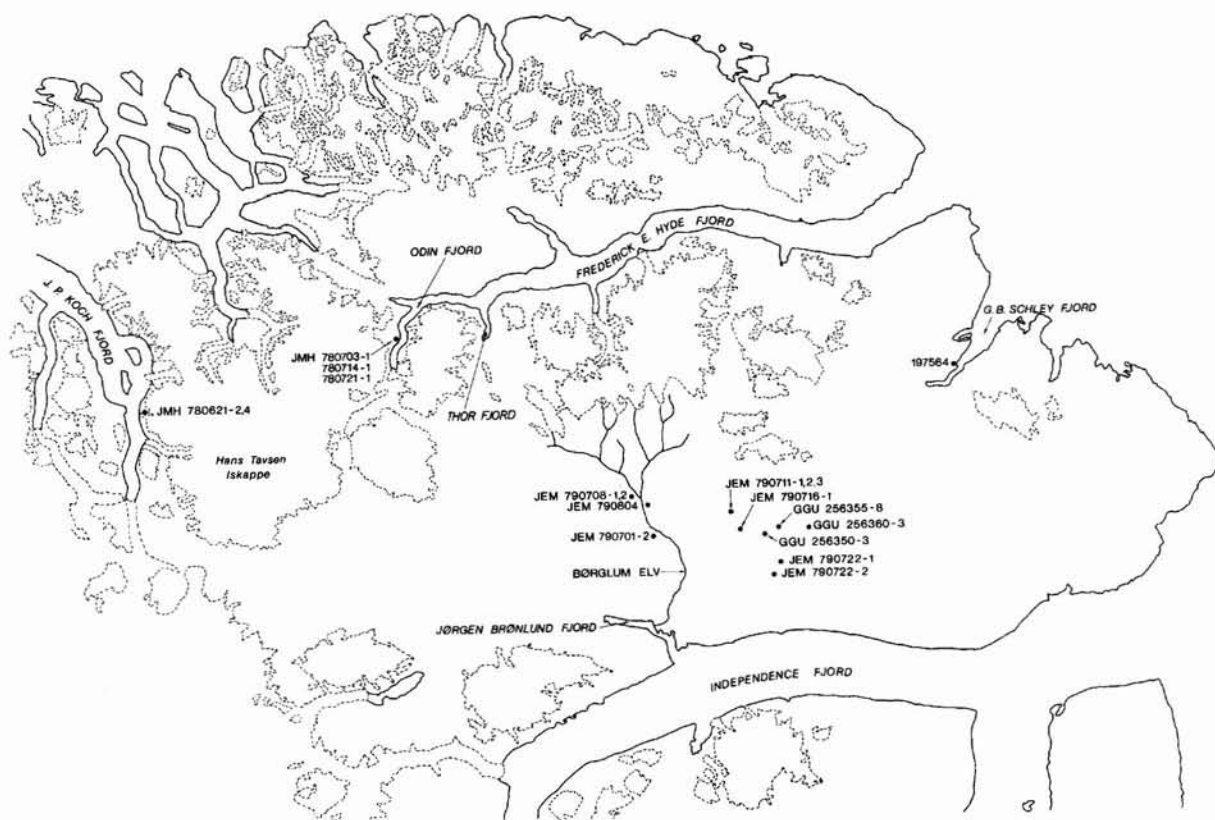


Fig. 3. Geological sections and spot sample localities in Peary Land. Sections are prefixed by the initials of the author (JEM, J. E. Mabillard; JMH, J. M. Hurst). Spot samples have GGU prefix. JMH 780703–1, see Hurst (1984, fig. 32); JMH 780714–1, see Hurst (1984, fig. 9); JMH 780721–1, see Hurst (1984, fig. 8). JEM 790701, see Hurst (1984, fig. 13); JEM 790708–1, see Hurst (1984, fig. 34, in part).

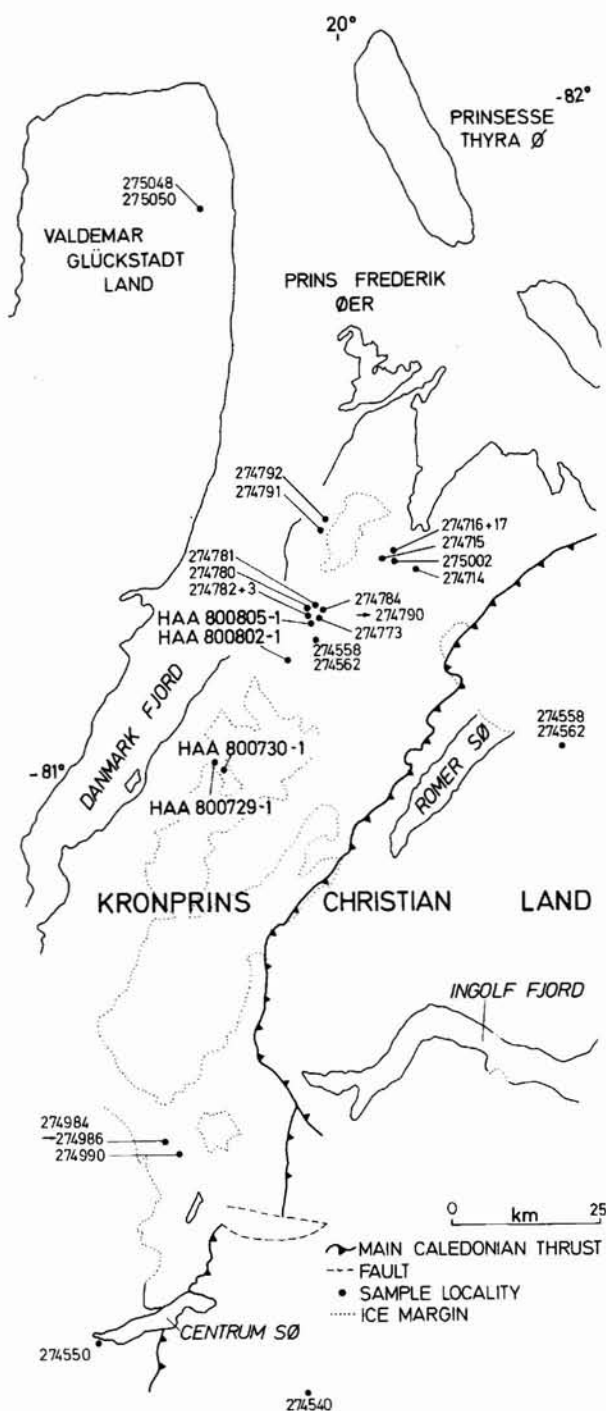


Fig. 4. Section and spot sample localities in Valdemar Glückstadt Land and Kronprins Christian Land. Spot samples are indicated by 6-figure GGU numbers. Section localities with prefix of name of author (HAA, Howard A. Armstrong).

Cephalopods and *Maclurites* occur rarely in the lower part of the formation; the upper part contains coquinas dominated by virgianid brachiopods.

The lower 40–50 m of this formation in Peary Land contain a moderately diverse though sparse conodont fauna which includes *Rhipidognathus symmetricus*, *Aphelognathus pyramidalis*, *Drepanoistodus suberectus*, *Plegagnathus dartoni*, *Oulodus* sp. indet. 1 and *Panderodus* species. This fauna indicates a late Ordovician (Richmondian) age and can be referred to Fauna 12 of Sweet *et al.* (1971).

The succeeding 20–30 m of strata contain only rare *Panderodus* and are followed by *Ozarkodina excavata* and *O. hassi*; both the latter species are indicative of the early Silurian. The Ordovician–Silurian boundary cannot be accurately placed but lies at approximately 65 m above the base of the formation. Strata below this level lacking age-diagnostic species and could correlate with the Gamachian of Anticosti Island (McCracken & Barnes, 1981). The remainder of the Turesø Formation contains only sparse conodonts which typically have long ranges; they are considered, however, to be early to middle Llandovery.

Ymers Gletscher Formation

The Ymers Gletscher Formation (figs 5–7, 10) comprises 25–45 m of pale, thin to medium-bedded, well-laminated limestones, crystalgalaminites and dark, laminated mudstones, suggesting that this formation was deposited in low-energy supratidal to shallow subtidal environments. Virgianid brachiopod coquinas and ostracode wackestones occur rarely and provide the only macrofossil data. Sparse conodonts including *Aspelundia fluegeli* from the type section at Odin Fjord and reference sections by Børglum Elv (figs 5, 6, 10) indicate a middle to late Llandovery age.

Odins Fjord Formation

The Odins Fjord Formation (figs 5–10) is between 200 m and 350 m thick and appears to thicken from south to north in Peary Land. It is characterised by medium to thick-bedded dark weathering skeletal limestones.

Hurst (1984) interpreted the lower part of the formation to be indicative of low-energy shallow subtidal environments; temporary low-energy peritidal environments recur in central and eastern Peary Land (Melville Land Member). In the north, around Odin Fjord and Thor Fjord (fig. 2), low-energy, possibly subphotic environments predominate in the upper part of the formation. Occasionally anoxic bottom conditions occur (Bure Iskappe Member). Detailed sedimentological

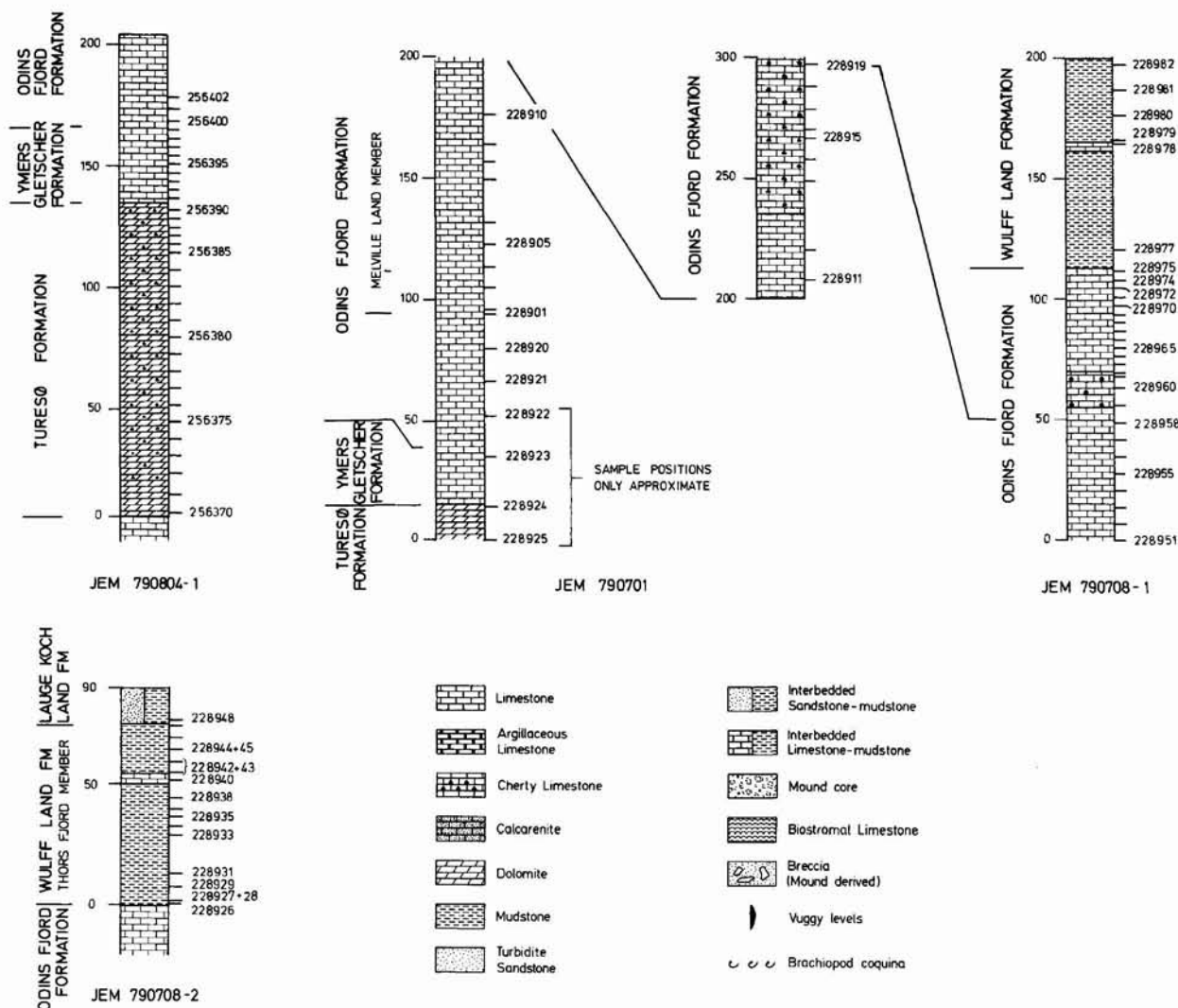


Fig. 5. Generalised section logs for localities in the valley of Børglum Elv, central Peary Land. For location of sections see fig. 3. Legend for all figures.

data are not available for Kronprins Christian Land; the available evidence suggests shallow subtidal depositional environments.

In the type section at Odin Fjord (Hurst 1984, fig. 9) *Virgianella* sp. and *Kulumbella* sp. occur 50–60 m above the base of the formation, suggesting a middle Llandovery age. *Harpidium* occurs 110 m above the base of the formation in a reference section to the north of the type section (Hurst, 1984, fig. 32) and is indicative of the late Aeronian and Telychian stages. Corals 110 m above the base of the formation at Børglum Elv suggest a similar age (Saied, 1979).

Conodonts are generally scarce in this formation, with taxa continuing from the Turesø and Ymers

Gletscher Formations. *Aspelundia fluegeli* occurs 110 m above the base of the formation at Odin Fjord (fig. 10) and suggests a late Llandovery age. The upper part of the formation, however, contains abundant and diverse conodont faunas indicative of the *Pterospathodus celloni* Biozone. In the type section *P. celloni* occurs 2 m below the top of the formation; in sections to the south this species first appears progressively lower in the formation (5 m below the top at southern Odin Fjord, 15 m at Børglum Elv and 25 m in eastern Peary Land). *P. celloni* has also been recorded approximately 1 m below the top of the formation at G. B. Schley Fjord (sample GGU 197564, Table 3). This evidence may suggest that the top of the Odin Fjord Formation in Peary Land is

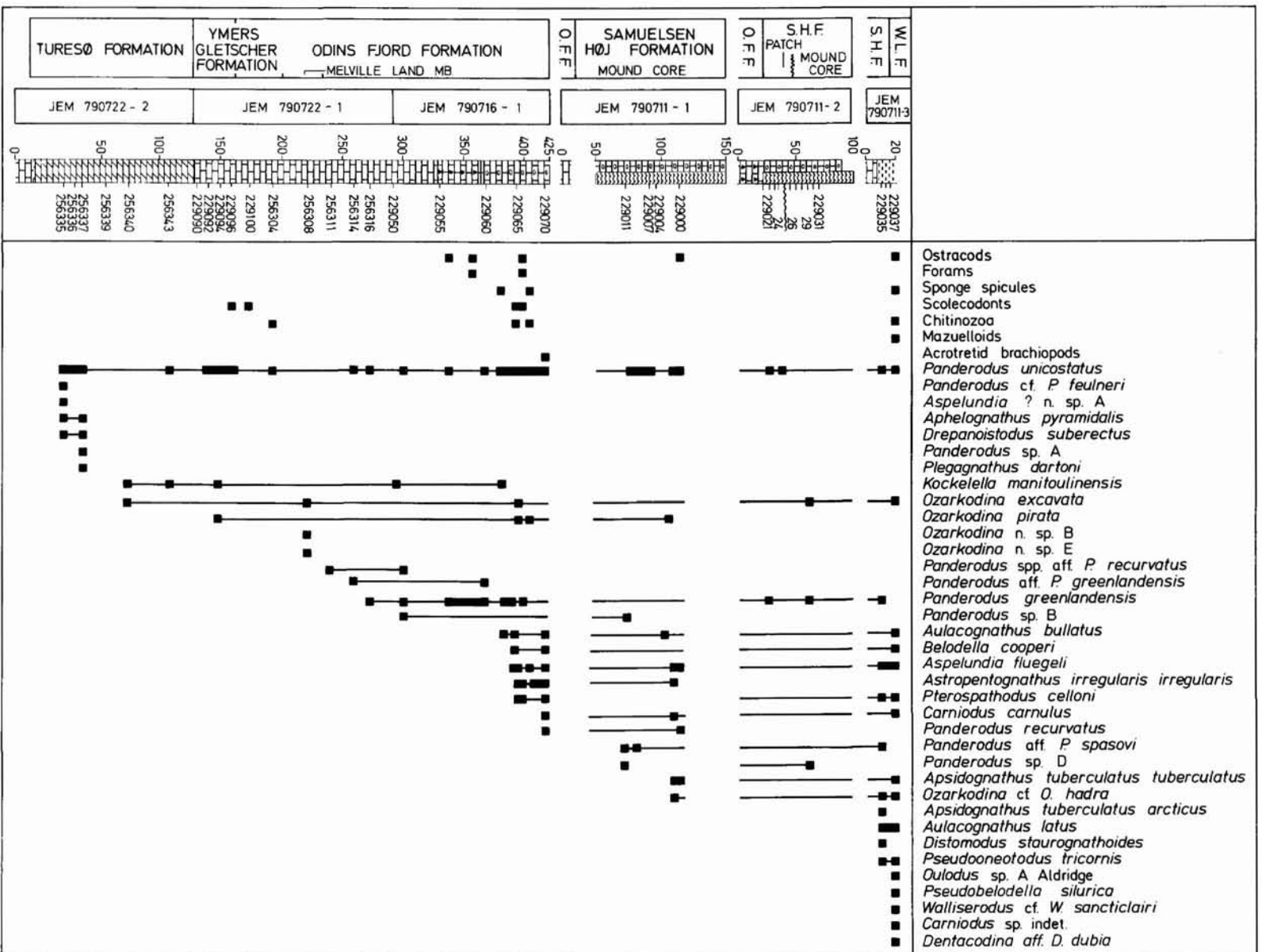
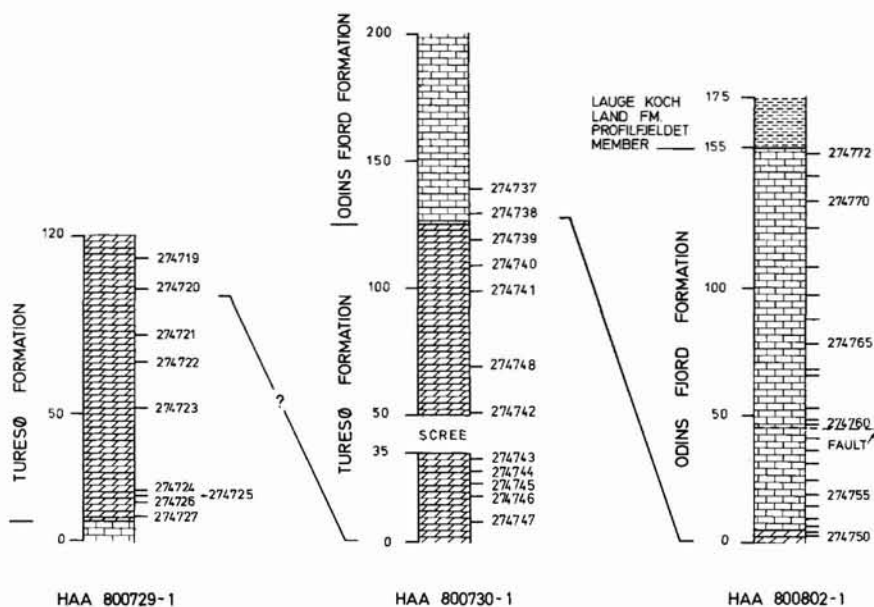


Fig. 7. Generalised section logs and conodont ranges for sections in eastern Peary Land. For location of samples see fig. 3; for legend see fig. 5. O. F. F., Odins Fjord Formation; S. H. F., Samuelsen Høj Formation; W. L. F., Wulf Land Formation.

Fig. 8. Generalised section logs and location of conodont samples in Kronprins Christian Land. See fig. 4 for localities and fig. 5 for legend.



diachronous, younging south (refer also to Hurst, 1984, p. 46).

Other species typical of the *Pterospirifer celloni* Biozone include *P. pennatus*, *Aulocognathus bullatus*, *Astropentagnathus irregularis irregularis*, *Apsidognathus tuberculatus*, *Aspelundia fluegeli*, *Distomodus staurognathoides*, *Belodella cooperi*, *Walliserodus curvatus* and several species of *Panderodus*. *A. bullatus* occurs some 30 m below the top of the formation (in GGU sample 274769) in Kronprins Christian Land (fig. 9), but with no other *P. celloni* Biozone species. *P. celloni* first occurs 20 m below the top of the formation along with a moderately diverse fauna including *A. bullatus*, *Ast. irregularis irregularis*, *Asp. fluegeli* and *Panderodus* species. This first appearance correlates well with those at Børglum Elv and eastern Peary Land suggesting little diachroneity from Børglum Elv south-east to Kronprins Christian Land.

Melville Land Member

This member is between 15 m and 30 m thick thinning from east to west and from south to north (Hurst, 1984). The Melville Land Member is absent at Odin Fjord and G. B. Schley Fjord and has not been described from Kronprins Christian Land or Valdemar Glückstadt Land. It contains rare ostracodes and brachiopods (Christie & Peel, 1977) considered to be middle Aeronian in age. The conodont fauna from this member is extremely poor yielding rare *Ozarkodina excavata*, *O.*

n. sp. B and *O.* n. sp. E from East Peary Land (figs 5, 6, 7).

Bure Iskappe Member

This member consists of characteristically thin to medium bedded skeletal limestones suggestive of deposition in low-energy, possibly anoxic, deep-shelf environments (Hurst, 1984).

Conodonts from Odin Fjord (fig. 10) and the brachiopod *Harpidium* sp. from the middle of the formation in its type section suggests middle to late Llandovery (Aeronian–Telychian).

Samuelsen Høj Formation

Hurst (1984) erected this formation to include the isolated carbonate mounds of Peary Land, Valdemar Glückstadt Land and Kronprins Christian Land. This formation does not occur west of central Peary Land. Isolated mounds vary in thickness from 50 m to 300 m. Core facies consist of massive lime mudstone and flank deposits of thick-bedded skeletal limestones. In Kronprins Christian Land the carbonate mound complexes are embedded in thinly-bedded black lime mudstones. The mounds were deposited in high-energy environments well within the photic zone, while the surrounding mudstones possibly represent hemipelagic deposition after mound development had terminated (Hurst, 1984).

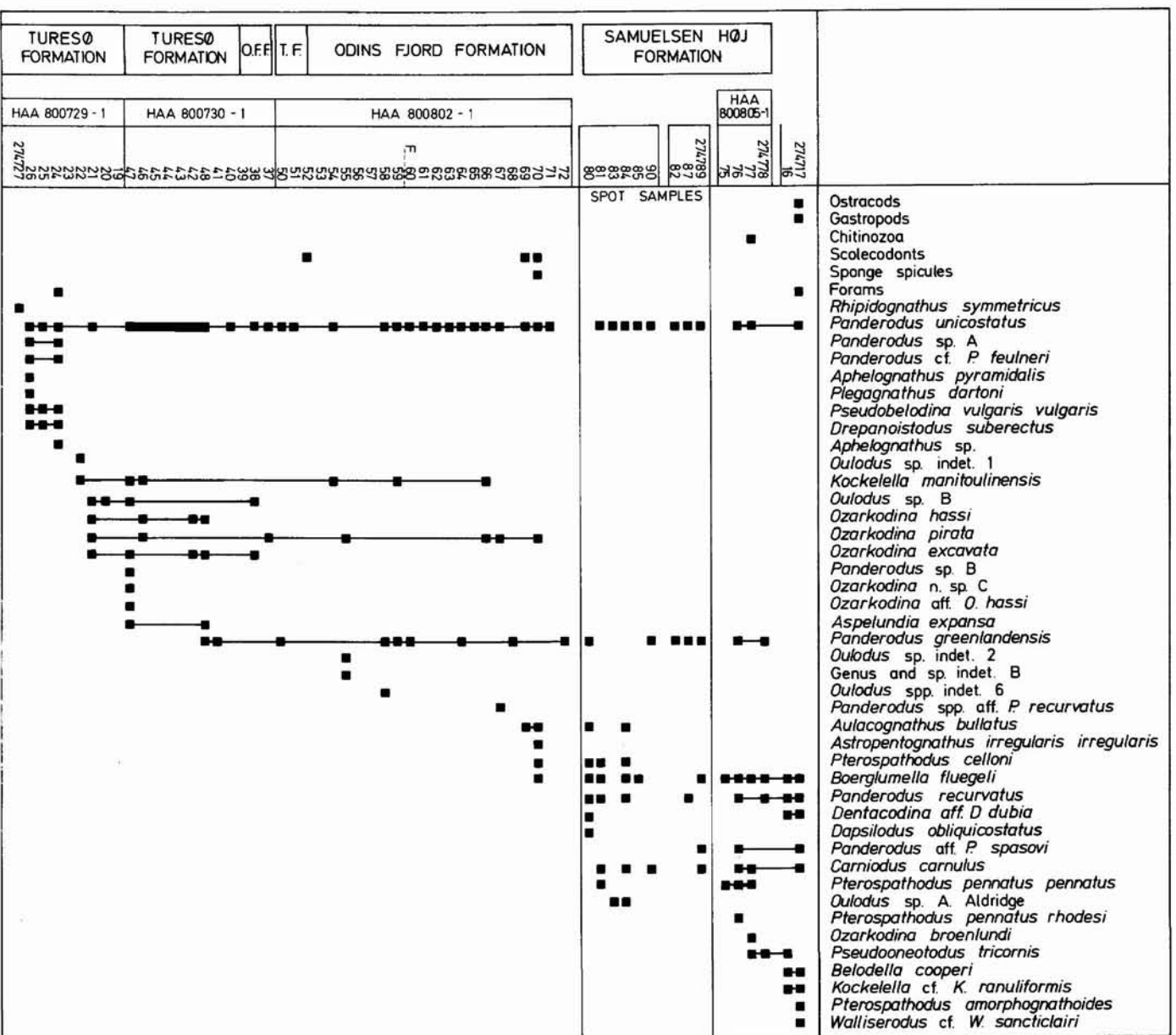
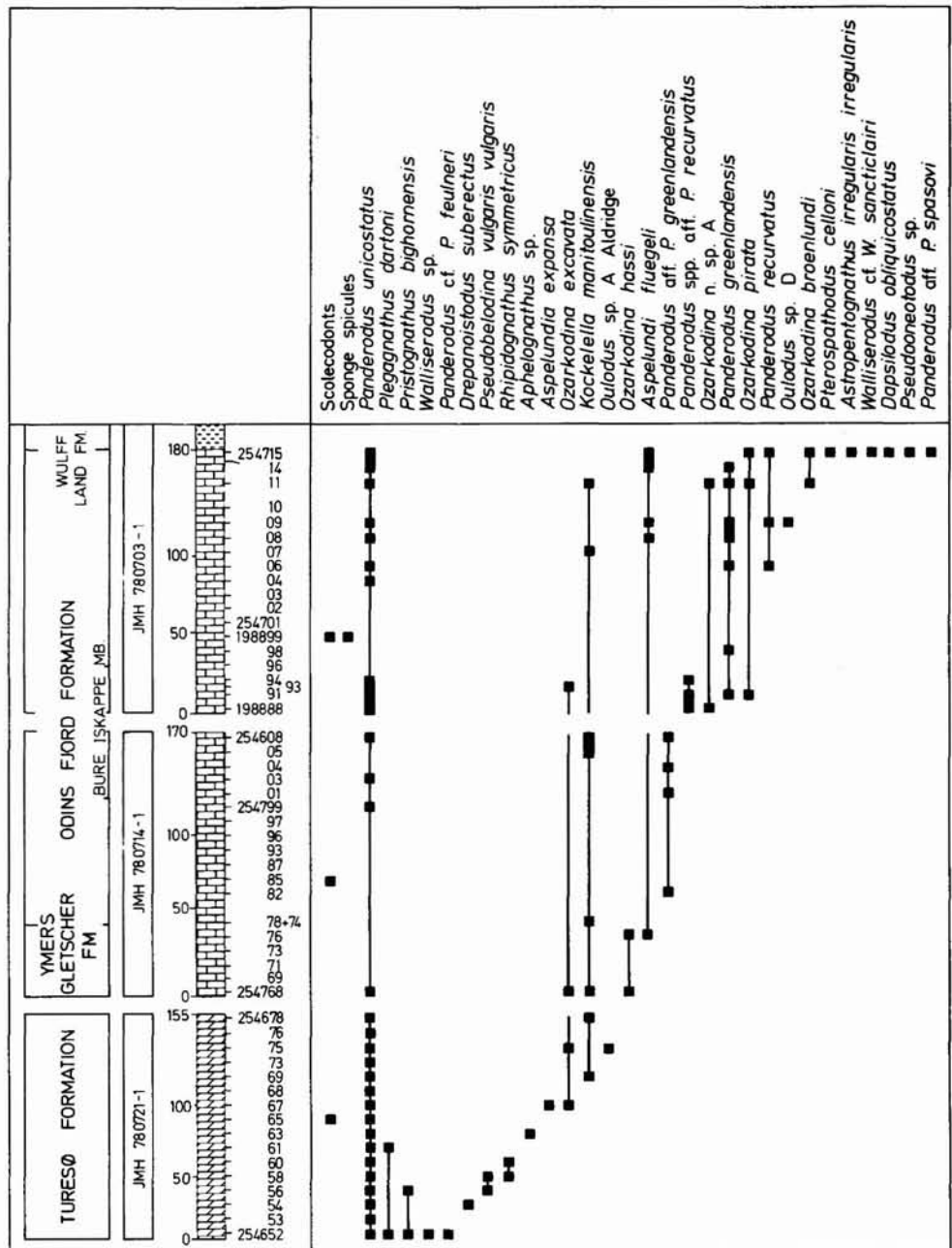


Fig. 9. Conodont range chart for Kronprins Christian Land. O. F. F., Odins Fjord Formation; T. F. Turesø Formation; F. fault. For localities see figs 4, 8.

Mounds from Peary Land and Kronprins Christian Land have yielded poor conodont collections indicative of the *Pterospathodus celloni* Biozone (figs 7, 9). Taxa are identical to those found in the Odins Fjord Formation below. The black limestones overlying some mounds in Kronprins Christian Land also contain an

Fig. 10. Generalised section logs and conodont ranges near Odin Fjord, Peary Land (fig. 3). See fig. 5 for legend.



abundant and diverse late *P. celloni* Biozone to lower *P. amorphognathoides* Biozone fauna. It would appear that the Samuelsen Høj Formation was deposited in an extremely short period of time within the *P. celloni* Biozone.

Peary Land Group

Wulff Land Formation

This formation (figs 5, 6) is 12–300 m thick and dominated by black mudstone, with subordinate siltstone and sandstone, considered to have been deposited in a lower slope and basin-plain margin setting (Hurst & Surlyk, 1982).

Thors Fjord Member

The Thors Fjord Member (12–150 m) is characterised by mudstone with starved ripples, thin fine sandstone or siltstone and turbidites (Hurst & Surlyk, 1982). Graptolites from the south of the outcrop suggest that this member ranges in age from the late Llandovery *spiralis* Biozone to the middle Wenlock *flexilis* or *linnarssoni* Biozones; in the north the member is contained within the late Llandovery *spiralis* Biozone (Hurst & Surlyk, 1982). In Peary Land conodonts from thin argillaceous limestone beds within the lowest 5 m of this member contain *Pterospathodus celloni*, *Apsidognathus tuberculatus arcticus*, *Aulocognathus latus*, *Distomodus staurognathoides*, *Pseudooneotodus tricornis*, *Pseudobellodella silurica*, *Walliserodus* cf. *W. sancticlairi* and *Denticodina* aff. *D. dubia*.

Lauge Koch Land Formation

The Lauge Koch Land Formation (850 – c. 1500 m) extends right across North Greenland from Kronprins Christian Land in the east to northern Hall Land in the west (Hurst & Surlyk, 1980; Larsen & Escher, 1985, 1987). In Kronprins Christian Land and north-eastern Valdemar Glückstadt Land, the formation rests on Silurian platform carbonates, farther to the east it overlies the Wulff Land Formation. The formation is dominated by sandstone and siltstone turbidites separated by mudstones.

Profilfjeldet Member

The Profilfjeldet Member is restricted to Kronprins Christian Land and Valdemar Glückstadt Land and includes discontinuous black mudstone and siltstone with the overlying sandstone turbidites (Hurst & Surlyk, 1982).

In north-east Kronprins Christian Land graptolites date the base of this member as *griestoniensis* Biozone or very low *spiralis* Biozone (Telychian). In western Kronprins Christian Land graptolites of the *spiralis* Biozone occur and in Valdemar Glückstadt Land graptolites of the late Llandovery *sakmaricus-laqueus* Biozone occur close to the base of this member (Hurst & Surlyk, 1982). Hurst & Surlyk thus concluded that the base of the Profilfjeldet Member was diachronous, oldest in the east, younging slightly northwards and westwards. Graptolite data from Lane (1972) indicate that the base of this member in southern Kronprins Christian Land is middle Wenlock; thus the member also youngs to the south.

Two samples collected from thin limestones in the

lower part of the Profilfjeldet member contained abundant and diverse conodont faunas. The lowest (GGU sample 274716) yields a *Pterospathodus celloni* Biozone fauna with, unusually, *Belodella cooperi* and *Kockelella* cf. *K. ranuliformis*. The upper sample (GGU 274717), collected 0.5 m higher, yields a *P. amorphognathoides* Biozone fauna with *P. amorphognathoides* and *Walliserodus* cf. *W. sancticlairi* (fig. 9). GGU sample 275048 from Valdemar Glückstadt Land (again from the lower part of the Profilfjeldet Member) contains *P. pennatus rhodesi* and *P. amorphognathoides*.

J. P. Koch Fjord and Wulff Land

Only scattered reconnaissance data were available from this general area of North Greenland, although subsequent field work during 1984–85 has permitted a full evaluation of the Upper Ordovician and Silurian sequences (Larsen & Escher, 1985, 1987; Sønderholm *et al.*, 1987; Smith *et al.*, 1989; Higgins *et al.*, in press).

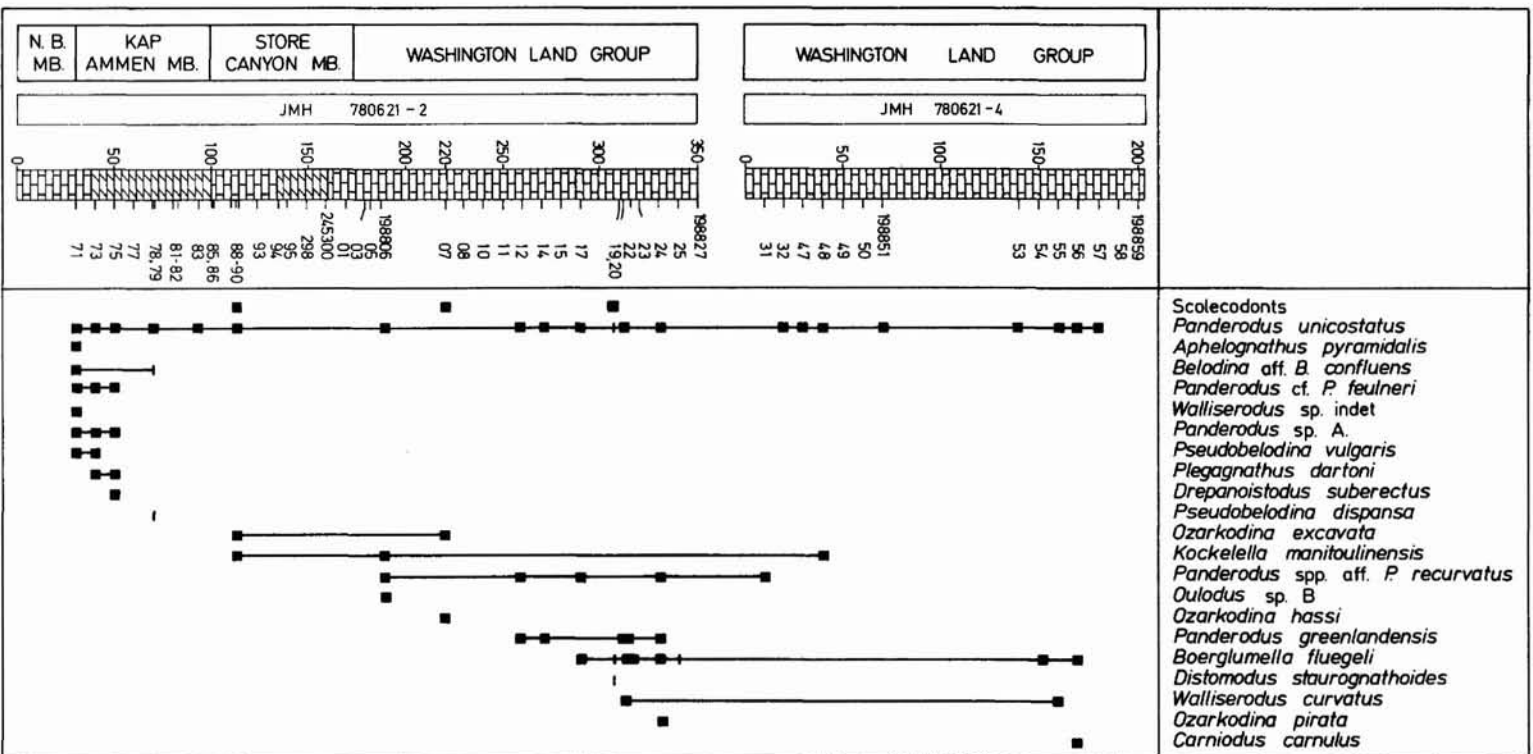
J. P. Koch Fjord

A full section through strata of the Franklinian Basin is seen in the walls of the prominent fjord, J. P. Koch Fjord, which marks the western extremity of Peary Land (fig. 3). Hurst (1979), on whose collections of samples the following comments are based, formally divided uppermost Ordovician to Upper Silurian carbonates in the southern fjord area into three formations which have been correlated by Sønderholm *et al.* (1987) with the formal lithostratigraphic schemes employed in Washington Land and Peary Land. Lithological descriptions are given by Hurst (1979), see also Sønderholm *et al.* (1987).

The J. P. Koch Fjord region is a transition region in terms of stratigraphy of the Morris Bugt Group, and strata can be assigned either to the units recognised further east in Peary Land (Børglum River and Turesø Formations) or to those recognised in more westerly regions (Kap Jackson and Aleqatsiaq Fjord Formations). Although the boundary between the latter two formations has lost its clarity at J. P. Koch Fjord on account of the easterly disappearance of the intervening Cape Calhoun Formation, they can be distinguished on outcrop near the section described by Hurst (1979; see present figs 3, 11). Thus, in a recent map compilation, the western terminology of Kap Jackson and Aleqatsiaq Fjord Formations has been employed as far east as Hans Tavsens Iskappe (J. S. Peel, personal communication, 1988).

The Børglum River Formation of Peary Land east of Hans Tavsens Iskappe is thus equivalent to the Kap

Fig. 11. Generalised section logs and conodont ranges at J. P. Koch Fjord, westernmost Peary Land (fig. 3). N. B. MB, Newman Bugt Member of the Aleqatsiaq Fjord Formation. See fig. 5 for legend.



Jackson Formation and the overlying lower member of the Aleqatsiaq Fjord Formation (AF1 of S nderholm *et al.*, 1987; Newman Bugt Member of Smith *et al.*, 1989).

In the following section, the original units of Hurst (1979) are re-interpreted in terms of this more recently available stratigraphic information.

Aleqatsiaq Fjord Formation

Kap Ammen Member

This corresponds to the Dolomite formation of Hurst (1979), and unit AF2 of S nderholm *et al.* (1987). It consists of some 70 m of thin to medium-bedded dark grey, limy dolomite and conformably overlies the Newman Bugt Member (unit AF1) of the Aleqatsiaq Fjord Formation. The lower part contains a moderately diverse fauna including *Rhipidognathus symmetricus*, *Aphelognathus pyramidalis*, *Belodina* aff. *B. confluens*, *Pseudobelodina vulgaris vulgaris*, *Plegagnathus dartoni*, *Drepanoistodus suberectus* and *Panderodus* species (fig. 11). The presence of *Pl. dartoni* and *Ps. vulgaris vulgaris* indicates a middle to late Richmondian age (Sweet, 1979).

The upper 25 m yield only rare *Panderodus unicostatus*. Macrofossils include recrystallised tabulate corals (*Favosites* and *Halysites*), stromatoporoids and orthocone cephalopods.

Store Canyon Member

This variable sequence of fossiliferous limestones with subordinate limy dolomites is 80 m thick and was referred to the Dark limestone formation by Hurst (1979). The basal beds contain coquinas of virgianid brachiopods, along with tabulate corals, cephalopods and stromatoporoids. A bed approximately 5 m from the base of the formation contains *Maclurites*, indicating an Ordovician age (J. S. Peel, personal communication, 1987). *Ozarkodina excavata* and *Kockeella manitoulinensis* occur 10 m above the base and indicate a Silurian age. The juxtaposition of these faunas restricts the Ordovician–Silurian boundary to within 5 m of strata, at the top of the barren horizon (a horizon found throughout Peary Land). If Fauna 12 as developed in North Greenland is equivalent in age to the Fauna 12 of Sweet *et al.* (1971), then the barren horizon may be coeval with the Gamachian Stage, defined on Anticosti Island (McCracken & Barnes, 1981).

The upper part of the formation is barren of cono-

donts though stromatoporoids and large ostracodes occur.

Washington Land Group

Strata placed here equate with the 'White limestone formation' of Hurst (1979). Hurst (1979) recorded rare favositids and *Harpidium* sp., together with brachiopods, trilobites, ostracodes and corals from near the top of these 380 m of homogeneous light grey limestone. GGU sample 198807 close to the base contains *Ozarkodina hassi* suggesting an early to middle Llandovery age.

The upper 100 m contain relatively abundant conodonts including *Aspelundia fluegeli*, *Distomodus staurogathides*, *Ozarkodina pirata*, *Panderodus greenlandensis*, *P. unicostatus*, *Walliserodus curvatus* and *Ozarkodina* n. sp. B., *D. staurogathoides* is not known from pre-mid Aeronian strata (fig. 24) *Carniodus carnulus* occurs 20 m from the top and indicates a probable Telychian age. From these data it appears that the 'White limestone formation' of the J. P. Koch Fjord area can be directly correlated with typical Washington Land Group as developed in Washington Land and the Odins Fjord Formation in Peary Land (see also S nderholm *et al.*, 1987). Transition to clastic deposition occurs within the Telychian.

Wulff Land

The lithostratigraphy of the area around 'Apollo S ' in eastern Wulff Land (fig. 2) was first described by Hurst & Peel (1980). The basinal clastic sequence has subsequently been assigned to the Peary Land Group (Hurst & Surlyk, 1982; Larsen & Escher, 1985, 1987) while the upper part of the Silurian carbonate platform sequence is now known to be part of the Washington Land Group (S nderholm *et al.*, 1987). The latter, however, was only informally subdivided into mapping units east of Washington Land by S nderholm *et al.* (1987) and hence the original informal stratigraphic scheme of Hurst & Peel (1979) is used in this paper. Descriptions of the regional setting of the units can be found in Hurst (1980a), S nderholm *et al.* (1987) and Higgins *et al.* (in press).

Aleqatsiaq Fjord Formation

The Aleqatsiaq Fjord Formation which straddles the Ordovician–Silurian boundary was defined in Washington Land (Peel & Hurst, 1980) where it reaches a thickness of 360 m in the environs of Bessels Fjord (fig. 14). Subsequently the formation has been divided into three units (AF1–3) by S nderholm *et al.* (1987) which were

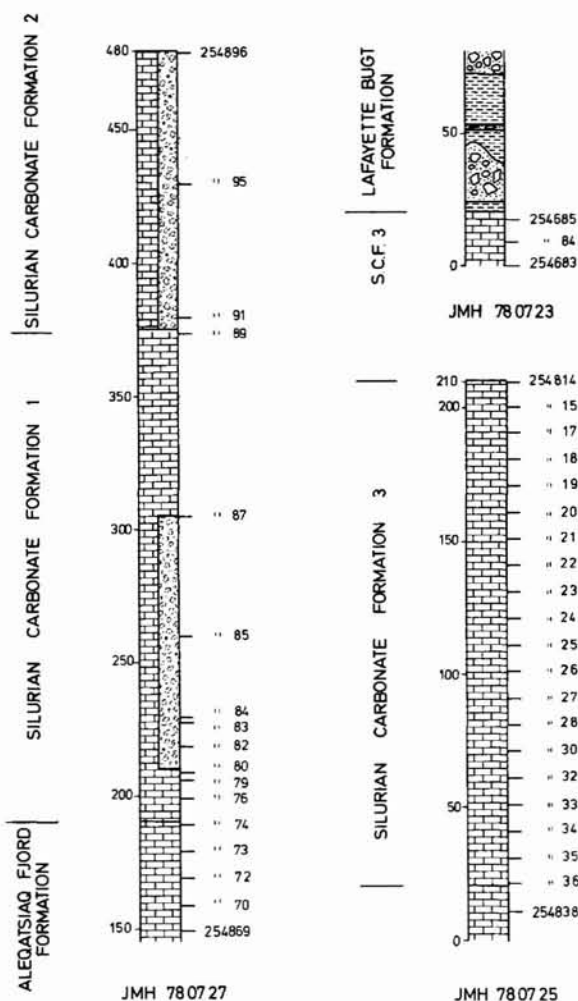


Fig. 12. Generalised section logs and conodont sample localities for sections north of Apollo Sø in Wulff Land (figs 1, 2). S. C. F. 3, Silurian carbonate formation 3. For legend see fig. 5.

given the names Newman Bugt, Kap Ammen and Store Canyon Members by Smith *et al.* (1989). These members can be followed across North Greenland and have also been recognised in Wulff Land where the formation has a measured thickness of 320 m at the northern end of 'Apollo Sø' (M. Sønderholm, personal communication, 1987). This figure is at variance with the thickness of 130 m recorded some kilometres north of 'Apollo Sø' by Hurst & Peel (1979). Examination of their figure 10, however, where the Aleqatsiaq Fjord Formation is exposed on an 850 m high hillside, shows that the 130 m must be an underestimate and that the formation is approximately 250 m thick at this locality. This means that the stratigraphical position of samples within the formation (fig. 12) is somewhat obscured, and that results must be treated with care.

The formation consists of generally dark weathering, mottled, skeletal limestones which are patchily dolomitised. Hurst & Peel (1979) recorded only a poor macrofauna from 'the upper part of the formation' consisting of tabulate corals, actinocerid cephalopods and *Maclurites*.

A single sample 30 m from the top of the formation contains *Belodina* aff. *B. confluens*, considered to be late Ordovician in age. A 10 m section with only *Panderodus unicostatus* follows; *Ozarkodina* n. sp. C and *Walliserodus curvatus*, 20 m from the top indicate an early Silurian age. Allowing for minor regional diachronism, the upper Aleqatsiaq Fjord Formation in Wulff Land correlates with that in Washington Land and Hall Land.

Washington Land Group

'Silurian carbonate formation 1'

This unit conformably overlies the Aleqatsiaq Fjord Formation and consists of a variable sequence of limestones and dolomites, approximately 185 m thick. It corresponds to the combined units WG1 and WG2 of Sønderholm *et al.* (1987); the oldest level of carbonate build-ups occurs within this formation (fig. 12).

The presence of *Aspelundia expansa* in GGU sample 254879, 20 m above the base of the formation and directly beneath the carbonate build-up, suggests a pre-early Aeronian age for the lower part of this formation which yields poor faunas, with the upper 140 m barren. *Ozarkodina hassi* occurs in GGU sample 254883, 42 m above the base, suggesting a pre-Telychian age for this part of the formation.

The conodont evidence suggests this mound complex was in part coeval with those found in the Adams Bjerg Formation, Pentamerus Bjerge Formation and Hauge Bjerge Formation (Kap Independence Member) of Washington Land.

'Silurian carbonate formation 2'

This unit consists of a variable sequence of limestone up to 180 m thick, containing a carbonate build-up complex (Hurst & Peel, 1979); it is referred to unit WG3 of Sønderholm *et al.* (1987). The carbonate mound originates close to the base of the formation and reaches 100 m in thickness in its core facies. Along strike and towards the south the mound complex grades into a monotonous sequence of thin-bedded, dark weathering, black, nodular lime mudstones. The formation only contains a poor macrofauna of disarticulated

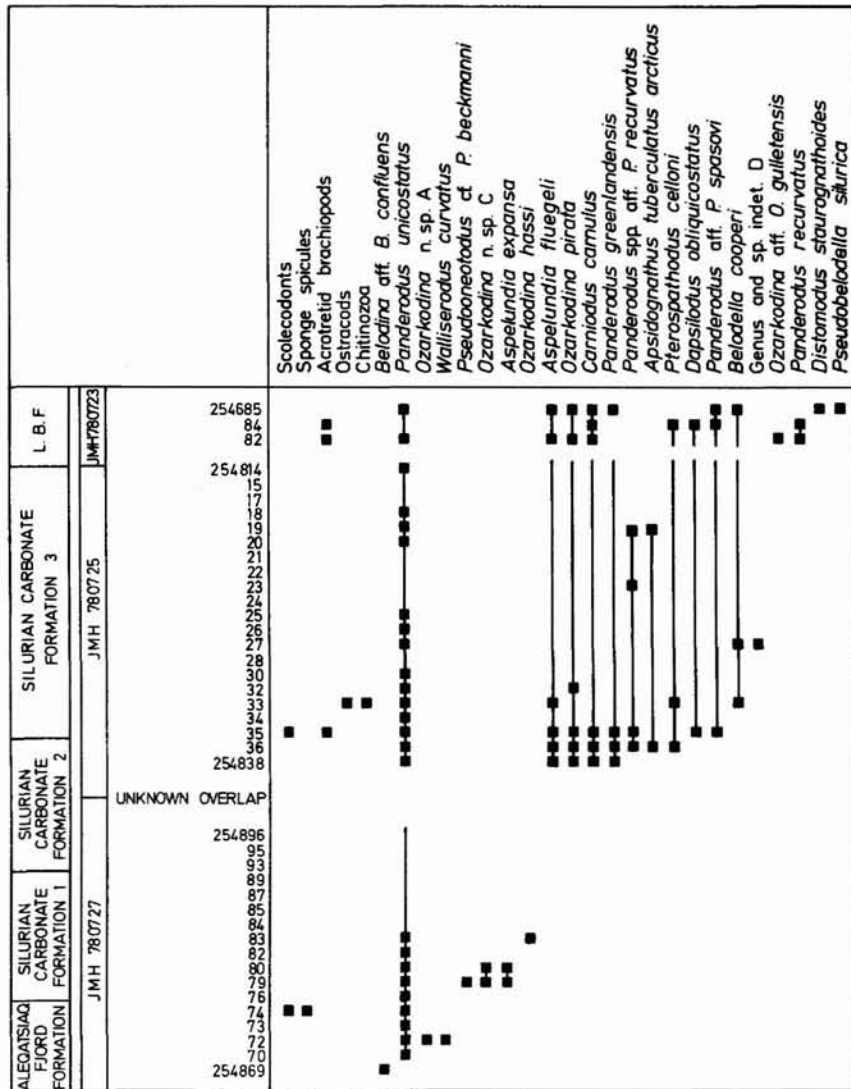


Fig. 13. Conodont range chart for sections north of Apollo SØ in Wulff Land (see figs 1, 2, 12 and fig. 5 for legend). L. B. F., Lafayette Bugt Formation; this is the shale and breccia formation of Hurst & Peel (1979, figs 9, 10), termed the Lafayette Bugt Formation by Hurst & Surlyk (1982).

pentamerids (*Harpidium* sp. ?) stromatoporoids and tabulate corals, suggesting a middle Aeronian age.

The unit is barren of conodonts until the top, where GGU sample 254836 contains a possible *Pterospathodus celloni* Biozone consisting of *Carniodus carnulus*, *Aspelundia fluegeli*, *Ozarkodina pirata* and *Panderodus greenlandensis* (fig. 13). *P. celloni* does not occur until 5.5 m above this sample, suggesting that the base of the *P. celloni* Biozone in Wulff Land occurs at or close to the boundary between Silurian carbonate formations 2 and 3.

'Silurian carbonate formation 3'

Silurian carbonate formation 3 of Hurst & Peel

(1979), equivalent to unit WG4 of SØnderholm *et al.* (1987), consists of a monotonous sequence of massively bedded skeletal limestones and mudstones some 200 m thick. The base of the formation is marked by a thick intraformational conglomerate. The formation contains a rich macrofauna of trilobites, corals, stromatoporoids, brachiopods and crinoid debris, suggested by Hurst & Peel (1979) to be of Aeronian or Telychian aspect.

Conodonts are moderately abundant and the whole formation yields a standard *Pterospathodus celloni* Biozone fauna (fig. 13). Conodonts are particularly abundant and diverse at the top of the formation in section JMH 780723 (figs 12, 13). The presence of *Pseudobelodella silurica* in GGU sample 254685, suggests a late *Pterospathodus celloni* Biozone age (latest Telychian).

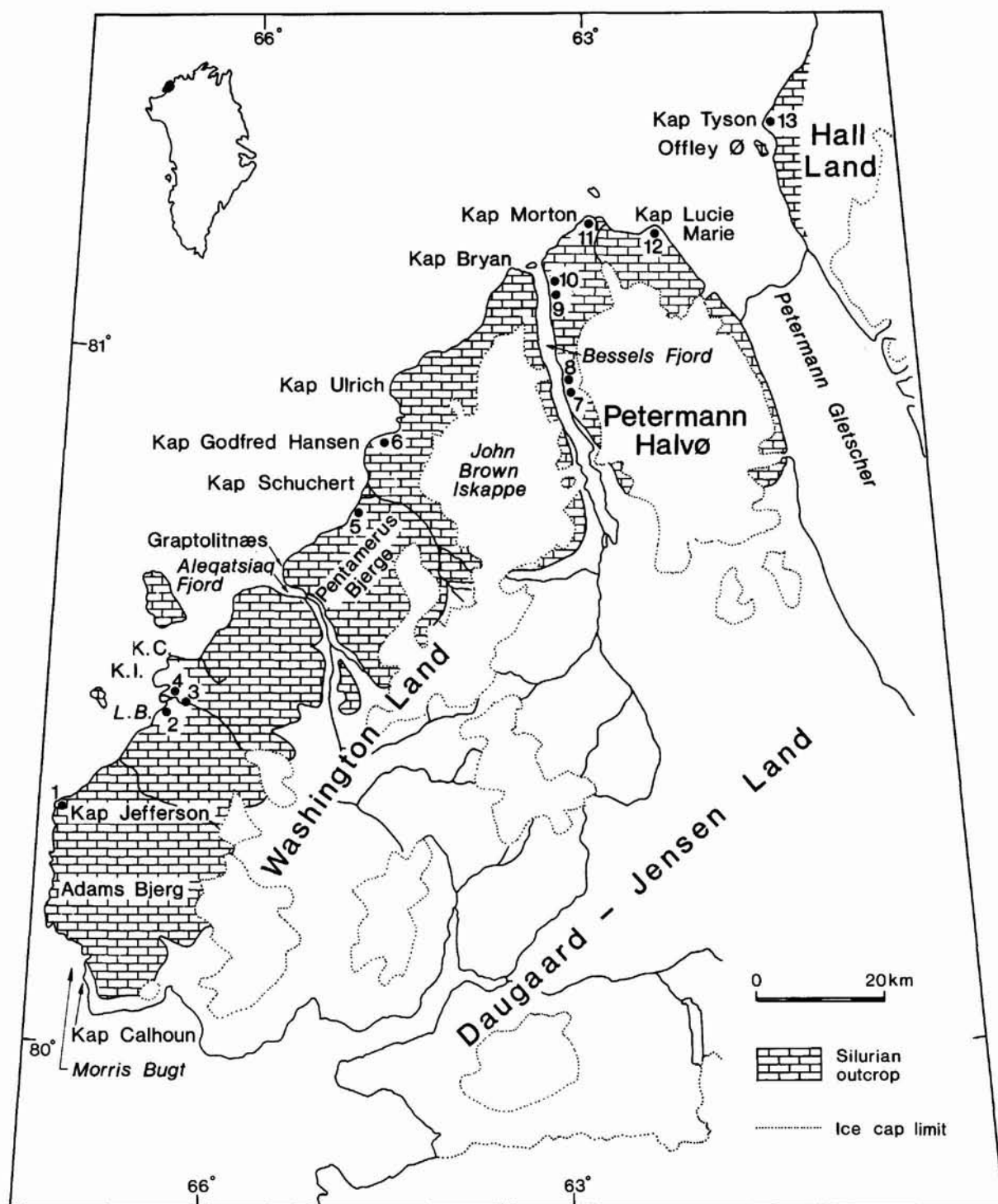


Fig. 14. Conodont localities in Washington Land and western Hall Land. Locality numbers refer to sections in figs 16-20. K. I., Kap Independence; K. C., Kap Constitution; L. B., Lafayette Bugt.

Washington Land and western Hall Land

Silurian sediments in Washington Land and western Hall Land (fig. 14) were deposited in two major environments (Hurst, 1980b). Platform carbonates are referred to the Morris Bugt Group (Peel & Hurst, 1980; Smith *et al.*, 1989) and the Washington Land Group (Hurst, 1980b), while slope deposits are referred to the Peary Land Group (Hurst, 1980b). Facies changes within and between these environments are complex and abrupt (fig. 15).

All formations, except the Pentamerus Bjerge and Kap Lucie Marie Formations, have yielded conodonts. Generally conodonts from this region are better preserved (Conodont Alteration Index 1–2) than those from Peary Land, but the majority of samples are small and species diversity is low in both environments. The stratigraphical distribution of conodont species in this region is summarised in fig. 16.

Morris Bugt Group

Aleqatsiaq Fjord Formation

This is the youngest formation in the predominantly Ordovician Morris Bugt Group. Hurst (1980b) considered these strata to represent deposition on an open marine, shallow shelf. Lithologically the formation consists of dolomitised massive lime mudstones and wack-

estones. Hurst (1980b) reported Ordovician conodont species identified by R. J. Aldridge to within 40 m of the top of this formation at Aleqatsiaq Fjord and at Kap Independence.

At Kap Jefferson (figs 14, 17) GGU samples 216719–29 within the upper Aleqatsiaq Fjord Formation (conformably beneath the Adams Bjerg Formation) contain *Aspelundia fluegeli*, *Dapsilodus obliquicostatus*, *Oulodus* spp., *Walliserodus bicostatus* and *Panderodus* spp., a fauna indicating an middle Aeronian age. Elsewhere the top of the Aleqatsiaq Fjord Formation lies close to the Rhuddanian–Aeronian boundary (fig. 23), suggesting either misidentification of this formation at Kap Jefferson or unusual local circumstances which allowed the continuation of Aleqatsiaq Fjord Formation 'facies' into the Aeronian.

Washington Land Group

Adams Bjerg Formation

The Adams Bjerg Formation (130–200 m, fig. 17) consists predominantly of white, creamy dolomite with stromatolitic laminae. At Kap Jefferson a mound-like build-up is developed, from the top of which Hurst (1980b) reported a single specimen of *Virgiana* sp., considered a pre-middle Aeronian form. The formation contains only undiagnostic *Panderodus unicostatus*. *Aspelundia fluegeli* in the underlying Aleqatsiaq Fjord Formation suggests a post middle Aeronian age.

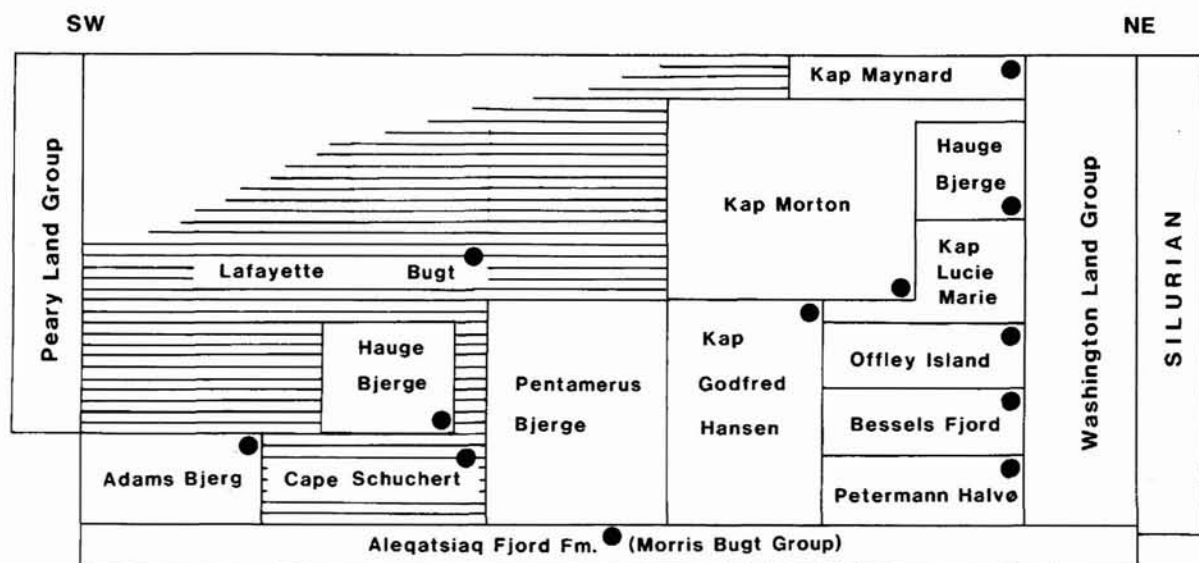


Fig. 15. Silurian stratigraphy in Washington Land and western Hall Land. Formations yielding conodonts are indicated by filled circles (from Peel, 1982, after Hurst, 1980b).

SECTION	LOCALITY	FORMATION - MEMBER	SAMPLE NUMBERS	Conodonts
13	HAUGE BJERGE FORMATION CAPE TYSON MBR		242909 07	<i>Apsidognathus tuberculatus tuberculatus</i> <i>Apsidognathus tuberculatus arcticus</i> <i>Astrapignathus irregularis irregularis</i> <i>Aulacognathus bullatus</i> <i>Aulacognathus latus</i> <i>Belodella cooperi</i> <i>Aspelundia fluegeli</i> <i>Aspelundia expansa</i> <i>Aspelundia ? n. sp. B</i> <i>Carniolus carnulus</i> <i>Dapsilodus obliquicostatus</i> <i>Decarionus fragilis</i> <i>Distomodus staurognathoides</i> <i>Distomodus n. sp.</i> <i>Kockellella manuilinensis</i> <i>Oulodus sp. A</i> <i>Oulodus sp. C</i> <i>Oulodus spp. indet. 2</i> <i>Oulodus spp. indet. 7</i> <i>Oulodus spp. indet. 8</i> <i>Ozarkodina braenlundii</i> <i>Ozarkodina excavata</i> <i>Ozarkodina aff. O. guileletensis</i> <i>Ozarkodina cf. O. hadra</i> <i>Ozarkodina pirata</i> <i>Panderodus cf. P. feulneri</i> <i>Panderodus greenlandensis</i> <i>Panderodus aff. P. greenlandensis</i> <i>Panderodus unicosatus</i> <i>Panderodus aff. P. unicosatus</i> <i>Panderodus recurvatus</i> <i>Panderodus spp. aff. P. recurvatus</i> <i>Panderodus aff. P. spasovi</i> <i>Pseudobelodella ? silurica</i> <i>Pseudooneotodus cf. P. beckmanni</i> <i>Pseudooneotodus bicornis</i> <i>Pseudooneotodus tricornis</i> <i>Pseudooneotodus n. sp.</i> <i>Pterospiriferus amorphognathoides</i> <i>Pterospiriferus celloni</i> <i>Pterospiriferus pennatus pennatus</i> <i>Denticodina aff. D. dubia</i> <i>Walliserodus bicostatus</i> <i>Walliserodus curvatus</i> <i>Walliserodus cf. W. sancticlairi</i> <i>Acrotreta brachiopods</i> <i>Mazuelloids</i> <i>Ostracods</i> <i>Sponge spicules</i> <i>Forams</i> <i>Scolecodonts</i> <i>Chitinozoa</i> <i>Thelodonts</i>
13	LAFAYETTE BUGT FM		242894 92 90 86 85 83 82	
13	OFFLEY ISLAND FORMATION		242879 77 75 73 70 69 68 67 66 60	
12	KAP MORTON FORMATION KAP LUCIE MARIE (not sampled) OFFLEY ISLAND FORMATION		242857 47 44 42 41 37 36 33	
11	KAP MORTON FORMATION		242856 55 54 53 52 50 49 46	
7	BESSELS FJORD FM		200379	
8	BESSELS FJORD FORMATION PETERMANN HALVØ FORMATION		200374 69 68 65 64	
10	KAP MAYNARD FORMATION KAP MORTON FM		211915 13 200400	
9	OFFLEY ISLAND FORMATION BESSELS FJORD FORMATION		200396 94 93 92 91 90 89	
6	KAP GODFRED HANSEN FORMATION		242915 14 11	
3	HAUGE BJERGE FM. KAP INDEPENDENCE MBR		216822 21	
2	LAFAYETTE BUGT FM		216778 74 73 72	
4	HAUGE BJERGE FM. KAP INDEPENDENCE MBR KAP SCHUCHERT FM		216809 04 02	
1	ADAMS BJERG FM. ALEQATSIQ FJORD FORMATION		216734 30 29 28 24 20 19	

Fig. 16. Stratigraphical distribution of conodonts in Washington Land and western Hall Land. For localities and geological sections see figs 14, 17-20. GGU 216778 is from the Lafayette Bugt Formation at Kap Independence (fig. 14), see Hurst (1980b, fig. 61, section height 107 m.

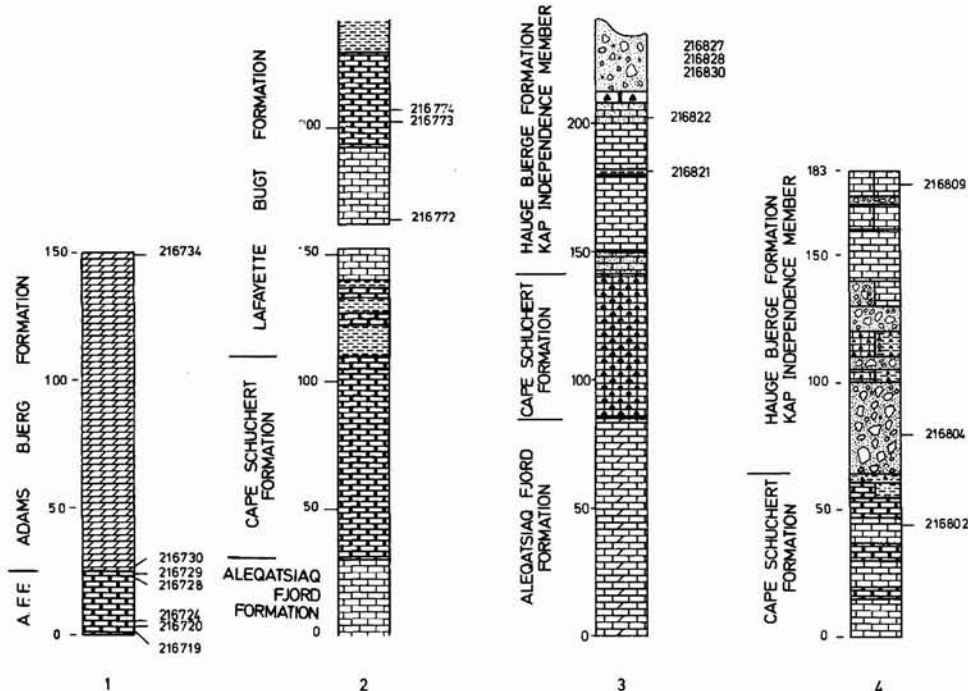


Fig. 17. Generalised section logs for localities 1–4 (fig. 14) in Washington Land. For legend see fig. 5. Derivation of logs: 1, Hurst (1980, fig. 16); 2, Hurst (1980b, fig. 58, in part); 3, J. M. Hurst (unpublished); 4, Hurst (1980b, fig. 56). GGU samples 216827, 216828 and 216830 were collected from loose blocks of Kap Independence Member lithologies.

Petermann Halvø Formation

In the type section the lower 20 m of the formation are composed of cream-yellow dolomite, the remaining 75 m are light grey massive dolomite with rare, calcareous pebble breccias and laminated crinoidal calcarenites (fig. 18). Hurst (1980b) interpreted these rocks as having been deposited on the shelf in marginal to open marine areas.

Diagnostic macrofossils have not been recorded from this formation and only few conodonts occur. If the top of the Aleqatsiaq Fjord Formation is synchronous, then the base of the Petermann Halvø Formation is late Rhuddanian to early Aeronian. *Ozarkodina pirata* and *Distomodus* sp. indet. are not age diagnostic forms but the former is found along with *Kockelella manitoulinensis* and *O. excavata* in the pre-Telychian strata of Peary Land.

Pentamerus Bjerger Formation

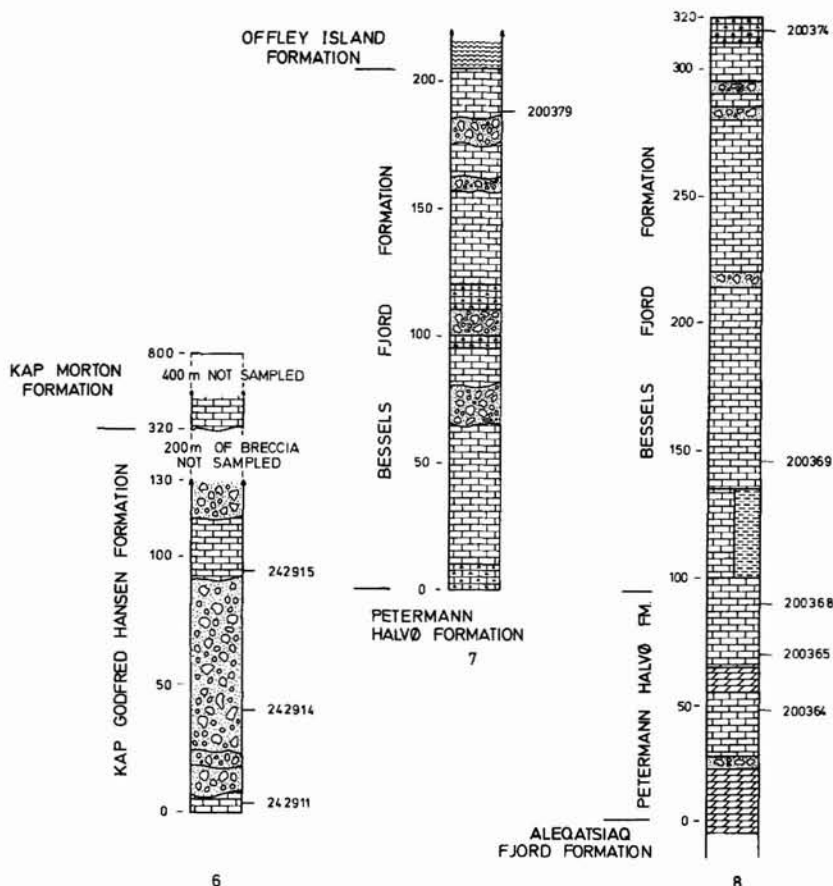
This formation represents a fringing reef complex located at the platform-slope boundary (Hurst 1980b; Hurst & Surlyk, 1983b). Conodonts provide indirect evidence for a maximum age of this formation in that

blocks occurring in breccia beds within the Lafayette Bugt Formation (fig. 21) derived from the Pentamerus Bjerger Formation contain a late *Pterospirifer celloni* or *P. amorphognathoides* Biozone fauna representing a Llandovery–Wenlock boundary age. This formation lies conformably above the Aleqatsiaq Fjord Formation and would therefore appear to range from the middle Llandovery into the Wenlock.

Kap Godfred Hansen Formation

The Kap Godfred Hansen Formation (250–300 m) consists of thick units of resedimented carbonate conglomerates derived from the Pentamerus Bjerger Formation and is interpreted to form part of a large submarine fan complex (Hurst 1980b; Hurst & Surlyk, 1983a). The formation conformably follows the Aleqatsiaq Fjord Formation in the type section. In the reference section (fig. 18, loc. 6) GGU sample 242911 yielded *Pterospirifer celloni*, *P. pennatus pennatus*, *Walliserodus* cf. *W. sancticlairei*, *Pseudobelodella silurica*, *Dentacodina* aff. *D. dubia* and *Ozarkodina* species (fig. 16). These suggest a late Telychian age. (fig. 16). From 50 to 130 m above this level, where the Lafayette Bugt and Kap Godfred Hansen Formations interdigitate, Hurst

Fig. 18. Generalised section logs for localities 6–8 (fig. 14) in Washington Land. For legend see fig. 5. Derivation of logs: 6, Hurst (1980b, fig. 26, in part); 7, Hurst (1980b, fig. 36D in part); 8, Hurst (1980b, fig. 36C).



(1980b) reported graptolites of latest Llandovery to early Wenlock age. At the top of the formation in the type section coquinas of *Kirkidium* (*Khodalovechia*) sp. occur, a genus not known elsewhere in strata older than middle Wenlock. The overlying Kap Morton Formation has elsewhere yielded conodonts of Wenlock age (see below); hence the Kap Godfred Hansen Formation ranges in age from early middle Llandovery to middle Wenlock.

Bessels Fjord Formation

The Bessels Fjord Formation (550–600 m, figs 18–20) is a complex unit of dark inter-mound sediments containing isolated carbonate build-ups. The build-ups consist of massive lime mudstones; intermound sediments are lithologically complex, comprising black, laminated, dolomitic limestone, chert, shale, dark lime mudstone and poorly laminated mudstone.

The formation has not yielded diagnostic conodont faunas, but lithostratigraphic evidence and the presence

of *Harpidium* sp. suggest a middle–late Llandovery age (Hurst, 1980b).

Offley Island Formation

The Offley Island Formation is a dominantly biostromal unit up to 450 m thick showing rapid lateral facies variations (figs 19, 20) representing an open, shallow marine shelf (Hurst, 1980b). The formation is conformably overlain by the Kap Lucie Marie Formation in Washington Land and by the Hauge Bjerger Formation (Cape Tyson Member) or Lafayette Bugt Formation in Hall Land.

Abundant macrofossil data are available from this formation indicating a late Llandovery age (Hurst, 1980b). Some 10 m above its base at Kap Lucie Marie (figs 14, 19), the formation contains a *Pterospirifer celloni* Biozone fauna (section 12, fig. 16). GGU sample 242894 (section 13, fig. 16), in the Lafayette Bugt Formation at Kap Tyson (fig. 20), contains *P. amorphognathoides*. Microfossil data thus suggest that the whole of this formation is of late Llandovery age.

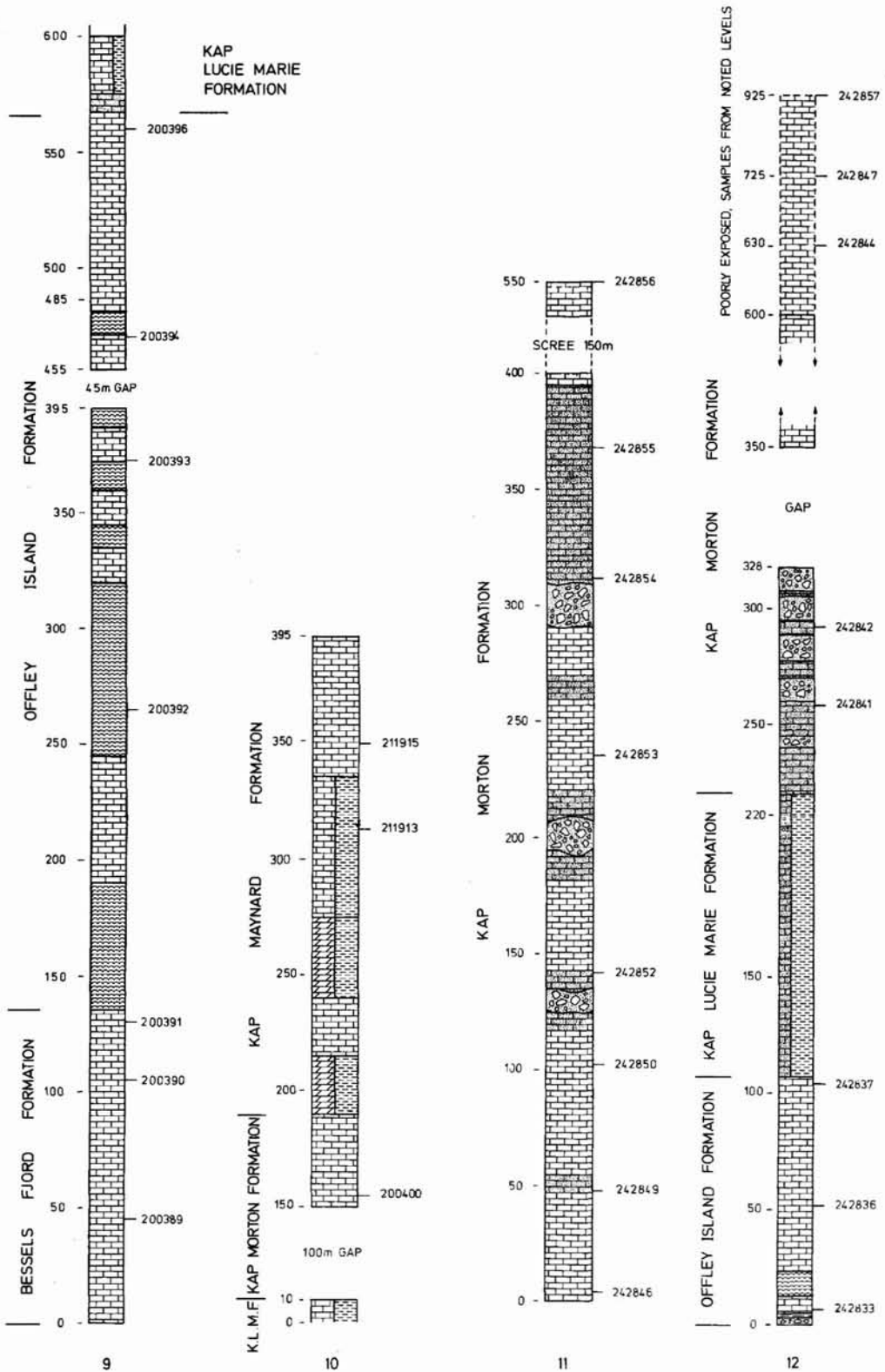
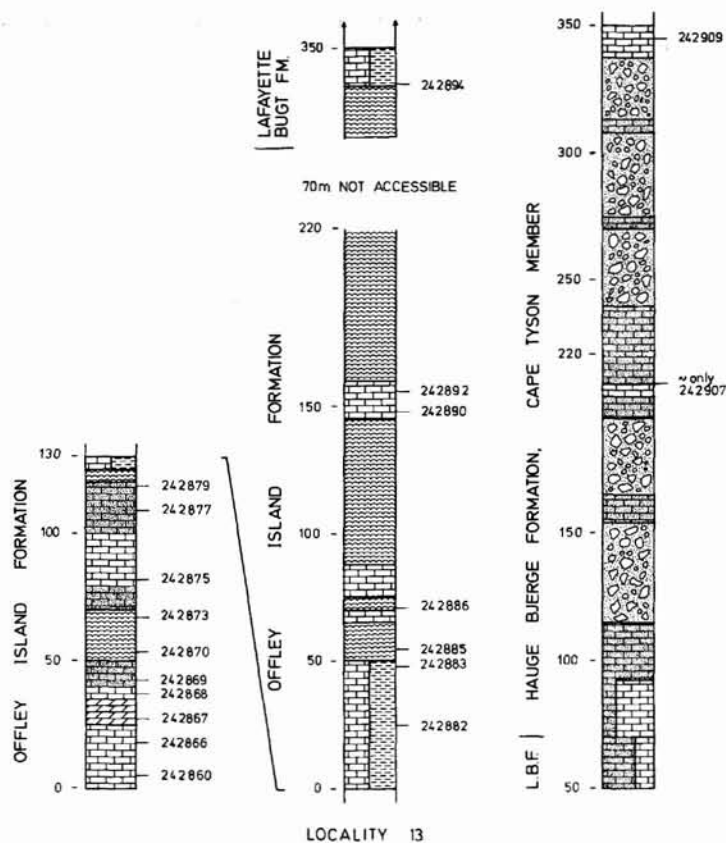


Fig. 19. Generalised section logs for localities 9-12 (fig. 14) in Washington Land. For legend see fig. 5. Derivation of logs: 9, Hurst (1980b, fig. 36A₁); 10, Hurst (1980b, fig. 36B₁); 11, Hurst (1980b, fig. 49); 12, Hurst (1980b, fig. 46).

Fig. 20. Generalised section logs for locality 13 (fig. 14) in Hall Land. For legend see fig. 5. See also Hurst (1980b, fig. 43).



Kap Lucie Marie Formation

This formation consists of a 25–135 m thick sequence of faintly laminated mudstones, silty, limy mudstones and, towards the top, graded calcarenites (fig. 19). Graptolites occurring 35 m above the base of the formation indicate the *M. spiralis* Biozone of late Llandovery age (Bjerreskov, 1981). Samples have not yielded conodonts.

Kap Morton Formation

The Kap Morton Formation varies in thickness from 150 to 700 m, and mainly consists of massive, light grey, lime mudstones (fig. 19). It was interpreted by Hurst (1980b) as deposited in open shelf to slope environments.

The Kap Morton Formation follows conformably upon the Kap Lucie Marie or Kap Godfred Hansen Formations and is conformably overlain by the Kap Maynard Formation. The presence of *Kirkidium* (*Rhodolovechia*) sp. in the Kap Godfred Hansen Formation below suggests that the whole of the Kap Morton Formation is post-middle Wenlock in age (Hurst, 1980b).

A low diversity conodont fauna is present throughout the formation, containing mainly coniform species assigned to *Dapsilodus obliquicostatus*, *Decoricornus fragilis*, *Panderodus recurvatus*, *P. unicastatus*, *P. aff. P. spasovi*, *Pseudooneotodus* cf. *Ps. beckmanni*, *Ps. bicornis*, *Ps. tricornis*, with elements of *O. excavata* (fig. 16).

Kap Maynard Formation

This formation consists of dolomites and light grey limestones, mudstones and green, limy shales (Hurst, 1980b) and is up to 200 m thick (fig. 19). Available conodont samples from Bessels Fjord were barren, but brachiopods assigned to *Kirkidium* (*Kirkidium*) sp. by Hurst (1980b) suggest a mid Wenlock to Ludlow age for the lower part of the formation. The upper age limit of the formation is unknown.

Hauge Bjerger Formation

This formation contains large carbonate mound complexes including core and flank deposits and was divided into two geographically separated members; the Kap

Independence and Cape Tyson Members by Hurst (1980b).

Kap Independence Member

This member overlies the Cape Schuchert Formation. Loose blocks of core facies collected in the Kap Independence area (fig. 17) contain a *Pterospathodus celloni* Biozone fauna. The age span of this member appears to be middle to late Llandovery; there is no internal faunal evidence of a middle Llandovery age but, considering facies relationships, it appears likely that some of the member is of that age.

Cape Tyson Member

Conodont samples collected at Kap Tyson (fig. 20) were barren. A reconnaissance sample (GGU 82687, Table 10) collected from Kayser Bjerg, Hall Land by P. R. Dawes contains a single *Pterospathodus amorphognathoides* Pa element and abundant *P. pennatus pennatus*. This confirms a late Llandovery to early Wenlock age for this member. Graptolites found in a small shale outcrop at the side of a carbonate mound are assigned to the *M. spiralis* Biozone (Hurst, 1980b; Norford, 1972).

Peary Land Group

This group was erected by Hurst (1980b) to contain slope and basinal sediments of Silurian – earliest Devonian? age deposited all across North Greenland (Hurst & Surlyk, 1982). In this paper only the slope deposits of the Cape Schuchert and Lafayette Bugt Formations in the Washington Land – Hall Land area will be dealt with. In Washington Land the Peary Land Group conformably rests on the Aleqatsiaq Fjord Formation and interdigitates with formations of the Washington Land Group: Adams Bjerg, Pentamerus Bjerge, Kap Godfred Hansen and Hauge Bjerge (Kap Independence Member) Formations (fig. 15). In Hall Land the group rests conformably upon the Offley Island Formation, and interdigitates with the Hauge Bjerge Formation (Cape Tyson Member).

Cape Schuchert Formation

The Cape Schuchert Formation (55–80 m) is dominated by thin-bedded black, bituminous, cherty limestones and mudstones. Shale beds are common and increase in thickness and abundance upwards. The Cape Schuchert Formation follows conformably upon the Aleqatsiaq Fjord Formation and is conformably

overlain by the Lafayette Bugt Formation and the Kap Independence Member of the Hauge Bjerge Formation (fig. 15). Hurst (1980b) suggested that it probably interdigitates with the Adams Bjerg Formation to the south, with the Pentamerus Bjerge Formation to the east and with the Kap Godfred Hansen Formation to the north.

Conodonts from the reference section (fig. 21) are abundant and well preserved, allowing the subdivision of this formation into two conodont biozones, a lower *Aspelundia expansa* Biozone and an upper *Aspelundia fluegeli* Biozone. The boundary between the two occurs at approximately 20 m above the base of the reference section. Associated conodonts are long-ranging, coniform species.

Graptolites collected in the type section were described by Bjerreskov (1981) as part of the *M. argenteus* Biozone (equivalent to the early Aeronian). This level is equivalent to 10–20 m above the base of the reference section (J. M. Hurst, personal communication, 1982) and allows independent dating of the *A. expansa* – *A. fluegeli* Biozone boundary. In the type section, graptolites 2 m above the top of the formation are indicative of the *M. convolutus* Biozone (middle Aeronian, B₂ of Jones, 1925). Some 10 m below the top of the formation in the reference section (fig. 21) graptolites indicative of the *M. turriculatus* Biozone of late Aeronian age were described by Bjerreskov (1981).

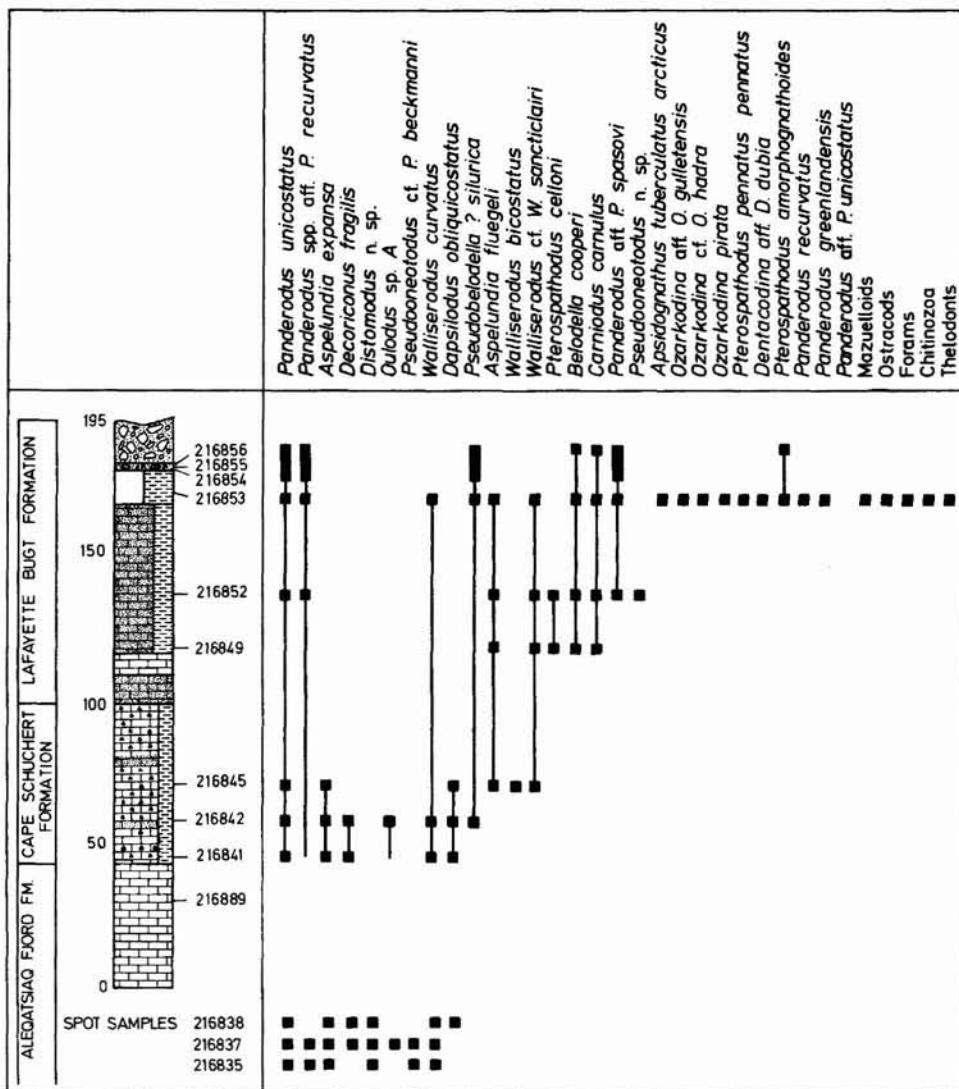
The Cape Schuchert Formation is thus apparently of early Aeronian age in the general area of the type locality (although the lower beds may be of Rhuddanian age). Away from this area the formation ranges up into the late Aeronian.

Lafayette Bugt Formation

The Lafayette Bugt Formation (up to 300 m exposed) consists dominantly of thick shale units interbedded with poorly-laminated lime mudstones and limestone conglomerate beds, up to 20 m thick. A thin string of probable stromatoporoid mounds and associated flank breccias at Kap Schuchert were included in this formation by Hurst (1980b).

The Lafayette Bugt Formation conformably follows the Cape Schuchert Formation and interdigitates with the Hauge Bjerge Formation (Kap Independence and Cape Tyson Members), Pentamerus Bjerge Formation and Kap Godfred Hansen Formation (fig. 15). The lower part of the formation yielded a *Aspelundia fluegeli* Biozone fauna (fig. 21). Standard *Pterospathodus celloni* Biozone species are present 35 m above the base, and at 50 m species indicative of the *Pterospathodus amorphognathoides* Biozone occur. Graptolites from

Fig. 21. Generalised section log and conodont ranges for locality 5 (fig. 14) in Washington Land. For legend see fig. 5.



the Lafayette Bugt Formation (Bjerreskov, 1981) indicate a middle Llandovery age for the base of the formation and an age range from Wenlock up into the Ludlow. The majority of outcrops are of late Llandovery age (Hurst, 1980b).

North Greenland conodont biozones

The work of Walliser (1964, 1972) in the Carnic Alps of Austria stimulated worldwide examination of Silurian faunas, and numerous zonal schemes have since been proposed. These have been assessed and discussed by Cooper (1980, p. 209) who concluded that no simple zonation is at present suitable as a standard reference scheme. He proposed the use of datum planes based on index taxa whose phylogeny is well understood, and

whose appearance and extinction can be documented throughout the world.

Cooper (1980) documented only two datum planes in the early Silurian. The *Distomodus staurogathoides* appearance datum has only been recognised reliably within the Washington Land Group at J. P. Koch Fjord. The *Pterospathodus amorphognathoides* appearance datum of Llandovery – Wenlock boundary strata is recognised in Washington Land, Valdemar Glückstadt Land and Kronprins Christian Land.

Silurian conodont faunas from North Greenland lack species which have proved biostratigraphically useful in other parts of the world. For example, *D. kentuckyensis* is absent and *D. staurogathoides* is rare, both taxa being important in the zonation of American Midcontinent Silurian strata. *Icriodella* species, important as

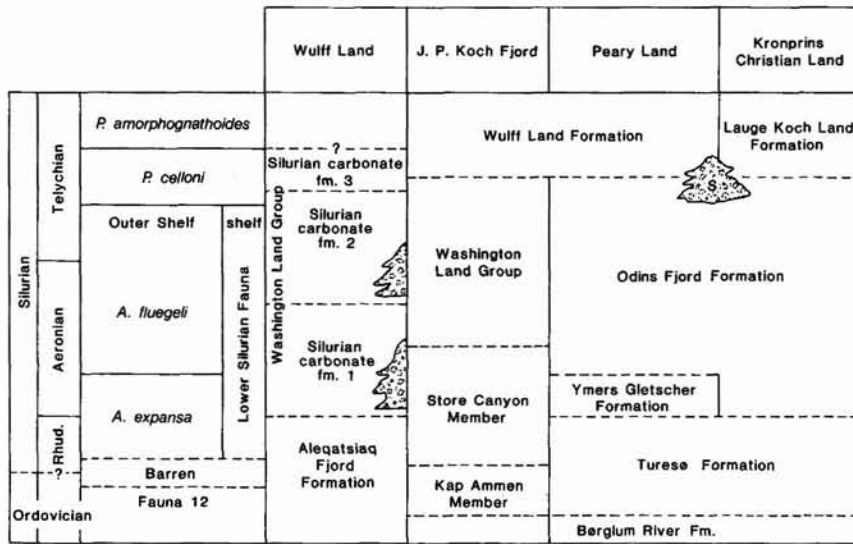


Fig. 22. Summary of section correlation and conodont biostratigraphy in the Wulff Land - Kronprins Christian Land region. Carbonate mounds are indicated schematically; S, Samuelsen Høj Formation.

zonal indices in part of the Welsh Borderland zonation proposed by Aldridge (1972, 1975), are also absent. Consequently a local conodont zonation is proposed herein for North Greenland (figs 22, 23).

Late Ordovician - middle Llandovery shelf biofacies

'Fauna 12'

A conodont fauna attributable to 'Fauna 12' of Sweet *et al.* (1971) occurs at the base of studied sections from Wulff Land eastwards to Kronprins Christian Land. The species present are typical of shallow water deposits in the American Midcontinent Province. Sweet (1979) described in detail the Late Ordovician conodonts and conodont biostratigraphy of the western part of the Midcontinent Province, and species ranges are taken from this work. Of the species recorded in Greenland *Aphelognathus pyramidalis*, *Rhipidognathus symmetricus*, *Drepanoistodus suberectus*, *Pseudobelodina vulgaris vulgaris*, *Pristognathus bighornensis* and *Plegognathus dartoni* are restricted to the Richmondian Stage but are, as yet, unknown from strata in the type area (Sweet, 1979). Barnes (1974) also recorded *P. dartoni* in strata of the Canadian Arctic Islands thought to be Maysvillian-Richmondian in age.

'Lower Silurian Fauna'

In shelf biofacies the Ordovician-Silurian boundary can be restricted to within 5 m of strata at J. P. Koch

Fjord. In this area 'Fauna 12' is succeeded by barren strata prior to the first appearance of *Ozarkodina hassi*. If the first appearance of *O. hassi* provides a reasonable basis for correlation, the underlying barren zone, which occurs throughout Peary Land, may be equivalent in part to the Gamachian Stage as defined on Anticosti Island (McCracken & Barnes, 1981).

In the shelf biofacies, pre-*Pterospirifer celloni* Biozone strata are characterised by *Kockella manitoulinensis*, *Ozarkodina hassi*, *O. excavata* and *Panderodus unicostatus*; these species have long ranges from the earliest Silurian. The most common pectiniform element in this biofacies is *K. manitoulinensis* which ranges into the *P. celloni* Biozone. The presence of *Aspelundia expansa* and *A. fluegeli* in small numbers in collections from Wulff Land, J. P. Koch Fjord and Kronprins Christian Land allows correlation with strata in the slope biofacies.

Early to middle Llandovery slope and outer shelf biofacies

The pre-*Pterospirifer celloni* Biozone in this biofacies can be subdivided into a lower *Aspelundia expansa* Biozone and an upper *Aspelundia fluegeli* Biozone. The most abundant and characteristic member of each is the nominate species; these occur together with long ranging coniform species.

In Washington Land the earliest occurrence of *A. expansa* corresponds with the base of the Cape Schuchert Formation of slope aspect (fig. 23). It appears close to the Ordovician-Silurian boundary in outer shelf sequences in Wulff Land, at J. P. Koch Fjord and in

		1	2	3	4	5	6	7-10	11	12	13	
Silurian	Wenlock	?					Kap Morton	Kap Maynard				
		<i>P. amorphognathoides</i>	Lafayette Bugt		?	Lafayette Bugt	Kap Godfred Hansen		Kap Morton			
	Telychian	<i>P. celloni</i>		Hauge Bjerge							Hauge Bjerge	
		<i>A. fluegeli</i>			?				Kap Lucie Marie		Kap Lucie Marie	Lafayette Bugt
	Aeronian	?				Cape Schuchert			Offley Island			Offley Island
		Adams Bjerg										
	Rhud.	<i>A. expansa</i>							Bessels Fjord			
Barren		Aleqatsiaq Fjord						Petermann Hajve				
Llandovery	?		Aleqatsiaq Fjord			Aleqatsiaq Fjord		Aleqatsiaq Fjord				
	?											
Ordovician	?											
	Fauna 12											

Fig. 23. Summary of section correlation and conodont biostratigraphy Washington Land and Hall Land (localities 1-13 in fig. 14).

Kronprins Christian Land. The upper limit of this biozone is defined at Kap Schuchert (fig. 21) by the first appearance of *A. fluegeli*, an event dated independently by graptolites as lower Aeronian, B₁₋₂ of Jones (1925).

The upper limit of the *A. fluegeli* Biozone is defined at Kap Schuchert by the first appearance of *P. celloni* of the *P. celloni* Biozone. The nominate species ranges into post-*P. amorphognathoides* Biozone strata.

Late Llandovery – *Pterospodus celloni* Biozone

The base of this biozone is recognised throughout North Greenland at the first appearance of *Pterospodus celloni*. The upper limit is drawn at the appearance datum of *P. amorphognathoides*. At Kap Schuchert *P. celloni* first appears between graptolite assemblages assigned to the *M. turriculatus* Biozone and the *M. spiralis* Biozone (Telychian as defined by Cocks *et al.*, 1984). In east Peary Land *Aulacognathus bullatus* occurs approximately 10 m below the first occurrence of *P. celloni*, though elsewhere their first appearances coincide. *A. bullatus* is restricted to the C₅ subdivision of the Telychian in Britain (Aldridge, 1975) and to the *P. celloni* Biozone in the Carnic Alps (Walliser, 1964). On Anticosti Island *A. bullatus* occurs beneath the first occurrence of *Icriodella inconstans* (Uyeno & Barnes, 1981), a zonal index species confined to the Telychian in Britain where it first appears before *P. celloni* (Aldridge, 1975, p. 153). *A. bullatus* is recorded in small numbers almost everywhere and may be of use locally in identifying strata of late Aeronian age in Greenland.

Llandovery–Wenlock boundary – *Pterospodus amorphognathoides* Biozone

The base of this biozone is recognised within the Lafayette Bugt Formation at Kap Schuchert in Washington Land. The nominate species also occurs in the lower part of the Profilfjeldet Member in Valdemar Glückstadt Land and Kronprins Christian Land. The upper limit of the biozone has not been recognised in Greenland.

Comparisons with other early Silurian conodont zonations

Pre-*Pterospodus celloni* Biozone collections from Greenland have little in common with those described elsewhere (fig. 24). At the classic section of Cellon Mountain in the Carnic Alps Walliser (1964) described an all-embracing Bereich I fauna, the exact age of which is uncertain. Serpagli (1967) and Schönlaub (1971) suggested that it was in part late Ordovician in age and Schönlaub (1980) subsequently considered the Ordovician–Silurian boundary to occur within sample 5 of Walliser (1964, pl. 1, Table 2). Conodont fragments assigned to *Icriodina irregularis* by Walliser (1964) occur in samples 6–8 but cannot definitely be assigned to the Silurian, as similar specimens from the Upper Ordovician have been figured by Orchard (1980, pl. 1, figs 22, 27). The base of the *P. celloni* Biozone occurs beneath sample 10 allg. of Walliser (1964), an horizon considered by Rexroad (*in* Craig, 1969) to be an unconform-

		CELLON 1	GREAT BRITAIN 2	U. S. MIDCONTINENT 3		
SILURIAN	Early	Wenlock	patula			
		Telychian	amorphognathoides	?	P. amorphognathoides	
			C ₆			
		Aeronian	celloni	I. inconstans	L. celloni	
			C ₅			
		Rhuddanian	Bereich I	H. staurognathoides	D. kentuckyensis	
				C ₃₋₄		
				C ₁₋₂	I. discreta – I. deflecta	
		"Gamachian"		?	?	
			A ₁₋₄			
ORD.	Late	?	A. ordovicicus	Fauna 12		

Fig. 24. Approximate relationships between Silurian conodont zonations. 1, from Walliser (1964); 2, in part from Aldridge (1972, 1975); 3, in part from Nicoll & Rexroad (1969), Pollock *et al.* (1970), Cooper (1975); 4, from McCracken & Barnes (1981); 5, from Uyeno & Barnes (1981). Ordovician conodont zonation from Nowlan (1981).

ity; if this is the case then much of the Llandovery is missing at Cellon.

In Britain, Aldridge (1972, 1975) divided pre-*P. celloni* Biozone strata of the Welsh Borderland into three conodont assemblage zones (fig. 24). His *Hadrognathus staurognathoides* assemblage zone occurs within the late Aeronian and can be correlated with the upper part of the *Aspelundia fluegeli* Biozone in Greenland (fig. 24). Aldridge (1972) noted few distinctive species present in this assemblage zone apart from the common occurrence of *A. fluegeli* which ranges from older strata in Greenland. He used the *Icriodella* lineage as the basis for his Llandovery zonation, but *Icriodella* is absent from the Greenland collections. The *I. inconstans* assemblage zone of Aldridge (1972) is restricted to C₅ strata in Britain and contains the first appearance of *P. celloni*.

Aldridge (1975, p. 609) reported an Aeronian fauna including *Ozarkodina hassi*, *O. abrupta* (questionably a junior synonym of *Kockelella manitoulinensis*) and *O. oldhamensis* along with *M. convolutus* Biozone graptolites from the Hamperly borehole, Church Stretton, in

the Welsh Borderland. Apart from the presence of *O. oldhamensis* this fauna closely resembles the shelf biofacies 'Lower Silurian Fauna' from Greenland.

Lower Llandovery strata from the Oslo graben have yielded a conodont sequence similar to that on Anticosti Island (Aldridge & Mohamed, 1982) with *Distomodus* and *Oulodus?* being common. *Ozarkodina hassi* is present close to the base of the Silurian, and is considered to be Rhuddanian (*O. nathani* Biozone) in age.

A comprehensive study of the conodonts from an apparently continuous upper Ordovician to Silurian (lower Wenlock) sequence on Anticosti Island has yielded large amounts of new information regarding the distribution of conodonts through the Llandovery (Nowlan & Barnes, 1981). They described a Richmondian conodont fauna (Fauna 12) similar to that in Greenland from the Vaureal Formation. It includes *Aphelognathus pyramidalis* and *Plegagnathus dartoni* which Nowlan & Barnes considered to be typical of nearshore environments. The overlying Ellis Bay Formation contains species in common with Greenland, *Drepanoistodus suberectus*, *Rhipidognathus symmetri-*

ANTICOSTI 4	ANTICOSTI 5	GREENLAND		
		SHELF	SLOPE	
	?			
	<i>P. amorphognathoides</i>	<i>P. amorphognathoides</i>	<i>P. amorphognathoides</i>	<i>P. amorphognathoides</i> datum
	<i>I. inconstans</i>	<i>P. celloni</i>	<i>P. celloni</i>	<i>P. celloni</i> datum
<i>D. kentuckyensis</i>	<i>O. aldridgei</i>	"Lower Silurian Fauna"	<i>A. fluegeli</i>	<i>D. staurognathoides</i> datum
	<i>D. staurognathoides</i>			
<i>I. discreta</i> – <i>I. deflecta</i>				
?				
<i>O. ? nathani</i>			<i>A. expansa</i>	
Fauna 13			?	
Fauna 12		Fauna 12		

Fig. 24 cont.

cus, *A. pyramidalis* and various *Panderodus* species, but it also includes *Gamachignathus*, a genus not recognised in Greenland (S. Tull, personal communication, 1988). In terms of the informal conodont faunas of Sweet *et al.* (1971) and Sweet & Bergström (1971), McCracken & Barnes (1981) considered the fauna in the Ellis Bay Formation to be significantly different from that in the underlying Vaureal Formation and consequently erected a new Fauna 13, characterised by the presence of *Gamachignathus ensifer* and *G. hastatus*.

Sections across the Ordovician–Silurian boundary yielding conodonts are rare. The newly defined stratotype at Dob's Linn (Cocks, 1985) is in graptolitic facies and has not yet yielded age diagnostic Silurian conodonts. On Anticosti Island, however, conodonts are moderately abundant and Barnes & McCracken (1980) drew the Ordovician–Silurian boundary at the first appearance of *Ozarkodina hassi*, *O. oldhamensis*, *Oulodus? nathani* and *Oulodus kentuckyensis*. McCracken & Barnes (1981) erected the *O. ? nathani* Biozone as the lowest conodont zone of the Silurian, and this biozone ranges up into the late Rhuddanian (Nowlan, 1981).

The *Distomodus kentuckyensis* Biozone, above, ranges from the late Rhuddanian to the Telychian. Based on the occurrence of graptolites in the Greenland sections, it would appear that the *Aspelundia expansa*–*A. fluegeli* Biozone boundary lies within the lower part of the *D. kentuckyensis* Biozone.

Other species recorded throughout the Ellis Bay, Becscie and Gun River Formations on Anticosti Island include *Icriodella discreta*, *I. deflecta*, *Spathognathodus elibatus*, *Ozarkodina hassi*, *O. oldhamensis* and *Walliserodus curvatus* (Fåhraeus & Barnes, 1981; McCracken & Barnes, 1981). The conodont zonations utilised for this part of the section (Uyeno & Barnes, 1981, 1983) compares closely with that proposed for the Welsh Borderland by Aldridge (1972).

Generally, faunas from the North American Mid-continent are similar to those described from elsewhere. However, Nicoll & Rexroad (1969) and Pollock *et al.* (1970) noted differences in faunas from the Cincinnati Arch and north Michigan–Ontario areas of the Mid-continent. The dominant taxon in the former area is *Distomodus*, and in the latter *Icriodella* and *Ozarkodina*

predominate. The northern area also yields abundant *Ozarkodina hassi*, *O. excavata* and *Kockelella manitoulinensis* and is similar to the shelf biofacies 'Lower Silurian faunas' of Greenland. These authors considered that these differences within the Midcontinent reflected provincialism. *Distomodus* and *Icriodella*, however, occur commonly together (e.g. Aldridge, 1972, in the Welsh Borderland), and the occurrence of a diverse *Ozarkodina* assemblage may be palaeo-ecologically controlled, as suggested by its distribution in Greenland (fig. 26).

Pterospathodus celloni Biozone faunas are widespread. The base of the *P. celloni* Biozone can be well defined in all sections in North Greenland where it provides the best datum for correlation. *P. celloni* ranges through the late Telychian (see Cooper, 1980, for a review). At Cellon, the *P. celloni* and *P. amorphognathoides* Biozones have mutually exclusive ranges and an unconformity has been suspected between them (Rexroad in Craig, 1969). Elsewhere the ranges of *P. celloni* and *P. amorphognathoides* overlap (Nicoll & Rexroad, 1969; Craig, 1969).

The *Pterospathodus amorphognathoides* appearance datum is important in worldwide correlation, occurring in Llandovery–Wenlock boundary strata in Britain (Aldridge, 1972), and in the Carnic Alps (Walliser, 1964; Schönlaub, 1971). Elsewhere in Europe the datum has been located in the Oslo graben (Aldridge, 1974; Aldridge & Mohamed, 1982), and it is reported from the USSR (Mashkova, 1977, 1979). *P. amorphognathoides* is also recorded widely in the United States and Canada (refer to Cooper, 1980; Uyeno & Barnes, 1981; Nowlan, 1981 for recent reviews). The *P. amorphognathoides* Biozone at Cellon extends into the middle Wenlock (Walliser, 1964; Cooper, 1980).

A conodont fauna of post middle Wenlock in the Kap Morton Formation contains predominantly simple cone species which cannot be correlated with coeval sections elsewhere.

Palaeo-ecological observations

The Greenland collections do not lend themselves to statistical analysis. Sections, particularly from Washington Land, have not been collected systematically, are widely separated and conodont yields are generally less than twenty five specimens per sample. Without the support of statistical comparisons it is difficult to hypothesise about conodont palaeo-ecology, but some major distributional differences within the North Greenland conodont fauna are discussed below. Analysis is restricted to the comparison of conodont distributions (figs 25–27) and diversity changes through time. Previously published interpretations of conodont distri-

butional patterns are used to elucidate those found in Greenland.

Late Ordovician faunas from North Greenland are characteristic of the American Midcontinent Province which was close to the equator (Spjeldnæs, 1961; Bergström, 1973). Limestones within this province are often closely associated with extensive evaporite deposits, and Barnes & Fåhraeus (1975) concluded that late Ordovician seas in this province would have tended towards hypersalinity and increased temperature.

Various shelf communities have been distinguished for the late Ordovician (Barnes & Fåhraeus, 1975; Le Fèvre *et al.*, 1976); several of these occur in Greenland. *Rhipidognathus* has been reported in abundance from tidal flat deposits in the Cincinnati Arch area (Kohut & Sweet, 1968) and in evaporite deposits (Barnes & Munro, 1973). The monogeneric sample at the base of the Turesø Formation in Kronprins Christian Land may therefore indicate extremely shallow water.

Plegagnathus, *Drepanoistodus*, *Oulodus*, *Rhipidognathus* and *Panderodus* are widespread in North Greenland. They are common genera in shallow, subtidal deposits (Barnes & Fåhraeus, 1975) and appear to have formed a widespread 'shelf' community.

On limited data, the association of *Walliserodus*, *Pristognathus* and *Pseudobelodina* at Odin Fjord and J. P. Koch Fjord may represent a deeper shelf community in Greenland.

Two regressive–transgressive cycles were documented in Upper Ordovician strata from the Hudson Bay Basin by Barnes & Fåhraeus (1975). The second regressive phase (resulting from the late Ordovician Gondwana glaciation during the latest Ordovician) is recorded elsewhere in the world (Berry & Boucot, 1973) and resulted in widespread extinction within the Conodonta. The North Greenland conodont fauna underwent a major crisis, with only a few coniform genera continuing into the Silurian. Currently, the only diverse conodont faunas described from this interval ('Gamachian') are from the deeper water sediments of the Gaspé Peninsula (Nowlan, 1981) and Anticosti Island (Nowlan & Barnes, 1981).

Conodonts during the early Silurian were generally low in abundance and diversity. During this time a well defined nearshore community comprising *Icriodella*, *Distomodus* and *Ozarkodina* species existed (Aldridge, 1976; Le Fèvre *et al.*, 1976). This may in part correlate with the shelf biofacies in Greenland; but major differences in the assemblage (absence of *Icriodella* and *Distomodus*) suggest that either these taxa did not reach Greenland until later in the Silurian or that environmental conditions were somewhat different from those in Europe and Canada. The closest relative to the

'FAUNA 12'	Washington Land								Hall Land							
	Wulff Land	J. P. Koch Fjord	Odin Fjord	G.B. Schley Fjord	Berglum Ely	E. Peary Land	V. G. Land	K. C. Land	Wulff Land	J. P. Koch Fjord	Odin Fjord	G.B. Schley Fjord	Berglum Ely	E. Peary Land	V. G. Land	K. C. Land
Aphelognathus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Belodina	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Drepanostodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Oulodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Panderodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Pilegnathus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Pristognathus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Pseudobelodina	A	A	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Rhipidognathus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Walliserodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•

'LOWER SILURIAN'	Washington Land													Hall Land				
	1	7-10	5	6	4	3	2	12	11	13	Wulff Land	J. P. Koch Fjord	Odin Fjord	G.B. Schley Fjord	Berglum Ely	E. Peary Land	V. G. Land	K. C. Land
Aulacognathus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Belodella	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Aspelundia	A	A	A	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Carniodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Dapsilodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Decoriconus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Distomodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Kockellella	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Oulodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Ozarkodina	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Panderodus	A	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Pseudooneotodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Walliserodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•

'P. celloni Biozone'	Washington Land													Hall Land				
	1	7-10	5	6	4	3	2	12	11	13	Wulff Land	J. P. Koch Fjord	Odin Fjord	G.B. Schley Fjord	Berglum Ely	E. Peary Land	V. G. Land	K. C. Land
Apsidognathus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Astropentagnathus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Aulacognathus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Belodella	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Aspelundia	A	A	A	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Carniodus	A	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Dapsilodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Decoriconus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Distomodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Kockellella	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Oulodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Ozarkodina	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Panderodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Pseudobelodella (?)	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Pseudooneotodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Pterospathodus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Dentacodina	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Walliserodus	A	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•

Fig. 25. Geographical and stratigraphical distribution of conodont genera in North Greenland. A, abundance greater than 25% of conodont fauna.

shelf biofacies in Greenland may be found in the fauna of the Manitoulin Island dolomites of Canada (Pollock *et al.*, 1970). In possibly more outer shelf sequences at J.

P. Koch Fjord and Kronprins Christian Land, a shelf biofacies fauna of simple cones and diminutive *Ozarkodina* species dominate lower to middle Llandovery strata. In Wulff Land an apparent mixture of shelf and slope genera occurs (fig. 25).

The slope biofacies of lower-middle Llandovery age, represented at Kap Schuchert, yields prolific, low diversity conodont faunas containing *Aspelundia*, *Dapsilodus* and *Decoriconus* almost to the exclusion of other genera. A similar biofacies has not previously been described, although Aldridge & Mabillard (1981) documented the preference of *Dapsilodus* and *Decoriconus* for shelf margin to slope environments in the Welsh Borderland. The *Pterospathodus celloni* Biozone from Greenland contains cosmopolitan species (fig. 25), suggesting uniform environmental conditions for eurytopic species.

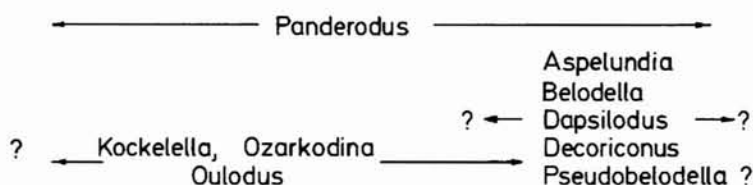
Aulacognathus, *Astropentagnathus* and *Apsidognathus* are relatively more abundant in Greenland than in the majority of described Silurian collections, but the significance of this observation is obscure. Similar abundances occur, however, in the Lee Creek Member of the Brassfield Limestone (Nicoll & Rexroad, 1969) and in Silurian collections from Ellesmere Island (Mirza, 1976). Coniform species are particularly abundant and diverse in the Greenland collections.

Pterospathodus celloni Biozone strata in other parts of the world witness the rapid increase in abundance and diversity of the Conodonta, and this increase is also readily distinguished in Greenland (fig. 27). Le Fèvre *et al.* (1976) considered the increase on the American midcontinent to be the result of migration of 'European' conodonts into the area which reflected the establishment of more open marine conditions. A European ancestral stock for many of the species recorded cannot be discounted; but it is difficult to conceive how the virtually instantaneous worldwide migration of these species into shelf habitats could have been accomplished unless all had a pelagic mode of life. An alternative hypothesis is that this fauna originally occupied slope or deeper shelf (lower salinity, cooler water) environments and subsequently migrated into shelf environments as the result of worldwide transgression.

A distinct littoral biofacies comprising *Icriodella*, *Ozarkodina*, *Distomodus* and *Lonchodina* has been documented from *P. celloni* Biozone strata (Aldridge, 1976) though this is not present in Greenland.

Coniform species are abundant and diverse throughout the Llandovery in Greenland and show apparent increase in diversity (fig. 27) during the *P. celloni* Biozone. This is mirrored in coeval strata in the Welsh Basin (Mabillard & Aldridge, 1985).

EARLY SILURIAN



FAUNA 12

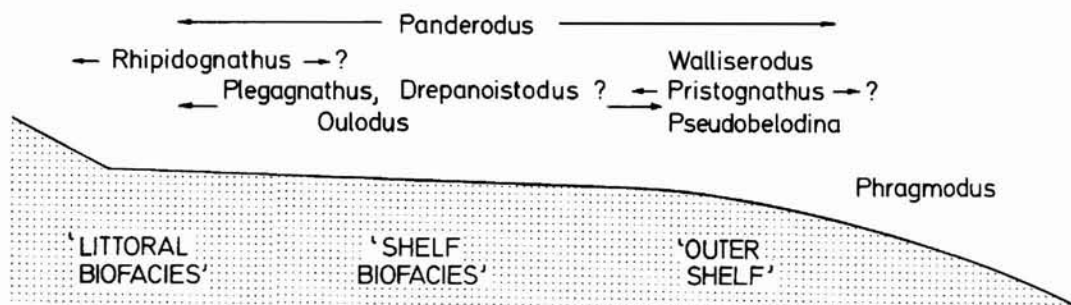


Fig. 26. Generalised palaeoecological distribution of conodont genera in North Greenland during the late Ordovician (Fauna 12) and early Silurian.

Diversity trends

A method of comparing the relative diversity of samples containing a variable number of individuals from a randomly sampled population is provided by an index formulated by Fisher *et al.* (1943):

$$S = a \log e (1 + N/a)$$

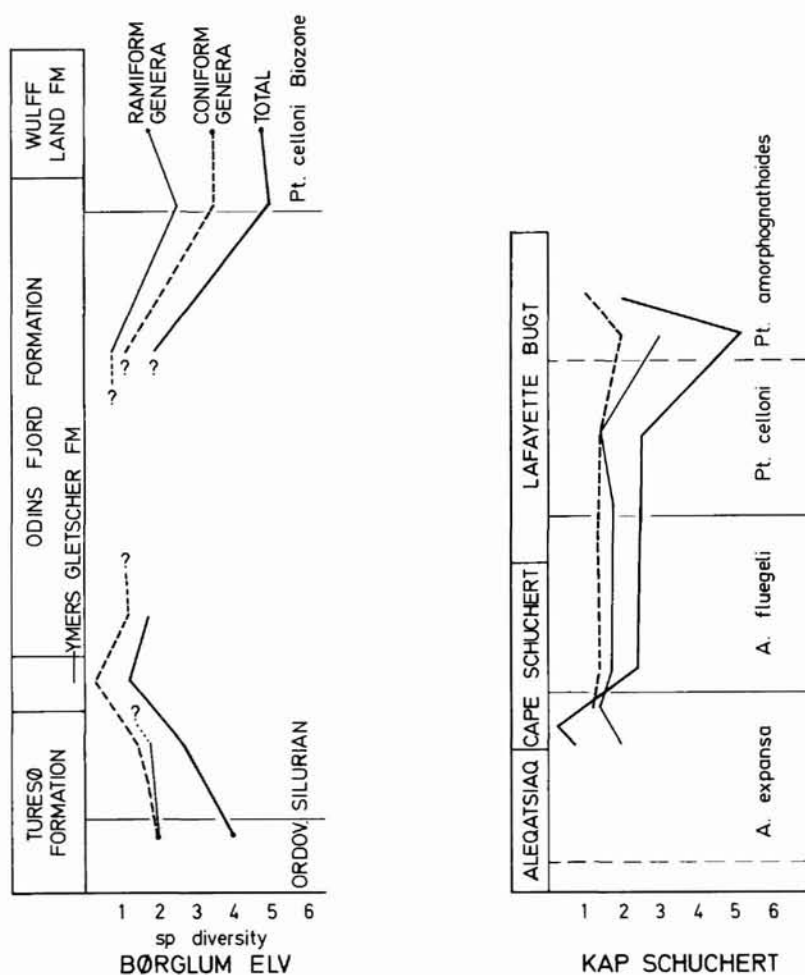
S is the number of species, N the number of individuals, and a is the index of diversity. The number of individuals within each species is not taken into account (Aldridge, 1976). In the present context measurement of conodont diversity is based entirely on multi-element species; changes in diversity are plotted in fig. 27. In all but the shelf biofacies at Børglum Elv in southern Peary Land and the slope biofacies at Kap Schuchert, the specimen abundances are too low to allow separate calculation for ramiform and coniform genera. Where possible, samples from each lithostratigraphical member or formation have been grouped to increase the effective sample size. At Kap Schuchert specimen abundances per sample are large enough to trace diversity trends between each sample. The low specimen abundances in Wulff Land, at J. P. Koch Fjord and at Odin

Fjord may in part reflect low sample sizes rather than palaeo-ecological factors.

Diversities measured in Upper Ordovician samples are moderately high and compare with the values for *Pterospirifer celloni* Biozone strata. In the Børglum Elv area of southern Peary Land and Kronprins Christian Land diversity decreases through the Turesø Formation reaching a low in the upper part of the formation. Above this, diversity increases only gradually. Typical of this part of the succession are occasional samples with high yields (e.g. GGU 228901, fig 6, Table 1). Le Fèvre *et al.* (1976) recorded a similar low diversity with occasional prolific horizons which they related to oscillation between intertidal (low diversity) and peri-reefal/subtidal conditions (higher diversity). Comparable environmental oscillation may account for variation in conodont abundance also in the Odin Fjord Formation.

The slope biofacies in Washington Land also displays a reduction in diversity within the upper *Aspelundia expansa* Biozone; this correlates with the reduction in the upper parts of the Turesø Formation in Peary Land. At Kap Schuchert, however, the fall in diversity is due to a massive increase in the number of specimens of *Dapsilodus obliquicostatus* which may represent the

Fig. 27. Changes in conodont diversity through time at Børglum Elv and Kap Schuchert.



temporary colonisation of the area by a low diversity, specialised, deeper water community. Diversity throughout the *A. fluegeli* Biozone remains constant at Kap Schuchert, with values comparable to those in coeval strata in Peary Land.

The late Ordovician worldwide regression has been correlated with the Gondwana glacial event (Berry & Boucot, 1970; McCracken & Barnes, 1981, for a review). The resultant shallowing would have led to a fall in the number of shelf habitats and a fall in species diversity. The diversity trend in the Turesø Formation mirrors this, with the reduction continuing into the earliest Silurian. Following the regression and mass extinctions the shelf fauna might be expected to be of low diversity, comprising a restricted number of opportunistic species, and a stable environment would inhibit rapid diversification (Valentine, 1973). The general similar-

ities between the diversity values in shelf and slope biofacies would initially suggest that the late Ordovician extinction event affected the whole conodont fauna.

The increase in diversity at the base of the *Pterospathodus celloni* Biozone is more difficult to interpret. Other authors have noted that there is no evidence for increased conodont diversity with depth (Aldridge, 1976; Barnes & Fåhræus, 1975). Similarly, Aldridge (1976) noted no general correlation between diversity and lithology though, in some situations, lithological changes may be concurrent with changes in conodont faunal composition and diversity. Coniform genera, however, show increased abundance in offshore environments in Greenland, supporting the postulation of Seddon & Sweet (1971), Aldridge (1972) and Barnes & Fåhræus (1975) that distribution patterns may be correlated with water-depth related factors.

SYSTEMATIC PALAEOLOGY

Conodont element terminology

Ramiform genera

The application of a more biological multi-element taxonomy has led to the development of a large number of notational schemes relating element shape and morphology to presumed position in the conodont apparatus (Sweet, 1981b, pp. W17–20). The notational scheme proposed by Sweet & Schönlaub (1975) modified by Cooper (1975), is adopted in this study as it is the most widely used amongst Silurian conodont workers. Apparatuses containing more than the standard six elements occur in the Greenland section e.g. *Astropentagnathus* and *Aspelundia*. Distinct multiple pairs of elements in this type of apparatus, which apparently occupied similar locations, are denoted by subscripts, e.g. Pa₁ and Pa₂. The major shape categories and morphological terminology employed herein are as described by Sweet (1981b).

Coniform genera

There is at present no widely accepted descriptive terminology for homologous elements within coniform multi-element apparatuses. Prior to the work of Barrick (1977) few attempts were made to reconstruct Silurian

coniform apparatuses. Cumbersome generically derived terminology, applied at that time to many non-coniform apparatuses, was adapted for use with coniform taxa (Lindström, 1964, 1971; Bergström & Sweet, 1966). This terminology had many problems associated with it (Barrick, 1977) and has largely been abandoned.

In an attempt to make coniform apparatus nomenclature more 'natural' Barrick (1977) applied the national scheme proposed by Sweet & Schönlaub (1975). This assumed the elemental positions in coniform and non-coniform apparatuses are directly comparable, which cannot be confirmed. The system also demands easily recognisable elemental positions within and between apparatuses. Inadequately known coniform 'bauplans' and intergrading element morphotypes cannot be adequately classified with this system. In addition, until the apparatuses of coniform and non-coniform genera can be shown to have analogous functions and similar origins, a separate notational system is advocated.

Barnes *et al.* (1979) classified coniform apparatuses into 'types' based upon the degree of elemental upper-lower compression, cross-sectional symmetry and curvature (fig. 28). This scheme is preferred as it is flexible, it highlights homologous elements, which leads to a greater understanding of phylogeny and may lead to a 'natural' supragenetic classification.

The Greenland collections contain a large number

A. *Panderodus*

Barrick (1977)	Sweet (1979)	Barnes et al (1979)	Greenland
Sa	similiform	p	sym.p
Sb	asimiliform		aq
Sc	arcuatiform		r
M	falciform	q	sq
	tortiform		tp

B. *Walliserodus*

Form taxa	Cooper (1975)	Barrick (1977)	Barnes et al (1979)	Greenland
<i>P. dyscritus</i>	costate el.	Sa	u	sym.p
<i>P. debolti</i>	costate el.	M	? t	ap
<i>A. unicastatus</i>	acodiform			
<i>A. curvatus</i>	costate el.	Sd	t	aq
<i>P. migratus</i>	costate el.	Sc	s	sq
	Not previously described			r

Fig. 28. Apparatus nomenclature applied to *Panderodus* and *Walliserodus*.

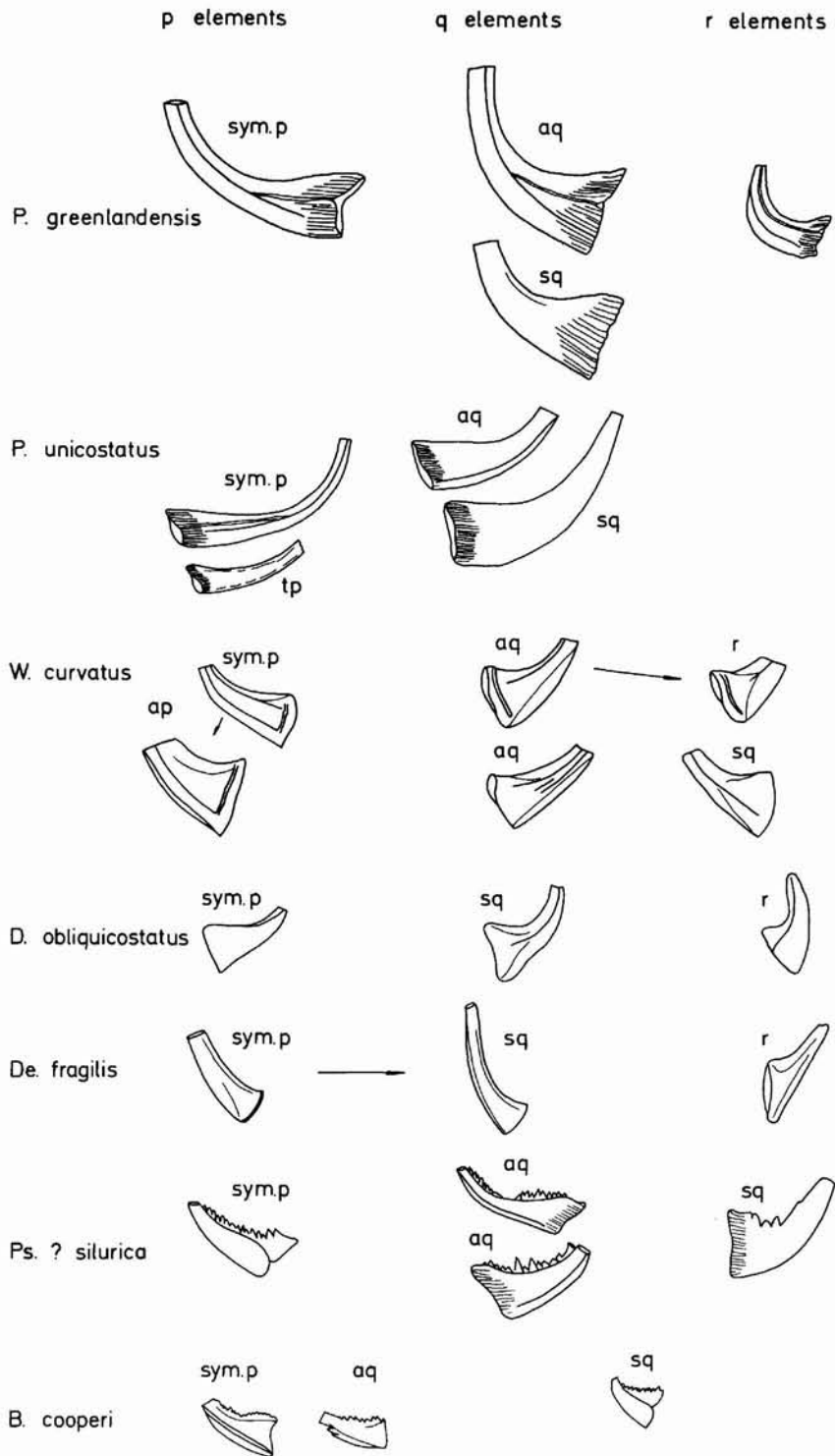


Fig. 29. Homologies between elements of coniform conodont genera encountered in the Greenland collections. Arrows indicate symmetry transition with intermediate forms.

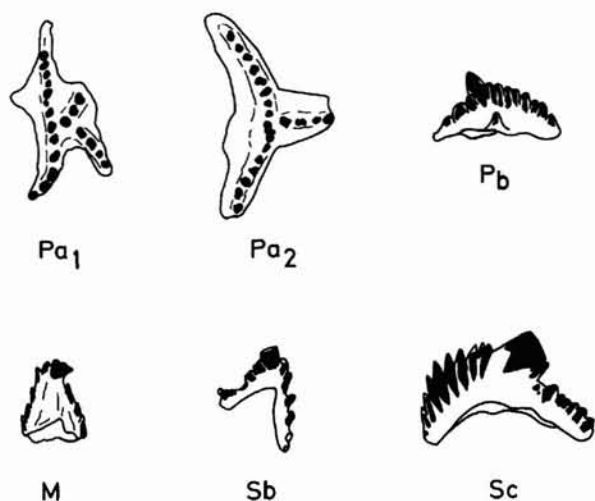


Fig. 30. The apparatus of *Astropentagnathus irregularis irregularis* Mostler. The shaded area represents the distribution of white matter. All figures are camera lucida drawings of the numbered specimens, $\times 30$ unless otherwise stated. Pa₁, MGUH 17.632; Pa₂, MGUH 17.633 $\times 20$; Pb, MGUH 17.634; M, MGUH 17.636; Sb, MGUH 17.638; Sc, MGUH 17.639.

and variety of coniform elements, and early in this study it was found that the morphological variation between the elements of a single apparatus could not be adequately covered by the simple p, q and r notation of Barnes *et al.* (1979). Modification of the scheme as outlined below solves this problem and is applicable to all Silurian coniform taxa (fig. 29).

Erect elements with a long base and short proclined cusp (p elements) can be subdivided into symmetrical p elements (sym. p) which are more or less bilaterally symmetrical and commonly develop antero-lateral and postero-lateral costae; asymmetrical p elements (ap) which are asymmetrical with respect to the location of the inner-lateral costa or costae; twisted p elements (tp; the tortiform element defined by Sweet, 1979), in which the cusp is laterally twisted with respect to the base, are commonly upper-lower compressed with a lenticular cross-section. This element has only been recorded rarely from the *Panderodus* apparatus.

From the more strongly recurved q elements two shape categories can be distinguished. Symmetrical q elements (sq) which are laterally compressed and have a cusp with a lenticular cross-section. Asymmetrical q elements (aq) which are strongly asymmetrical, commonly bearing only a single inner-laterally directed costa on the lower edge. This element is generally the most abundant and exhibits the greatest intra-elemental variation.

The highly recurved r elements are commonly morphologically transitional from the aq element by increased curvature of the cusp, costa distribution is also similar. This shape category in all Silurian genera (except *Panderodus*) is acodontan in style, rather than oistodontan as found in Upper Ordovician coniform apparatuses.

The elemental notation employed in this study does not presuppose a locational position within an apparatus. Very few coniform natural assemblages are known (Aldridge, 1982) and the apparatus structure of many is poorly understood. Ratios of elements within a single apparatus suggest that multiple pairs of each element category may have occurred, for example ratios of elements in *Dapsilodus obliquicostatus* from Greenland are p,1 : q,10 : r,5. This suggests that as many as 32 single elements may have occurred within the *D. obliquicostatus* apparatus. Aldridge (1982) described a coniform cluster *Besselodus arcticus* from the Upper Ordovician which contained several sq elements and one r element. Close study of this cluster shows the sq elements to differ slightly in minor detail, i.e. slight difference in the twisting and inclination of the cusp or slightly different positions of the lateral costae, characters also seen to differ in large collections of discrete elements. The significance of such minor changes cannot adequately be assessed until additional clusters are isolated. If found to be significant, these differences can be accommodated in the proposed scheme by the use of subscripts.

Denticulate coniform genera from the Ordovician, *Pseudobelodina* Sweet (1979) and *Plegagnathus* Ethington & Furnish (1959) are described using the nomenclature of Sweet (1979). *Pseudooneotodus* Drygant (1974c) cannot be described using existing nomenclatural schemes, and a descriptive morphological terminology is applied to the elements of its apparatus.

It is considered somewhat premature to firmly accept any familial classification (Clark, 1981) before a fuller understanding of apparatus structure and phylogeny of coniform genera can be achieved. Using the modified Barnes scheme it is possible to compare directly the apparatus structures of lower Silurian coniforms which may form the basis for a suprageneric classification.

Attempts have been made to study all relevant holotypes, though this was not always possible. Where available, topotype material within the University of Nottingham, Department of Geology, Micropalaeontology Unit collections has been examined to support taxonomic conclusions.

Synonymy lists for Silurian species are comprehensive and annotated as recommended by Matthews (1973, after Richter, 1948). Ordovician collections are small and synonymy lists for these species have been short-

ened to include: the original species designation; any subsequent important taxonomic changes; the most recent full synonymy list.

Silurian conodont systematic palaeontology

Genus *Apsidognathus* Walliser, 1964

1964 *Apsidognathus* 1964, p. 29.

1964 *Astrognathus* 1964, p. 30.

Type species. *Apsidognathus tuberculatus* Walliser, 1964, p. 29.

Emended diagnosis. Apparatus comprised of a broad pastiniscaphate platform element, with variable platform ornament; a lenticular element with an inner-laterally extended platform and reduced or absent outer platform; an anguliscaphate ambalodontan element; a cruciform, astrognathodan element with a narrow laterally restricted basal cavity; a strongly arched and highly characteristic lyriform element; a laterally compressed element and a coniform element which develops short rudimentary lateral processes and a costa on the posterior edge.

Remarks. All elements are distinctive and species are characterised particularly by the variable ornament of the platform element and the shape and ornament of the lyriform element.

Apsidognathus contains similar elements to the Pa₁ and Pa₂ elements of *Astropentagnathus* (plate 3, figs 1–2); the platform develops multiple inner and outer processes and the lenticular element with a single lateral process. The ambalodontan element of *Apsidognathus* can be homologised with the Pb element of *Amorphognathus* (*sensu* Bergström, 1971, p. 132, fig. 13, N-T) though sinistral and dextral morphotypes are identical in *Apsidognathus*. The M elements in *Amorphognathus* and *Astropentagnathus* and the coniform element of *Apsidognathus* are teriopede and develop rudimentary lateral processes; additionally all three are rare in known collections. Assuming these similarities represent true homologies in the platform complex of these genera the remaining elements should represent the ramiform complex. In order to understand the possible homologies of these elements an *a priori* decision as to the location of the astrognathodan element has to be made. This element is bilaterally symmetrical and quadriramate and could occupy either the Sa or Sd positions in the apparatus. If the former is correct, then the logical homology would be to have the lyriform as the

Sb and the compressed element equivalent to the Sc element. The direction of compression thus changes between Sb and Sc elements, a feature of the symmetry transition series in better known apparatuses.

If the astrognathodan, however, represents the Sd element in a ramiform complex similar to that of *Amorphognathus*, it is then likely that the lyriform element either occupied both Sa and Sb positions or that no Sa element has yet been found. It is pertinent to note that the squat conical element of *A. ruginosus* (*sensu* Mabilard & Aldridge, 1983) is bilaterally symmetrical and may be the Sa element of this species. As currently perceived *Apsidognathus* could have an apparatus plan intermediate between that of *Amorphognathus* and *Astropentagnathus*, having the platform structure of the latter and the ramiform structure of the former.

Apsidognathus tuberculatus tuberculatus Walliser, 1964

Plate 1, figs 12–16; plate 2, figs 1–4

- 1962 n. gen B n. sp. Walliser, p. 282, fig. 1, no. 4.
 v*1964 *Apsidognathus tuberculatus* Walliser, p. 29, pl. 5, fig. 1; pl. 12, figs 16–22; pl. 13, figs 1–5.
 v1964 *Ambalodus galerus* Walliser, p. 27, pl. 6, fig. 1; pl. 12, figs 1–7.
 v1964 *Astrognathus tetractis* Walliser, p. 30, pl. 5, fig. 4; pl. 14, figs 1, 2.
 v1964 *Pygodus lyra* Walliser, p. 68, pl. 5, fig. 5; pl. 12, figs 8–14.
 v1964 *Pygodus lenticularis* Walliser, p. 67, pl. 4, fig. 17; pl. 12, fig. 15.
 1965 *Apsidognathus tuberculata*; Brooks & Druce, p. 375, pl. 1, figs 1, 9, 10.
 v1969 *Apsidognathus tuberculatus*; Nicoll & Rexroad, p. 24, pl. 3, fig. 8.
 1970 *Apsidognathus tuberculatus*; Moskalenko, pl. 1, figs 4, 5, 6a, 6b.
 1970 *Pygodus lyra*; Moskalenko, pl. 1, figs 9, 10.
 1970 *Ambalodus galerus*; Moskalenko, pl. 1, fig. 3.
 1971 *Astrognathus tetractis*; Schönlaub, p. 46, pl. 2, fig. 15.
 1971 *Pygodus lenticularis*; Schönlaub, p. 48, pl. 2, figs 13, 14.
 v1972 *Apsidognathus tuberculatus*; Aldridge, p. 165, pl. 2, figs 7, 9.
 v1972 *Ambalodus galerus*; Aldridge, p. 166, pl. 3, figs 6, 8.
 v1972 *Astrognathus tetractis*; Aldridge, p. 166, pl. 3, fig. 1.
 v1972 *Pygodus? lyra*; Aldridge, p. 210, pl. 3, fig. 2.
 v1975 *Apsidognathus tuberculatus*; Aldridge, pl. 1, figs 1, 2.
 v1975 *Ambalodus galerus*; Aldridge, pl. 3, fig. 9.
 v1975 *Pygodus? lenticularis*; Aldridge, pl. 3, figs 22, 23.
 1980 *Apsidognathus tuberculatus*; Helfrich, pl. 1, figs 25, 29.
 1981 *Apsidognathus tuberculatus*; Nowlan, pl. 7, figs 7, 12–14, figs 7, 12–14, 17.
 1981 *Apsidognathus tuberculatus*; Uyeno & Barnes, pl. 1, figs 14–17.
 1983 *Apsidognathus tuberculatus*; Nowlan, figs 4A, 4B.
 1985 *Apsidognathus tuberculatus*; Aldridge, pl. 3.2, figs 20–24.

- 1985 *Apsidognathus tuberculatus*; Savage, p. 715, figs 5A-N.
 p1986 *Apsidognathus tuberculatus tuberculatus*; Bischoff, p. 150, pl. 1, figs 1-7, 11-13, 22, 25-28; pl. 2, figs 1-4.
 1987 *Apsidognathus tuberculatus*; Over & Chatterton, pl. 4, figs 8, ?9, 10-14, 20, ?21.

Holotype. *Apsidognathus tuberculatus* Walliser, 1964, p. 28, pl. 5, fig. 1; pl. 12, fig. 18. Pa element from Cellon, layer 10D, Carnic Alps, Austria.

Emended diagnosis. The lyriform is diagnostic of the apparatus and has a short free anterior blade, its posterior platform is flattened-oval in outline with a straight posterior margin. The anterior and lateral platform margins are raised and bear an ornament of reticulate or transverse rugae. The platform element has a short free blade and nodose ridges which radiate from the centre of the element.

Description. Platform element. Falls within the range of morphology illustrated by Walliser (1964, pl. 13, figs 1, 2).

Lyriform element. Arched, planate element which is more or less bilaterally symmetrical longitudinally. Anterior free blade is short and slender, triangular in upper view with a reticulate ornament of low, sinuous rugae. A transverse ridge or swelling may separate the free blade from the main platform. The platform is narrow and has rounded anterior 'shoulders'; it flares towards the posterior and may be slightly inwardly curved. Its upper surface displays raised marginal ridges which bear an ornament similar to that of the free blade. The ornament extends for approximately two-thirds of the length of the platform. Centrally the platform has a

broad depression which is narrow anteriorly and broadens rapidly towards the posterior. The lateral faces of this depression are shallowly concave to convex and are unornamented. Towards the posterior a low medial ridge may be developed; this can extend up to the midlength of the platform. The posterior margin is smoothly concave when this medial ridge is absent, often indented when it is present.

In lower view the undersides of the marginal ridges are steeply inclined upwards and inwards. The basal cavity is restricted to a broad groove in the centre of the lower surface. It is deeply excavated, and surrounded by a narrow raised zone of recessive basal margin. Anteriorly the cavity terminates beneath the junction of the free blade and the platform, though the lower surface of the former may be shallowly excavated; posteriorly the basal cavity extends almost to the posterior margin of the element. Commonly the cavity is partially infilled with a thin layer of basal material, in these specimens the posterior eighth of the cavity is completely infilled and the remaining basal material develops a narrow slit-like depression in its lower surface (plate 2, fig. 2).

Ambalodontan element. Arched, anguliscaphate, with a prominent cusp at the apex of the element. The anterior process is longer and taller than the postero-lateral and has a more or less straight upper edge. The postero-lateral process forms an angle of 170°-175° to the anterior process, and is steeply inclined distally. This element has a widely flared base which is roughly oval in outline, the basal edge on several specimens bears small irregular nodes. The basal cavity commonly contains basal material.

Astrognathodan element. Cruciform, stelliplanate element comprising a slightly arched blade and more

Plate 1

Figs 1-11. *Apsidognathus tuberculatus arcticus* n. ssp.

- 1, upper view of platform element, × 40; MGUH 17.640 from GGU 216773.
- 2, upper view of lenticular element, × 40; MGUH 17.641 from GGU 275048.
- 3, oblique upper view of ambalodiform element, × 40; MGUH 17.642 from GGU 229035.
- 4, outer-lateral view of compressed element, × 40; MGUH 17.643 from GGU 229035.
- 5, posterior view of astrognathiform element, × 60; MGUH 17.644 from GGU 275048.
- 6, upper view of lyriform element, × 40; MGUH 17.645 from GGU 216773.
- 7, upper view of lyriform element × 40; MGUH 17.646 from GGU 229035.
- 8, 9, upper and lower views of lyriform element, × 40; MGUH 17.647 from GGU 229035 (holotype).

- 10, upper view of lyriform element, × 40; MGUH 17.648 from GGU 229035.
- 11, upper view of lyriform element, × 40; MGUH 17.649 from GGU 229035.

Figs 12-16. *Apsidognathus tuberculatus tuberculatus* Walliser. All specimens from GGU 82687.

- 12, upper view of platform element, × 40; MGUH 17.650.
- 13, inner-lateral view of ambalodiform element, × 40; MGUH 17.651.
- 14, posterior view of astrognathiform element, × 40; MGUH 17.652.
- 15, inner-lateral view of coniform element, × 60; MGUH 17.653.
- 16, upper view of lyriform element, × 40; MGUH 17.654.



strongly arched lateral processes; all the processes are denticulate. The anterior process is approximately twice as long as the posterior; the upper edge of the posterior process is steeply inclined downwards to the posterior. Both anterior and posterior processes bear up to five completely fused nodose denticles. The lateral processes are of similar length, normal to the blade and juxtaposed. The basal cavity is deeply excavated and slightly enlarged beneath the junction of the processes. The cavity extends as a narrow groove along the anterior and posterior processes, but not under the lateral processes.

Compressed element. Laterally compressed with a much deeper outer than inner face. Rounded triangular in lateral view the anterior and posterior edges are sharp and irregular. The posterior edge is concave and extended, basally to form a rudimentary posterior process; the basal margin is broadly convex downwards. The outer face is almost vertical and ornamented by longitudinal and oblique low rugae. Centrally two subparallel main rugae extend downwards from the apex; the anterior of the two extends to the basal margin. The posterior ruga terminates slightly below midheight where a series of short radiating rugae extend along the posterior process. Below the midheight short inclined rugae are situated along the anterior edge of the outer face, and are separated from the anterior longitudinal ruga by an unornamented gap. Inter-rugae areas are commonly smooth, but rarely bear discrete slender nodes. The inner face is again almost vertical with a narrow ledge of thickening at approximately one-third the height of the face. Beneath the thickening the face is inwardly inclined. The basal cavity is narrow and deeply excavated, with commonly a thin lining of basal material.

Coniform element. Tall slender tertiopedate element with a conspicuous ledge-like lower margin. The cusp is tall, approximately twice as high as broad and triangular in cross section. Its edges are extended to form short postero-lateral processes, its posterior face is shallowly

concave and bears a central longitudinal costa. The inner postero-lateral process is longer than the outer and bears three to four nodose denticles, which are fused almost to their tips; the outer process is little more than a thickened flange. In posterior view the upper edges of the lateral processes are inclined steeply downwards. The base of the cusp is expanded laterally to form a heart-shaped platform, narrow anteriorly and broad posteriorly with a concave indentation on the inner side just posterior of the inner-lateral process. The platform is ornamented by low discrete to coalescing nodes. Below the upper surface of the platform the lateral edges are steep with a deep, centrally situated, v-shaped groove which runs around the element. The entire lower surface is excavated and commonly has a thin layer of basal material within it.

Remarks. The majority of specimens of the platform element develop rows of nodes (as in Walliser, 1964, pl. 12, fig. 21) which differ from those of the holotype of *A. walmsleyi* Aldridge (1974, fig. 1A) by being well spaced; the inner and outer platforms are subequally developed in the Greenland specimens, and deep v-shaped depressions are developed between the processes.

The ambalodontan element compares closely with that previously described as *A. galerus* Walliser (1964), and specimens referred to that taxon by Aldridge (1974, p. 299) were regarded by him to be part of the *A. walmsleyi* apparatus. The Greenland specimens differ from those from Norway in possessing a more or less straight upper edge to the anterior process, thus approaching the morphology of Walliser's specimen (1964, pl. 2, fig. 6).

The lyriform element from the Greenland collection has a slightly more restricted basal cavity than the specimens figured by Walliser as *P. lyra* and the specimens of *P. lyra* Walliser (Aldridge, 1972, p. 210, pl. 3, fig. 2). The prominence of the postero-central ridge varies from

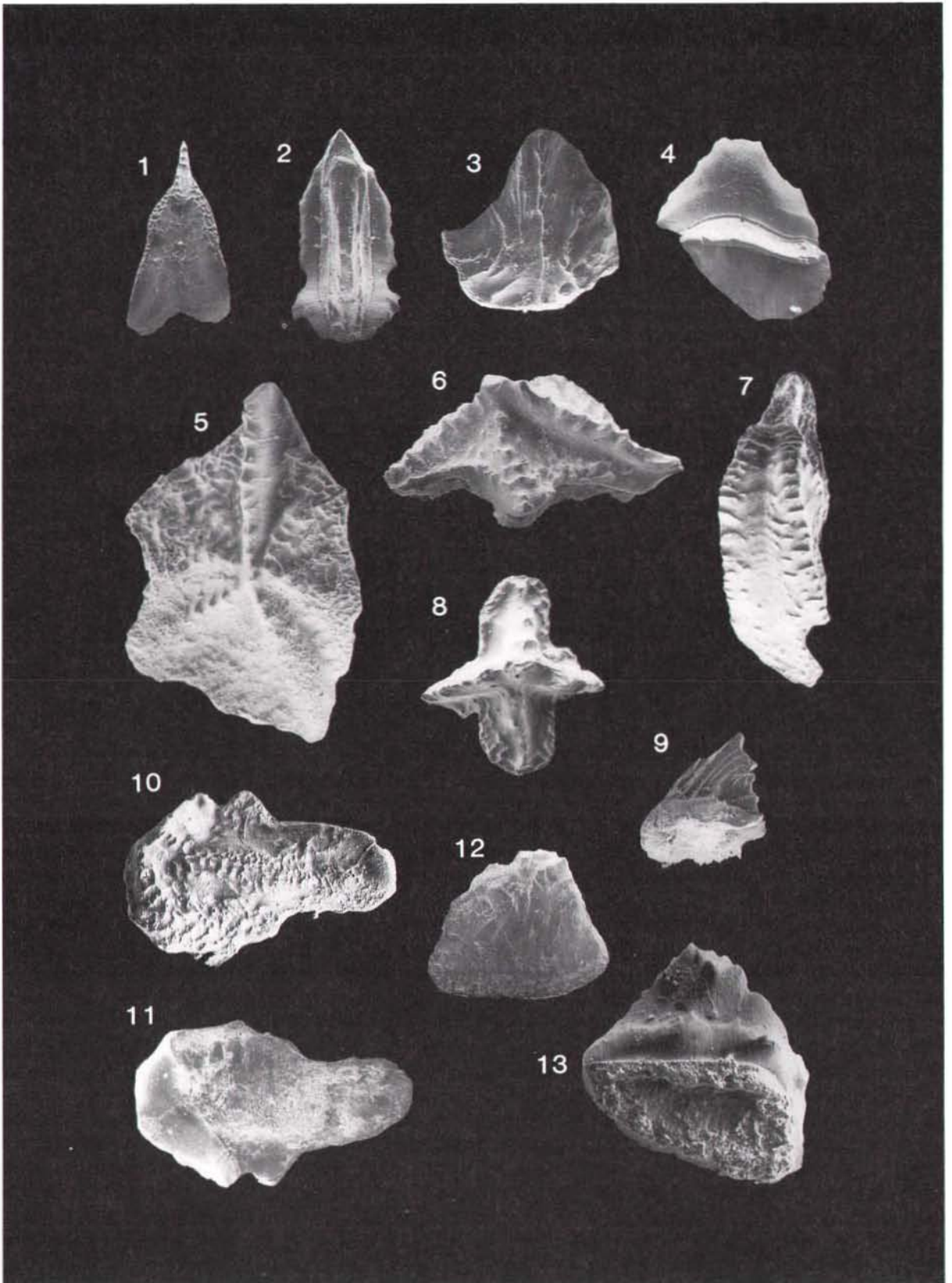
Plate 2

Figs 1-4. *Apsidognathus tuberculatus tuberculatus* Walliser.
All specimens from GGU 82687, × 40.

- 1, upper view of lyriform element; MGUH 17.655.
- 2, lower view of lyriform element; MGUH 17.656.
- 3, outer-lateral view of compressed element; MGUH 17.657.
- 4, inner-lateral view of compressed element; MGUH 17.658.

Figs 5-13. *Apsidognathus* n. sp.
All specimens from GGU 275048.

- 5, upper view of platform element, × 20; MGUH 17.659.
- 6, oblique upper view of ambalodontan element, × 40; MGUH 17.660.
- 7, upper view of lyriform element, × 20; MGUH 17.661.
- 8, upper view of astrogathiform element, × 40; MGUH 17.662.
- 9, outer-lateral view of coniform element, × 40; MGUH 17.663.
- 10, 11, upper and lower views of lenticular element, × 40; MGUH 17.664.
- 12, 13, outer-lateral and inner-lateral views of compressed element. Fig. 12, × 25, fig. 13, × 40; MGUH 17.665.



absent to barely prominent in the Greenland collections, the former being the most abundant. A range in the degree of prominence in this ridge is also shown by specimens from Gullet 4 (compare specimens, Aldridge 1972, pl. 3, fig. 2, with Aldridge 1975, pl. 1, fig. 2). The significance of this variation as a taxonomic criterion is unknown, and it does not appear to be ontogenetic as specimens of similar size occur with the ridge present or absent. The lyriform element of *A. walmsleyi* Aldridge (1975, figs 1C, 1D) has a strongly developed median posterior ridge and lobate antero-marginal ridges.

The astrogathodan elements of *A. tuberculatus tuberculatus*, *A. tuberculatus arcticus* and *A. walmsleyi* are similar, differing only in the relative lengths of the lateral, anterior and posterior processes; those of the former are more or less equal in length. That of *A. walmsleyi* has shorter, poorly denticulate anterior and posterior processes (Aldridge & Mohamed, 1982).

Occurrence. Found abundantly in GGU sample 82687 of *P. celloni* Biozone age from Hall Land, less abundantly in the uppermost *P. celloni* Biozone of Peary Land.

Apsidognathus tuberculatus arcticus n. ssp.

Plate 1, figs 1–11

Name derivation. From its apparent geographical restriction to Arctic Greenland.

Holotype. Specimen MGUH 17.646, a lyriform element from GGU 229035, plate 1, figs 8, 9.

Diagnosis. Characterised by the lyriform element which is robust, strongly arched and bears prominent marginal ridges and medial-posterior process.

Description. *Platform element.* Indistinguishable from that of *A. tuberculatus tuberculatus* (Walliser).

Lenticular element. Scaphate, platform well developed inner-laterally, narrow or absent outer-laterally. In upper view the platform is heart-shaped to spatulate in outline, narrowing inner-laterally. A low curved carina forms the outer-lateral margin; anteriorly this has steeply inclined lateral faces and a weakly serrate to irregular upper edge. Posteriorly the carina broadens and its midlength is inwardly curved, forming an angle of 140°–170° between the anterior and posterior processes. The posterior process is broadly rounded, lobate in large specimens and bears an ornament of low sinuous rugae which may coalesce to form a reticulum.

Outwardly the posterior process may be flared slightly to form a narrow outer-lateral process. In small specimens the posterior process does not extend to the steeply inclined posterior edge of the platform. On the inner side the narrow platform extends up to twice the longitudinal length. Centrally a broad, rounded ridge extends at 90° from the point of maximum curvature of the carina. The ridge has the same ornament as the posterior process. Its anterior and posterior faces are shallowly inclined and weakly ornamented to smooth. The posterior edge of the inner-lateral platform is upturned slightly and bears a narrow, outwardly tapering zone of ornament. The entire lower surface of the element is shallowly excavated; a deep groove beneath the carina may be differentiated. Commonly the lower surface is infilled with basal material.

Ambalodontan element. Arched, pyramidal, pastiniscaphate element with a prominent apical denticle. The anterior process maintains a constant height though inclined downwards; it bears eight to ten, low almost completely fused, nodose denticles. The postero-lateral process, forming an angle of 160°–170° with the anterior process, is shorter and more steeply downwards inclined than the anterior process. It is also only weakly denticulate; its lateral faces are steeply inclined and have a broad, outwardly convex lower margin. The inner-lateral face of this element may develop a broad, lobate, inner-lateral process. This arises centrally from the base of the apical denticle, is directed slightly antero-laterally and broadens distally. When this process is present, the lower margin of the element is indented between the processes. The inner-lateral process may bear a weak ornament of low nodes or sinuous rugae and nodes. The entire lower surface is deeply excavated.

Astrogathodan element. Cruciform, stelliplanate element with a prominent apical denticle. The anterior process is slightly longer than the posterior, and both are slightly longer than the lateral processes. Both anterior and posterior processes are straight. The former bears four to six nodose, fused denticles, and decreases in height distally. The posterior process bears one or two discrete short nodes and is steeply inclined downwards towards the posterior. Basally the posterior process flares forming a narrow platform which is ornamented by a weak reticulum of low sinuous rugae. The lateral processes are subequal in length and are orientated normal to the 'blade'. They are tall proximally and are inclined steeply downwards distally. Each bears four to six low, fused nodes. Basally the lateral processes may be arched, slightly more strongly downwards than the blade. A narrow zone of recessive basal margin surrounds the basal cavity, which is restricted to a narrow, deeply excavated groove beneath the anterior and

posterior processes. The basal cavity tapers distally and terminates before the tips of the processes.

Lyriform element. Longitudinally arched, robust, scaphate element. More or less bilaterally symmetrical about its long axis, though rare asymmetrical forms occur (plate 1, fig. 11). Anterior free blade is short and broad with an ornament of irregular nodes or short sinuous rugae, which are usually concentrated along a rounded central ridge. The lateral faces of the free blade are steeply inclined and occasionally bear an ornament of discrete nodes. A low transverse ridge or zone of ornament separates the free blade from the main platform. The platform is elongate with a rounded anterior margin. Two strongly posteriorly arched marginal ridges extend from the anterior margin; at approximately the platform midlength they are directed steeply downwards. Commonly the inner marginal ridge is slightly shorter than the outer. Both marginal ridges are ornamented with a low reticulum of sinuous rugae, the prominent elements of which run transversely. The ornament decreases in prominence posteriorly, in several specimens ornament is absent from the posterior half of the marginal ridges. The centre of the platform is shallowly depressed, varying from smooth to developing a similar ornament to the marginal ridges. A broad, rounded to rectangular posterior process arises from the centre of the platform and is free from the platform for the greater part of its length. The posterior process has a similar ornament to the marginal ridges and free blade, the distribution of this ornament varies from covering the entire process to being restricted to the posterior tip and lateral edges of the process. In this latter case the central area of the process may be shallowly depressed, only rarely ornamented by isolated nodes or sinuous low ridges. The lateral faces of the posterior process are almost vertical and usually devoid of ornament. The entire lower surface of the element is deeply excavated, beneath the free blade the cavity narrows and becomes shallower. The basal cavity is commonly infilled with basal material which may extend beyond the lower edge of the element. The variation within this element is illustrated in plate 1, figs 6–11.

Compressed element. Highly laterally compressed, scaphate element, the outer face is approximately half the length of the inner face. In inner-lateral view the element is rounded triangular in outline. The anterior edge is more or less straight with a central sinuous longitudinal costa along most of its length. The posterior edge is vertical to posteriorly inclined, postero-basally extended to form a short, rudimentary posterior process. The basal margin of the element is broadly convex downwards. The inner face bears an ornament of low, sinuous rugae. A prominent ruga extends down-

wards from the apex which just below the midlength furcates into a series of radiating short rugae, each terminating before the basal margin of the element. A low reticulum of rugae may be developed on inner face of the posterior process. The anterior half of the basal margin bears a narrow zone of shallow pits or low reticulum. The outer face of this element is smooth occasionally with an ornament of scattered low sinuous rugae. The basal cavity is deeply excavated and rounded triangular in outline, it is broad posteriorly and narrows anteriorly. The outer-lateral edge of the cavity is thickened slightly to form a narrow ledge. The basal cavity is commonly infilled by basal material.

Remarks. A coniform element such as those present in *Apsidognathus* n. sp. and *A. tuberculatus tuberculatus* has not been recognised. The lyriform element of *A. walmsleyi* Aldridge (1974, p. 301, figs 1C, 1D) has a similar overall morphology. It displays, however, smaller marginal ridges and develops a narrow ridge-like medial-posterior process.

The lenticular platform element of *A. tuberculatus arcticus* differs from its counterpart in *Apsidognathus* n. sp. in the prominence of the lateral process and difference in upper surface ornament.

Occurrence. Found in moderate abundance in GGU 216773 from Washington Land and GGU 229035 from eastern Peary Land. In GGU 275048 it occurs with *Apsidognathus* n. sp. Specimens occur infrequently in the *P. celloni* Biozone strata of Wulff Land.

Apsidognathus n. sp.

Plate 2, figs 5–13

p1986 *Apsidognathus tuberculatus*; Bischoff, p. 150, figs 17–21, 23–24.

Description. Platform element. Scaphate with long carina, two inner-lateral processes and three outer-lateral processes. The platform is slightly longer than broad, is broadly oval in upper outline, shallowly indented between the lateral processes. Anteriorly the free blade is short, high and slightly laterally expanded; it continues posteriorly across the platform as a nodose carina. At midlength the carina is low and sharply inwardly curved, an angle of approximately 120° being developed between the anterior and posterior processes. The posterior process is low and lobate and broadens distally where it becomes increasingly indistinct. Occasionally the posterior bears a central row of diffuse nodes. The inner side of the platform is approximately half the width of the outer platform. From the point of maxi-

imum curvature of the carina two lobate processes diverge antero- and postero-laterally, the anterior process at an angle of 10° – 20° from the anterior carina and the posterior process by 20° – 30° from the posterior carina. Both inner-lateral processes are narrow, rounded ridges which decrease in height and broaden distally. At approximately two-thirds of their length they become difficult to distinguish. Both bear an ornament of low, sinuous, transverse rugae or nodes. The process inter-areas have a reticulate ornament to low sinuous rugae; the most prominent rugae join with those on the processes. On the outer side three processes diverge from the point of maximum curvature of the carina. The most anterior is lower and less prominent than the others, diverging at an angle of 30° from the carina, from which it is separated proximally at an angle of 80° – 90° from the posterior carina. The remaining process bisects the angle developed between the antero- and postero-lateral processes. At their midlength the outer-lateral processes broaden rapidly, occasionally developing a bifurcating distal end. The processes have an ornament of closely spaced low, transverse rugae which extend into the concentrically orientated rugae of the process inter-areas. The lower surface is shallowly excavated and commonly contains a thin layer of basal material.

Lenticular element. Scaphate with a well developed inner platform, the outer platform is absent or reduced to a flaring of the posterior process. In upper outline the element is a flattened oval with broadly rounded lateral ends. A low, broadly rounded carina forms the outer-lateral margin, anteriorly this is weakly, inwardly bowed; at its midlength this is incurved and broadens to a rounded lobate process. Anteriorly the carina bears an ornament of low longitudinal rugae, posteriorly it bears a low reticulum of rugae; the more prominent of these are orientated transversely. On the inner side the platform is approximately twice as broad as long. Centrally it is raised to form a broadly rounded indistinct process which bears an ornament of irregular low rugae and low diffuse nodes. The entire lower surface of the inner platform is shallowly excavated and commonly contains a thin layer of basal material.

Ambalodontan element. Arched, pyramidal, pastiniscaphate element with a prominent apical denticle. The anterior process decreases in height anteriorly; it bears up to eight low partially fused denticles. The postero-lateral process is directed inwards to form an angle of approximately 170° with the anterior process, it is commonly lower than the anterior and bears six tall, almost completely fused denticles. An inner-lateral process diverges from the centre of the apical denticle and is anteriorly directed, forming an angle of 70° – 80° with the anterior process. It is broader than the other processes,

possessing an ornament of high transverse ridges. The lateral faces of the element are steeply inclined and the lower margin is strongly indented between the processes on the inner side. The entire lower margin is thickened, ornamented by coalescing nodes, whose prominence varies around the element. Scattered small nodes may develop on the lateral faces. The entire surface is deeply excavated.

Astrognathodan element. Cruciform, stelliplanate element with a prominent apical denticle. The anterior process is longer than the posterior and both are slightly longer than the lateral processes. The anterior process is straight, bearing four or five nodose, fused denticles. The posterior process is straight to inwardly curved and in all specimens has no well preserved denticles. The lateral processes are juxtaposed just posterior of the midlength of the blade. They are equal in length, tall proximally and decreasing in height distally; each bears two or three nodose denticles. Basally the anterior and posterior processes flare to form a narrow platform which in upper view is rounded rectangular in outline; it is not extended to the tips of the lateral processes. The margin of the platform is raised and bears an ornament of low sinuous rugae and small coalescing nodes. A narrow zone of recessive basal margin surrounds the basal cavity thus restricting it to a narrow, deeply excavated groove beneath the anterior and posterior processes. The cavity tapers distally and terminates before the tips of the processes.

Lyriform element. Arched, scaphate element, which is more or less bilaterally symmetrical, longitudinally. Anterior free blade is short and broad with an ornament of irregular nodes to low sinuous rugae. A low transverse ridge separates the blade from the main platform. The platform is narrow and consists of two, narrow raised marginal ridges separated by a broad central depression. The platform flares posteriorly and is strongly arched; it may be slightly inwardly curved. The marginal ridges decrease in height and flare slightly at their midlength. Both bear an ornament of low transverse rugae; posterior of midlength these are reduced in length rarely extending beyond the midpoint of the marginal ridge. On larger specimens short inner and outer transverse rugae alternate along the posterior half of the marginal ridges, and larger rugae may extend across the whole platform. Posteriorly the platform margin is weakly concave and ornamented by a narrow zone of small, low discrete to coalescing nodes. The lower surface has a marginal, narrow zone of recessive basal margin, centrally the lower surface is deeply excavated, under the free blade the cavity is narrow and groove-like, but still deep.

Compressed element. Laterally compressed, scaphate

element, rounded triangular in lateral view with a broadly rounded apex. The anterior edge is broadly convex, the posterior edge anteriorly inclined and postero-basally extended to form a short rudimentary process. The basal margin may be more or less straight to convex downwards. The inner face is approximately twice as long as the outer and bears an ornament of irregular, low, sinuous rugae. These tend to become oblique towards the edges of the face and on larger specimens may be more common here. The lower margin of the inner face is ornamented with a narrow zone of discrete and coalescing nodes which becomes more diffuse and disappears upwards. The outer face is basally thickened and bears occasional scattered nodes. Above this edge the face is steep and commonly smooth, but rarely bearing isolated, low nodes. In outer-lateral view the basal cavity has a rounded-triangular outline, tapering along the posterior process. The cavity is deeply excavated and commonly has a thin layer of basal material.

?*Coniform element*. A single poorly preserved, sphaerate pyramidal element. Laterally compressed; inner-laterally it has a tall rounded triangular outline, postero-basally extended as a short postero-lateral process; this has a serrated upper edge. The inner face is ornamented by up to eight longitudinal costae. On the outer side a short flange-like postero-lateral process diverges from the anterior edge of the element. The lower margin of the element is thickened, broadly rounded and rarely has an ornament of scattered isolated nodes. The entire lower surface is excavated.

Remarks. All elements of *Apsidognathus* n. sp. differ from those of previously described species of *Apsidognathus* though there is some morphological similarity to *A. ruginosus* Mabillard & Aldridge (1983), particularly in the platform and lyriform elements. The platform element of *Apsidognathus* n. sp. typically has an ornament of concentrically arranged low rugae only on the outer side of the platform, whereas the whole platform of *A. ruginosus* has this ornament. The lyriform element of both species has a similar upper outline, but that of *Apsidognathus* n. sp. has narrower marginal ridges and a moderately broad central depression which is generally unornamented.

The astrogathodan and ambalodontan elements of *Apsidognathus* n. sp. have a thickened and ornamented basal margin, which is absent in their counterparts in *A. ruginosus*. Additionally the ambalodontan element of the former is much narrower and more strongly pyramidal and develops an inner-lateral process; that of *A. ruginosus* is flattened, almost circular in upper outline and lacks an inner-lateral process. These characters also

distinguish the ambalodontan and astrogathodan elements from their counterparts in *A. tuberculatus arcticus*, *A. tuberculatus tuberculatus* and *A. walmsleyi*.

Mabillard & Aldridge (1983) included slender conical and squat conical elements in the apparatus of *A. ruginosus*. The squat element is comparable with that named *Pseudooneotodus* n. sp. by Cooper (1977a, pl. 2, figs 12, 13). The coniform(?) element of *Apsidognathus* n. sp. differs from both of the conical elements of *A. ruginosus* in possessing two short postero-lateral processes and an inner face ornamented by up to eight longitudinal costae.

Until larger collections of *A. ruginosus* and *Apsidognathus* n. sp. are available, the intraspecific variation of their constituent elements cannot be assessed. *Apsidognathus* n. sp. may prove to be synonymous with, or a geographical subspecies of, *A. ruginosus*.

Occurrence. Occurs with abundant *Pterospathodus pennatus rhodesi*, *P. amorphognathoides* and *A. tuberculatus arcticus* in GGU 275048 Valdemar Glückstadt Land.

Genus *Aspelundia* Savage, 1985

Type species, *Aspelundia capensis* Savage, 1985, p. 725.

Emended diagnosis. Septimembrate comprising digyrate (Pa) and angulate (Pb) elements with twisted processes; dolabrate, alate, tertiope date, modified tertiope date and bipennate elements form the ramiform complex. All elements are highly compressed.

Remarks. Savage (1985, p. 725) erected *Aspelundia* n. gen. to include elements of late *Pterospathodus amorphognathoides* Biozone age which had pronounced lateral processes, small or no basal cavity and a high degree of lateral compression. Within the apparatus of the type species, *A. capensis*, he placed a digyrate Pa (figs 19A,B), digyrate Pb (figs 19E,F), digyrate M (figs 19G-I), tertiope date Sb (figs 19M,N) and a digyrate Sc (fig. 19L). He also figured and described an alate Sa element (figs 19Q-T) though did not include this in the diagnosis.

Based upon the large collections from the *Pterospathodus celloni* Biozone of North Greenland and the lower *P. amorphognathoides* Biozone of the McKenzie Mountains (Over & Chatterton, 1987) it is apparent that species attributable to *Aspelundia* had a septimembrate apparatus, by virtue of bearing elements with strong lateral compression, variably twisted lateral processes, small basal cavity and similar white matter distribution.

The emended generic concept can be illustrated by

comparing homologous elements in *A. fluegeli* (herein) and '*Aspelundia*' n. sp. 1 Over & Chatterton, 1987. The platform complex comprised a digyrate (Pa) element (plate 3, fig. 1 with plate 5, figs 11, 14) and an angulate (Pb) element (plate 3, fig. 2 with plate 5, fig. 1). The ramiform complex contained a dolabrate (M) element (plate 3, fig 3 with plate 5, fig. 13), an alate (Sa) element (plate 3, fig. 4 with plate 5, fig. 17), tertiopeadate (Sb) elements (plate 3, figs 5–7 with plate 5, fig. 16) and bipennate (Sc) elements (plate 3, figs 11, 12 with plate 5, fig. 15). *A. fluegeli* also possessed a modified tertiopeadate (Sd) element (plate 3, figs 8–9) which has not been described for the other species.

Using the revised concept for the genus it is apparent that Savage (1985) only figured a partial reconstruction for the type species, Pa (figs 19A–L), ?Sa (figs 19Q–T) and Sb (figs 19M–P). Samples 3, 17 and 19 from the Heceta Limestone contain abundant *A. capensis* and *Pandorinellina plana* elements. The latter has an identical apparatus plan to that proposed for *Aspelundia*. The Pa element (figs 18B, ?D–E; *non* fig. 18C which is an Sc element) has the root of a lateral process just to the posterior of a prominent cusp, a characteristic of the Pa element of '*Aspelundia*' ?n. sp. 2 Over & Chatterton (1987, plate 5, fig. 19). The Pb element (Savage, 1985, figs 18F,H) is large, robust, has rounded denticles and possesses a narrow ledge-like platform beneath the denticle row. This may be an element of *Oulodus*, a gerontic *Aspelundia* Pb element or an aberrant form. The remaining elements, M (figs 18H–J), Sa (figs 18V–Y) and Sc (figs 18O–Q) are typical of *Aspelundia* species. From the illustrations it is difficult to decide whether or not these elements belong to *A. capensis sensu* Savage. This species is a partial reconstruction based upon common occurrence of the elements in the Heceta Limestone and which may have had vicariously shared Pb,

M, Sa and Sc elements with '*Aspelundia*' n. sp. 2 Over & Chatterton, 1987.

It is apparent from Pa morphology that the evolution of *Aspelundia* involved a reduction in the size of the basal cavity and an increase in the twisting of the processes and the number of denticles on the Pa, Pb and Sa elements. *Aspelundia* and some species of *Ozarkodina* appear to be closely related, particularly with *O. polinclinata* (Nicoll & Rexroad) *sensu* *Oulodus* Cooper (1977a, p. 1058) and *O. pirata* McCracken & Barnes (*O. aff. O. polinclinata sensu* Aldridge, 1979) which have almost indistinguishable M and Sc elements from *Aspelundia* species.

Aspelundia expansa n. sp.

Plate 3, figs 13–20

Name derivation. '*expansa*' refers to the broadly expanded basal cavity present in all elements of the apparatus of this species.

Holotype. Specimen MGUH 17.687, plate 3, fig. 13; a Pb element from sample GGU 216837, Cape Schuchert Formation, Kap Schuchert, Washington Land, western North Greenland.

Diagnosis. *Aspelundia* species in which the elements have compressed robust denticles and a broad, shallowly excavated basal cavity. Modified angulate Pa element.

Description. *Pa element.* Modified angulate element consisting of a prominent cusp and anterior and outwardly twisted and occasionally bowed posterior process. The cusp is laterally compressed, posteriorly in-

Plate 3

Figs 1–9. *Aspelundia fluegeli* (Walliser).
All specimens from GGU 216852, × 60.

- 1, inner-lateral view of Pb element; MGUH 17.675.
- 2, inner-lateral view of Pa element; MGUH 17.676.
- 3, inner-lateral view of M element; MGUH 17.677.
- 4, lower view of Sa element; MGUH 17.678.
- 5, posterior view of Sb₁ element; MGUH 17.679.
- 6, posterior view of Sb₂ element; MGUH 17.680.
- 7, posterior view of Sb₃ element; MGUH 17.681.
- 8, posterior view of Sd element; MGUH 17.682.
- 9, posterior view of Sd element; MGUH 17.683.

Fig. 10. *Aspelundia* n. sp. 1 (Over & Chatterton).
MGUH 17.684, from GGU 216852, × 60.

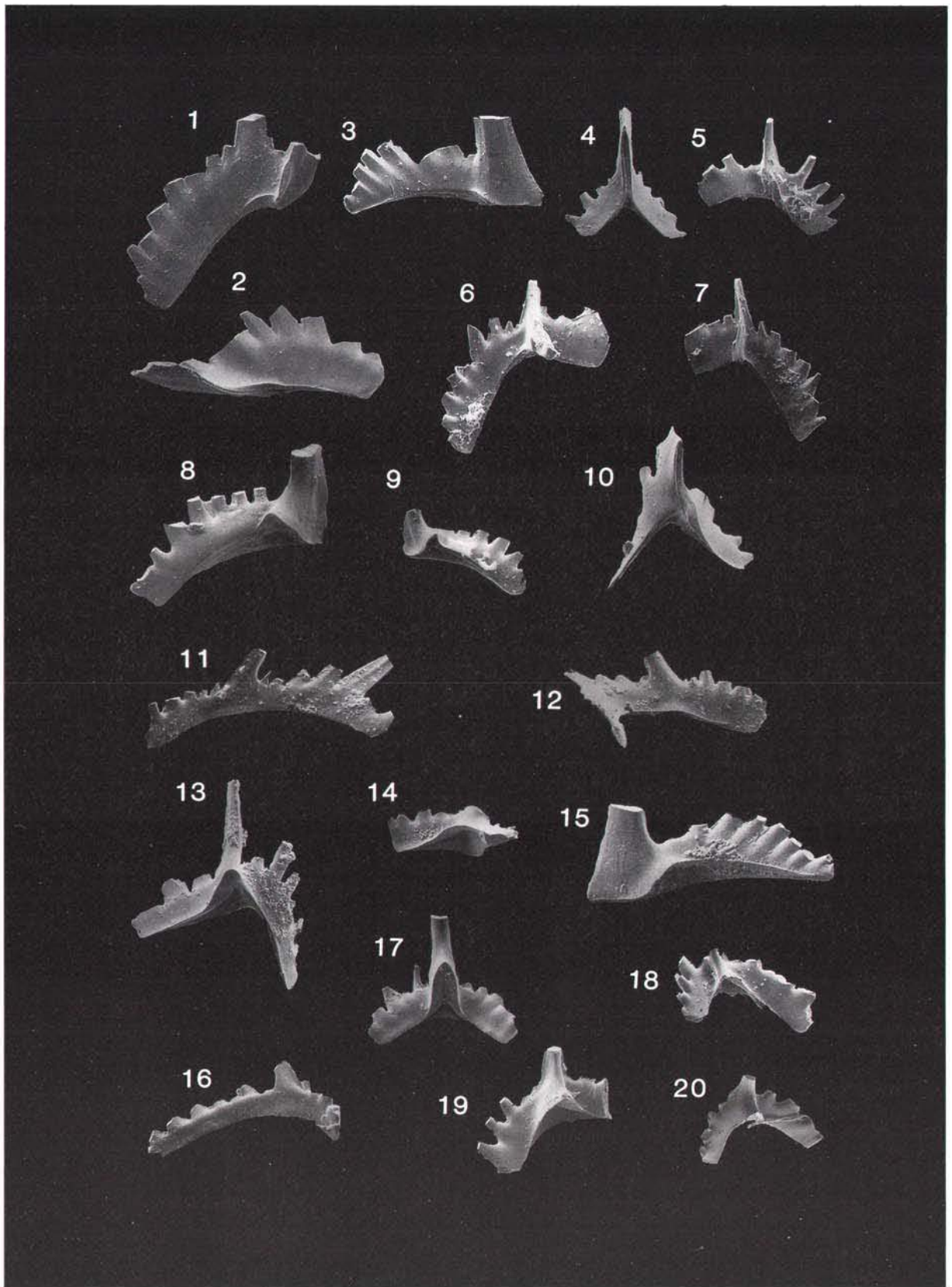
- 10, lower view of Pa element.

Figs 11–12. *Aspelundia fluegeli* (Walliser).

- 11, inner-lateral view of Sc element; MGUH 17.685.
- 12, inner-lateral view of Sc element; MGUH 17.686.

Figs 13–20. *Aspelundia expansa* n. sp.
All specimens from GGU 216837, × 60.

- 13, oblique lower view of Pb element; MGUH 17.687 (holotype).
- 14, inner-lateral view of Pa element; MGUH 17.688.
- 15, inner-lateral view of M element; MGUH 17.689.
- 16, inner-lateral view of Sc element; MGUH 17.690.
- 17, lower view of Sa element; MGUH 17.691.
- 18, posterior view of Sb₂ element; MGUH 17.692.
- 19, posterior view of Sb₁ element; MGUH 17.693.
- 20, posterior view of Sb₁ element; MGUH 17.694.



clined and lenticular in cross section. The anterior process lies in the plane of the cusp, is shorter than the posterior process and bears up to three laterally compressed, partially fused, posteriorly inclined denticles. The posterior process bears up to four compressed, posteriorly inclined denticles, separated by v-shaped spaces. The basal cavity is broadly excavated beneath the cusp and oval in lower outline, extending as a broad, tapering groove to the tips of the processes. White matter forms blocks completely filling each denticle and the cusp.

Pb element. Digyrate element consisting of a small cusp and two denticulated lateral processes; the inner process is the shorter and is twisted anteriorly. Occasionally a short adenticulate inwardly directed projection is present beneath the first proximal denticle of the inner-lateral process. The cusp is small, rarely broader than the denticles, laterally compressed and inclined slightly towards the inner-lateral process. It has a flattened lenticular cross section. The outer-lateral process is straight and downturned, forming an angle of 100° with the lateral edge of the cusp. It bears four to ten laterally compressed, partially fused denticles, these are inclined towards the cusp. The inner-lateral process bearing up to ten compressed denticles, of which the two most proximal are smaller than the others. The basal cavity is broadly expanded beneath the cusp, its lower posterior edge is upturned and asymmetrically inclined towards the inner-lateral process. In lower view it is rounded in outline and tapers rapidly to a narrow groove which extends to the tips of the processes.

M element. Dolabrate, with large laterally compressed, posteriorly inclined cusp and a long inwardly bowed posterior process. The cusp is separated slightly from the posterior process and is inwardly twisted; its anterior edge is sharp, its posterior edge rounded. The posterior process is compressed, directed outwardly and bowed inwardly. It bears six to eight compressed, posteriorly inclined denticles, which are separated from the cusp. The denticles increase in size towards the centre of the process. The basal cavity is shallowly excavated beneath the cusp, its inner, lower edge is upturned and flares laterally beneath the posterior edge of the cusp and process.

Sa element. Alate, the cusp is oval in outline and is highly inclined to the posterior. Compressed lateral processes of equal length arise from the antero-lateral edges of the cusp; these are bowed posteriorly and downwardly directed, in posterior view forming an angle of 160° between their lower edges. Each bears up to five compressed partially fused, tall denticles. The basal cavity is laterally expanded, extending as a broad

groove beneath the cusp and as a narrower groove along the processes.

Sb₁ element. Tertiopectate element with a short posterior projection at the base of the cusp. The cusp is laterally compressed with a broadly rounded anterior and sharp costate posterior edge; it is rounded triangular in midheight cross section and inclined towards the inner-lateral process. The lateral processes diverge, antero-laterally and arch downwards, the outer is longer and more steeply inclined than the inner. An asymmetrical arch of some 110° is produced between the lower edges of the processes, both bearing up to five, compressed, discrete, but closely packed denticles which are inclined away from the cusp. Denticles on the outer-lateral process are more closely packed than those on the inner-lateral process. The posterior edge of the basal cavity is posteriorly expanded and upturned beneath the cusp, where it is laterally restricted; extending as a rapidly tapering groove to the tips of the processes. In lower view the cavity beneath the cusp is triangular.

Sb₂ element. Similar to but much rarer than the *Sb₁* element. Differing only in the morphology of the cusp and basal cavity outline. Both the anterior and posterior edges of the cusp are rounded, the posterior edge lacking the costa of the *Sb₁* element. Accordingly the basal cavity margin is broadly rounded, oval in outline beneath the cusp. The basal cavity extends as a tapering groove to the tips of the lateral processes.

Sc element. Bipennate element consisting of a short anterior and a long posterior process. The cusp is laterally compressed, posteriorly inclined, and rounded lenticular in cross section. The anterior process is directed downwards, forming an angle of 110° to the anterior edge of the cusp, and slightly inwardly bowed along its length. It bears up to six compressed, closely packed denticles. The straight posterior process is also directed slightly downwards and bears six to eight compressed, posteriorly inclined denticles. The basal cavity is expanded beneath the cusp extending as a narrow groove to the tips of the element.

Remarks. The apparatus structure is similar to *A. fluegeli*, although no *Sd* element has been found in the Greenland collections.

Occurrence. Common in the middle Llandovery of Washington Land, found infrequently in Wulff Land and Kronprins Christian Land.

Aspelundia fluegeli (Walliser, 1964)

Plate 3, figs 1-9, 11, 12

- v*1964 *Lonchodina fluegeli*, p. 44, pl. 6, fig. 4; pl. 32, figs 22-24.
- v1964 *Neoprioniodus planus* Walliser, p. 51, pl. 4, fig. 10; pl. 6, fig. 3; pl. 29, figs 12, 13, 15.
- v1964 ?*Roundya trichonodelloides* Walliser, p. 72, pl. 6, fig. 2; pl. 31, figs 22-25.
- 1966 *Lonchodina fluegeli* Spasov & Filipović, p. 42, pl. 2, fig. 10.
- 1968 *Roundya?* sp. D Igo & Koike, p. 18, pl. 3, fig. 29.
- p1968 *Trichonodella symmetrica*; Igo & Koike; p. 19, pl. 3, fig. 10; non fig. 11.
- 1968 *Plectospathodus extensus*; Igo & Koike, p. 15, pl. 3, fig. 12.
- ?1968 *Roundya* sp. B Igo & Koike, p. 17, pl. 1, figs 1, 2.
- ?1968 *Neoprioniodus planus*; Igo & Koike, p. 12, pl. 1, figs 15, 18; pl. 3, fig. 21.
- v1972 *Hibbardella? trichonodelloides*; Aldridge, p. 182, pl. 6, figs 17, 18.
- v1972 *Lonchodina detorta*; Aldridge, p. 190, pl. 8, fig. 6.
- v1972 *Lonchodina fluegeli*; Aldridge, p. 190, pl. 8, fig. 7.
- v1972 *Neoprioniodus planus*; Aldridge, p. 195, pl. 5, fig. 23.
- p1975 *Ozarkodina plana*; Sweet & Schönlaub, p. 52, pl. 1, figs 1, 3, 4, 25, 6 only; non fig. 2.
- v1979 *Oulodus? fluegeli*; Aldridge, p. 14, pl. 2, figs 6-11.
- 1980 Gen. and sp. indet. A Helfrich, p. 568, pl. 1, figs 7-12.
- 1982 *Oulodus? fluegeli*; Aldridge & Mohamed, pl. 11, figs 26, 27.
- 1983 *Oulodus? cf. O.? fluegeli*; Uyeno & Barnes, p. 19, pl. 1, figs 1-6.
- v1983 *Oulodus? fluegeli*; Mabillard & Aldridge, pl. 2, figs 15, 16.
- v1985 *Oulodus? fluegeli*; Aldridge, p. 80, pl. 3.1, figs 18-23.
- 1985 *Oulodus? fluegeli*; Norford & Orchard, p. 11, pl. 1, figs 2, 9, 10, 12-14, 16-18, 20, 21.
- 1986 *Oulodus planus planus*; Bischoff, p. 80, pl. 19, figs 39-41; pl. 20, figs 1-7, 17-44; pl. 21, figs 1-12.
- 1987 *Oulodus? fluegeli*; Over & Chatterton, p. 23, pl. 1, figs 30-38.

Holotype. *Lonchodina fluegeli* Walliser, 1964, p. 44, pl. 6, fig. 4; pl. 32, fig. 24. From the Llandoverly of Cellon in the Carnic Alps (Austria).

Emended diagnosis. A species of *Aspelundia* in which all the elements are characterised by a narrowly expanded basal cavity and compressed denticles; the Pa, Pb, M and Sc elements have variably twisted and flexed processes.

Description. *Pa element.* Modified angulate, pectini-form element, with two laterally compressed denticulated processes. The cusp is posteriorly inclined, laterally compressed and lenticular in cross section. The

anterior process is generally shorter than the posterior and bears four or five discrete, though closely packed, denticles. The inclination of these varies from vertical to slightly posteriorly inclined. The posterior process has four or five denticles, its upper edge is twisted outwards, almost becoming horizontal in some specimens. Distally the posterior process may be slightly inwardly bowed. The basal cavity is only slightly flared beneath the cusp and extends as narrow grooves to the tips of the processes. In lateral view white matter, in the form of regular separate blocks, completely fills and is restricted to each denticle and the cusp. The base of these white matter blocks never extends below the midheight of the processes.

Pb element. Digyrate element with two lateral processes and occasionally a short posterior or postero-lateral process. The cusp is tall and slender, rarely broader than the denticles; it is laterally compressed and has a lenticular midheight cross section. The outer-lateral process is straight and downturned forming an angle of approximately 120° with the outer lateral edge of the cusp. It bears up to ten compressed partially fused denticles, which are inclined slightly towards the cusp. The inner-lateral process is usually the shorter of the two and is downturned and sharply anteriorly twisted. Maximum twisting occurs beyond the first proximal denticle. This process bears up to five closely packed compressed denticles which are inclined away from the cusp. Beneath the cusp or under the first proximal denticle on the outer-lateral process, a short posterior or postero-lateral denticulate process is occasionally developed; this is broken in all specimens. The basal cavity is shallowly excavated, broadest beneath the cusp and tapering rapidly to a groove which extends to the tips of the processes. White matter is distributed as in the Pa element.

M element. Dolabrate with a tall, laterally compressed, posteriorly inclined cusp and posterior process. The anterior edge of the cusp is sharp, the posterior variously rounded to sharp. The cusp is offset from the plane of the posterior process, rotated slightly inwards. The posterior process is compressed and flexed, and bears six to eight closely packed denticles. These are commonly fused to midheight and increase in height towards the centre of the process. The lower edge of the element steps up to beneath the posterior edge of the cusp and posterior process. The lower margin is slightly flared inwards. The basal cavity is shallowly excavated and most widely flared beneath the posterior edge of the cusp; it extends as a narrow groove to the tip of the posterior process. White matter distribution is comparable with that in the Pa element.

Sa element. Symmetrically arched, alate element,

comprising a long, compressed posteriorly inclined cusp, two long anterior-lateral processes and a much reduced posterior process. The cusp is strongly compressed, flattened lenticular in midheight cross section. Compressed, antero-lateral processes, equal in length, diverge from the anterior edge of the cusp; these are arched antero-laterally forming an angle of 90°. Each process bears up to eight small, compressed denticles, which are only partially fused. The basal cavity is deepest beneath the cusp, extending posteriorly as a long, narrow groove; beneath the lateral processes the cavity is narrower, the cavity extends to the tips of all the processes.

Sb elements. Sb₁-tertiopedate element with a short posterior process. The cusp is inclined inwards, laterally compressed and lenticular in midheight cross section; it is extended posteriorly at its base as a prominent longitudinal costa, which may develop into a short posterior process, bearing two or three compressed denticles (plate 3, fig. 6). Alternatively this process may be absent (Sb₂) (plate 3, fig. 5) in which case the posterior edge of the basal cavity is arched upwards, laterally restricted and inclined towards the inner process. Two compressed antero-lateral processes diverge from the anterior edge of the cusp. The inner of the two is shorter and bears up to four broad partially fused denticles, the outer process bears up to seven denticles. The basal cavity is shallowly excavated beneath the cusp and extends as a broad groove beneath the processes. White matter distribution is as described for the P elements.

Sc element. Bipennate with a short, inwardly bowed anterior process and longer posterior process. The cusp and denticles are laterally compressed and posteriorly inclined, the cusp is lenticular in cross section. The denticles are closely packed, usually fused on the anterior process; there are up to six denticles on the anterior process and six to eight on the posterior process. The distal tip of the posterior process is commonly twisted inwards, occasionally recurved to be directed anteriorly (plate 3, fig. 12). The basal cavity is wide beneath the cusp, extending as a narrow groove to the tips of the processes. A secondary widening of the cavity may occur beneath the distal flexure of the posterior process.

?Sd element. Modified tertiarypedate element, consisting of a laterally compressed, posteriorly expanded cusp and long, downwardly arched outer-lateral process. The lateral edges of the cusp are sharp. The outer process diverges from the base of the cusp, forming an angle of 100°–120° with the edge of the cusp; it bears up to eight compressed denticles which are separated from the cusp by a narrow gap. The posterior edge of the basal cavity is posteriorly extended and broadly arched. The basal cavity is broad beneath the cusp, shallowly excavated,

extending beneath the outer process as a narrow groove. White matter distribution is similar to that of the outer elements.

Remarks. *A. fluegeli* differs from the stratigraphically older *A. expansa* n. sp. in the morphology of the Pb and Sb elements and the narrower basal cavity of all elements. The Sd element described herein is rare, occurring only in large collections. This may be a separate member of the apparatus or an aberrant M/Sb element. Two Sb morphotypes are associated with *A. fluegeli* elements, differing on the presence or absence of a posterior process.

Apparatus bauplans with multiple Sb elements are not uncommon. From the Upper Silurian, Kuwano (1982) has recorded two Sb elements in the apparatus of *Ozarkodina excavata excavata* (Branson & Mehl) and Sparling (1981, p. 304) has suggested that *Oulodus elegans* (Walliser) may have had a seventh element assignable to a second Sb position. The Devonian *Oulodus angulatus* (Hinde), described by Nicoll (1977) from a natural assemblage in the fish gut of a palaeoniscoid fish, contains two Sb elements which compare closely in postero-basal cusp morphology with the two Sb morphotypes of *Aspelundia fluegeli*. By the Carboniferous apparatus structures with two Sb elements appear to have become extremely common (Norby, 1976). Over & Chatterton (1987, pl. 5, figs 22–23) figure two similar Sb morphotypes in their reconstruction of *Oulodus?* n. sp. 2 a species probably synonymous with *A. capensis*.

As first revisors Sweet & Schönlaub (1975) included within their concept of *Ozarkodina plana* a mixture of elements attributable to *A. fluegeli* and *Ozarkodina excavata* (Aldridge, 1979, p. 15). Subsequently, Aldridge (1979) erected a new species *Oulodus? fluegeli* placing in synonymy the Pb, Sb and M elements of *Ozarkodina plana*. The planiform M element formerly referred to *Neoprioniodus planus* of Walliser (1964) is extremely difficult to distinguish from the M element of *Ozarkodina polinclinata* (Nicoll & Rexroad), reconstructed by Cooper (1977, p. 1058). Consequently, the specific name *planus* may be considered a *nomen dubium* and the action of Aldridge (1979) is supported, this species bearing the name *A. fluegeli* rather than *A. plana*.

Occurrence. Extremely abundant in middle-upper Llandovery samples at Kap Schuchert (fig. 21). Here *A. fluegeli* is associated with abundant *Dapsilodus obliquicostatus* almost to the exclusion of other species. In Peary Land *A. fluegeli* is restricted to the *P. celloni* Biozone. The M and Sc elements of this species are indistinguishable from those of *Ozarkodina pirata* and,

when the two species occur together these elements may have been misidentified.

Aspelundia n. sp. 1 (Over & Chatterton, 1987)

Plate 3, fig. 10.

- 1969 *Diadelognathus* spp. Nicoll & Rexroad, p. 29–31, pl. 6, figs 1–10.
 1983 *Oulodus? fluegeli* subsp. A. Uyeno in Uyeno & Barnes, p. 18–19, pl. 7, figs 11–20, ?22.
 1983 *Oulodus? fluegeli*; Mabillard & Aldridge, pl. 2, figs 15–16.
 1987 *Oulodus? n. sp. 1* Over & Chatterton, p. 23, pl. 5, figs 11–17.

Diagnosis. Refer to Over & Chatterton (1987, p. 23).

Remarks. This species occurs rarely in late *P. celloni* Biozone samples from Washington Land. In these collections it can be distinguished from *A. fluegeli* only by its Pa element which bears a large compressed cusp, an undenticulated process over the basal cavity and a narrow basal cavity. This species differs from *Oulodus planus borenorensis* Bischoff (1986, p. 84) in which the Pa element has an additional denticulated process above the basal cavity.

Aspelundia? n. sp. A

Plate 4, figs 1–5

Description. Only a single specimen of each element occurs in the Greenland collection.

Pa element. Carminate, laterally compressed element with large denticle and a small cusp situated just posterior to the midlength. The cusp is posteriorly inclined, laterally compressed and lenticular in cross section. The posterior process is shorter and shallower than the anterior and bears three discrete, laterally compressed triangular denticles; the most proximal of these is fused to the cusp below its midheight. The most distal denticle on the posterior process is much smaller and separated from the central denticle by a 'u-shaped' rather than 'v-shaped' gap. The anterior process bears four triangular, pointed denticles which are fused to midheight. These are smaller than those on the posterior process. The lower edge of the element is higher beneath the cusp and posterior process than the anterior process. The basal cavity is expanded slightly beneath the cusp, extending as a rapidly tapering narrow groove, to the tips of the processes.

Pb element. Digyrate, comprising compressed lateral processes and an antero-posteriorly compressed cusp. The outer-lateral process is broken, though directed

slightly towards the anterior and bears the remains of two laterally compressed denticles. The inner-lateral process is complete and bears five tall, laterally compressed, partially fused denticles. The basal cavity flares posteriorly beneath the cusp, and is asymmetrically inclined towards the outer-lateral process. The cavity extends as a rapidly narrowing groove to the tips of the lateral processes.

M element. A dolabrate element, consisting of a laterally compressed cusp and a short denticulate posterior process, occurs with the Pa element. The cusp is inclined posteriorly with a straight posterior edge and flexed anterior edge. The posterior process projects at an angle of 90° from the base of the cusp and bears four posteriorly inclined, laterally compressed, completely fused denticle stubs; the most proximal of which is much smaller than the others from which it is separated by a gap. The basal cavity is expanded slightly beneath the posterior edge of the cusp, extending posteriorly as a rapidly tapering groove to the tip of the posterior process.

?Sb₂ element. Tertiopedate, in posterior view the cusp is broad and antero-posteriorly compressed; the outer-lateral process bears seven compressed denticles. The most distal of these is small, peg-like and discrete from the other denticles. The inner-lateral process is broken and bears two compressed denticles. An angle of 160° is developed between the lower ledges of the lateral processes. The posterior edge of the basal cavity is expanded slightly, upturned and offset towards the inner-lateral process, extending laterally, and terminates just before the tip of the inner-lateral processes.

Sc element. Bipennate with a short, inwardly curved, downturned, short anterior process; the posterior process is long and slightly downturned, it bears six compressed, discrete denticles which are separated by 'v-shaped' spaces. The anterior process bears a single denticle which is fused to the antero-lateral edge of the cusp. The basal cavity is slightly expanded beneath the cusp, oval in lower outline and extends as a narrow groove to the tip of the anterior process, but terminates posteriorly before the tip of the posterior process.

Remarks. These elements are morphologically similar to those of *Boerglumella* and appear to fit the same apparatus plan. Until an Sb₁ element is recognised this species can only be questionably assigned to this genus, but it may represent the oldest known representative of the *Aspelundia* lineage.

Occurrence. Found in GGU sample 256335, from the upper Ordovician part of the Turesø Formation of eastern Peary Land.

Aspelundia? n. sp. B

Plate 4, figs 6-13

Description. Pa element. Digyrate with small laterally compressed cusp, short anterior process and longer posterior process. The anterior process consists of a single, inner-laterally twisted, large compressed denticle, fused to the anterior edge of the cusp; the posterior process is inwardly bowed and bears four denticles which are posteriorly and inwardly inclined and separated from the cusp by a narrow gap. The lower surface is expanded to form a narrow platform which is broader posteriorly than anteriorly. The basal cavity is shallowly excavated and a deep basal pit is located beneath the cusp. In lateral view the denticles are filled with angular blocks of white matter, the bases of these blocks define a sharp linear trace at the midheight of both processes.

Pb element. Angulate and slightly inwardly bowed, the cusp and denticles are laterally compressed, posteriorly inclined and lenticular in cross section. The anterior process is slightly longer and deeper than the posterior and bears four large, partially fused denticles; the most distal of these is much smaller than the rest. The posterior process bears only three denticles, which are fused to midheight. The basal cavity is narrowly flared beneath the cusp, extending to the tips of the processes as a narrow, shallowly excavated groove. In lateral view white matter fills each denticle.

M element. Dolabrate with a tall, erect, laterally compressed cusp, denticulate posterior process and adentic-

ulate anticusp. The posterior process extends slightly downwards from the base of the cusp, forming an angle of approximately 100° with the lower edge of the anticusp. It bears six triangular, laterally compressed denticles; the four proximal to the cusp are partially fused, the two most distal are discrete. The anticusp is more or less parallel to the anterior edge of the cusp. Beneath the cusp the basal cavity is slightly, inwardly flared, extending as a narrow groove to the tip of the posterior process.

Sa element. Alate, the cusp is posteriorly curved, compressed and subrounded in midheight cross section. Two symmetrically disposed antero-lateral processes diverge at an angle of 60° - 75° beneath the cusp, each bears three discrete, compressed denticles, separated by 'u-shaped' spaces. The posterior process extends from the lower posterior edge of the cusp and bears up to six laterally compressed, posteriorly inclined, partially fused denticles. The basal cavity extends beneath the posterior process as a broad groove, and along the lateral processes as a narrower groove. White matter distribution is similar to that described for the Pb element.

Sb₁ element. Tertiopedate, the cusp is erect and laterally compressed, with a costa on the posterior edge; it is triangular in midheight cross section. The inner-lateral process is less steeply inclined than the outer, an angle of approximately 100° being developed between the lower edges of the lateral processes. Each lateral process bears four or five compressed, discrete denticles. The posterior process, bears two or three compressed denticles. The basal cavity extends to the tips of

Plate 4

Figs 1-5. *Aspelundia?* n. sp. A.
All specimens from GGU 256335, $\times 60$.

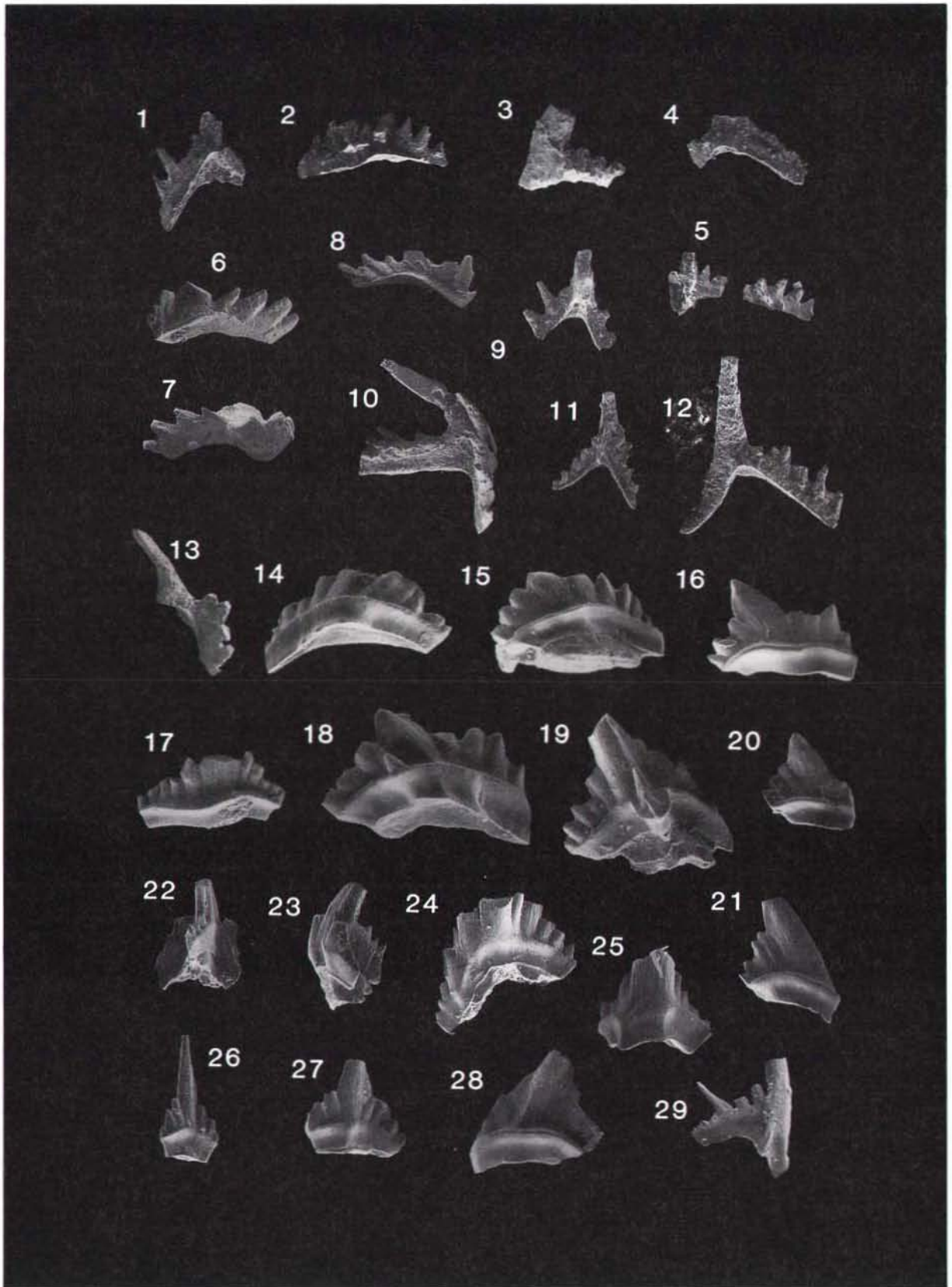
- 1, oblique lower view of Pb element; MGUH 17.695.
- 2, inner-lateral view of Pa element; MGUH 17.696.
- 3, inner-lateral view of M element; MGUH 17.697.
- 4, posterior view of ?Sb₂ element; MGUH 17.698.
- 5, inner-lateral view of Sc element; MGUH 17.699.

Figs 6-13. *Aspelundia?* n. sp. B.
All specimens from GGU 216809, $\times 60$.

- 6, lateral view of Pa element; MGUH 17.700.
- 7, upper view of Pa element; MGUH 17.701.
- 8, inner-lateral view of Pb element; MGUH 17.702.
- 9, posterior view of Sa element; MGUH 17.703.
- 10, inner-lateral view of Sc element; MGUH 17.704.
- 11, posterior view of Sb₁ element; MGUH 17.705.
- 12, posterior view of M element; MGUH 17.706.
- 13, inner-lateral view of ?Sb₂ element; MGUH 17.707.

Figs 14-29. *Carniodus carnulus* Walliser.
All specimens from GGU 216853, $\times 60$.

- 14, lateral view of carinthiaciform element; MGUH 17.708.
- 15, lateral view of carinthiaciform element; MGUH 17.709.
- 16, lateral view of carinthiaciform element; MGUH 17.710.
- 17, lateral view of carinthiaciform element; MGUH 17.711.
- 18, lateral view of carinthiaciform element; MGUH 17.712.
- 19, inner-lateral view of modified carinthiaciform element; MGUH 17.713.
- 20, inner-lateral view of carnuliform element; MGUH 17.714.
- 21, inner-lateral view of neoprioniodan (M) element; MGUH 17.715.
- 22, posterior view of latialatiform element; MGUH 17.716.
- 23, lateral view of latialatiform element; MGUH 17.717.
- 24, posterior view of carniform element; MGUH 17.718.
- 25, anterior view of (?)carniform element; MGUH 17.719.
- 26, posterior view of carnuliform element; MGUH 17.720.
- 27, posterior view of carnuliform element; MGUH 17.721.
- 28, lateral view of carnuliform element; MGUH 17.722.
- 29, outer-lateral view of subcarniform element; MGUH 17.723.



all the processes as a narrow groove. White matter distribution is as described for the other elements.

?Sb₂ element. Modified teriopede element with a single outer antero-lateral process. The cusp is tall, posteriorly recurved, and laterally compressed; it is extended slightly, postero-basally. The outer-lateral process is inclined steeply downwards and bears four compressed denticles. The basal cavity forms a narrow groove beneath the cusp and lateral process. White matter is distributed as in the other elements.

Sc element. Bipennate element, dominated by a posteriorly recurved cusp; antero-lateral and posterior processes diverge from its edges. The antero-laterally directed process is sharply downturned and twisted posteriorly; it bears up to four long, slender, discrete, compressed denticles. The posterior process extends horizontally from the base of the cusp bearing up to four posteriorly inclined and closely packed denticles; this process is usually longer than the anterior process. The basal cavity is narrowly expanded beneath the cusp extending as a narrow groove to the tips of the processes. White matter distribution is again similar to that of the other elements.

Remarks. This species is based upon the elements from a single sample. These are well preserved and show similar denticulation, basal cavity morphology and white matter distribution which allows their reconstruction into a single apparatus. The *?Sb₂* element (plate 4, fig. 13) is similar to the *Sd* element of *A. fluegeli* but has a more strongly laterally compressed cusp, a laterally restricted basal cavity and differs in the wider spaced denticles. This element has a similar morphology to the *?M* element of *Icriodella discreta* Pollock, Rexroad & Nicoll *sensu* Aldridge & Mohamed (1982, pl. 1, fig. 15). It differs in having a more sharply posteriorly curved antero-lateral process; the basal cavity is also less broadly flared beneath the cusp.

Occurrence. Found in GGU sample 216809, from the Kap Independence Member of the Hauge Bjerge Formation of Washington Land.

Genus *Astropentagnathus* Mostler, 1967

Type species. *Astropentagnathus irregularis* Mostler, 1967, p. 298.

Emended diagnosis. Apparatus septimembrate; *Pa₁* stelliscaphate with a bifurcate outer-lateral process and anteriorly directed inner-lateral process. *Pa₂* pastiniscaphate; *Pb* anguliscaphate, *M* pyramidal; *Sa* alate; *Sb*

modified teriopede lacking a posterior process; *Sc* bipennate. The ramiform elements are characterised by deep lateral processes.

Remarks. *Astropentagnathus* was originally described by Mostler (1967) on the basis of the *Pa₁* element alone. Bischoff (1986, p. 156–157) emended the generic diagnosis to include *Pa*, *Pb*, *M*, *Sa* and *Sb* elements.

The inclusion herein of the *Pa₂* element in the apparatus of *Astropentagnathus* follows Schönlaub (1971, p. 43) and is based upon its common occurrence with the other elements and shared morphological characters with the *Pa₁* element, for example white matter distribution and denticulation.

Astropentagnathus is distinct from *Aulacognathus* Mostler in having *Pa* elements with a centrally situated nodose carina along each process. The lateral processes of the *Pa* element of *Aulacognathus* species bear irregular rows of sinuous ridges. A *Pa₂* element has not been recognised in the apparatus of *Aulacognathus*, and the remaining elements are readily distinguishable (figs 30, 31).

Mostler (1967, p. 301, fig. 4) proposed a phylogeny in which *Astropentagnathus* was the common ancestor of *Apsidognathus* and *Aulacognathus*. In Greenland and on Anticosti Island (Uyeno & Barnes, 1983) *Aulacognathus* occurs in Telychian strata before the first appearance of *Pterospathodus celloni*, *Astropentagnathus* and *Apsidognathus* do not appear until the base of the *P. celloni* Biozone becoming abundant during the middle-upper *P. celloni* Biozone. On stratigraphical evidence the phylogeny suggested by Mostler (1967) cannot be sustained. It is more probable from apparatus structure that *Astropentagnathus* is closely related to *Amorphognathus* and *Apsidognathus* and that *Aulacognathus* has a separate ancestry.

Astropentagnathus irregularis Mostler, 1967

Remarks. Two subspecies of *Astropentagnathus irregularis* are present in Greenland. The nominate subspecies occurs in the *P. celloni* Biozone across the whole of Greenland. *A. irregularis* n. ssp. is distinguished by its morphologically distinct *Pa₂* element and has been found only in the *P. celloni* Biozone of Hans Egede Land; it is probable that this subspecies is a geographical variant of the nominate subspecies.

Astropentagnathus irregularis irregularis Mostler, 1967

Plate 5, figs 1–10

- *1967 *Astropentagnathus irregularis*, p. 298, pl. 1, figs 1–11.
 1967 *Spathognathodus tyrolensis* Mostler, p. 302, pl. 1, figs 17, 19, 20, 23.
 1971 *Hadrognathus irregularis*; Schönlaub, p. 42, pl. 1, figs 1–11.
 p1971 *Hadrognathus ceratoides*; Schönlaub, p. 43, pl. 1, figs 12, 13, 16, 19 only.
 1971 '*Rhynchognathus*' n. sp. Schönlaub, p. 48, pl. 3, figs 15–19.
 1971 *Falcodus?* n. sp. Schönlaub, p. 47, pl. 3, figs 1–3.
 1971 *Synprioniodina typica* Schönlaub, p. 49, pl. 3, figs 4–5.
 v1972 *Astropentagnathus irregularis*; Aldridge, p. 166, pl. 2, fig. 5.
 v1975 *Astropentagnathus irregularis*; Aldridge, pl. 3, fig. 14.
 1976 *Neospathognathodus tyrolensis*; Miller, fig. 8, no. 37.
 1976 *Hadrognathus irregularis*; Miller, fig. 8, no. 38.
 1976 *Ozarkodina media*; Miller, fig. 8, no. 35.
 1978 *Pterospathodus tyrolensis*; Miller, p. 341, pl. 4, figs 5, 6.
 1981 *Astropentagnathus irregularis*; Uyeno & Barnes, pl. 1, fig. 13.
 1983 *Astropentagnathus irregularis*; Nowlan, fig. 4D.
 v1985 *Astropentagnathus irregularis*; Aldridge, pl. 3.2, fig. 1, 2.
 1986 *Astropentagnathus irregularis*; Bischoff, p. 158, pl. 2, figs 27–29; pl. 3, figs 1–14.
 1987 *Astropentagnathus irregularis*; Over & Chatterton, pl. 2, figs 1–9.

Holotype. *Astropentagnathus irregularis* Mostler, p. 298, pl. 1, fig. 3, from Westendorf Schicht, Wi 19.

Emended diagnosis. Septimembrate apparatus characterised by its pastiniscaphate Pa_2 element which has a single centrally situated outer process and lacks an inner process.

Description. Pa_1 element. Stelliscaphate with a bifurcating outer-lateral process and anteriorly directed inner-lateral process, all processes have a narrow ledge-like platform, the margin of which may be upturned or differentially thickened. The anterior process is straight and bears fourteen nodose, fused denticles. The posterior process is shorter and curved inwards; at the point of maximum curvature it may have a slightly larger denticle. The outer-lateral process diverges close to the midpoint of the carina and bifurcates at the first proximal denticle. The branches of the process are separated by an angle of 90° . The postero-lateral process is longer and bears nodes. The inner lateral process is situated just anterior of the outer-lateral process, diverging from the carina at approximately 45° and bears a central

carina of up to three nodes. In small specimens the position of this process is marked by a flexure or slight thickening of the lateral platform. The entire lower surface is shallowly excavated. White matter distribution for all elements is illustrated in fig. 30.

Pa_2 element. Pastiniscaphate with a single outer-lateral process situated just posterior of the midlength; a narrow platform is developed around all the processes. The anterior and posterior processes bear a continuously inwardly curving carina of up to seventeen fused, nodose denticles. The posterior process may be more sharply inwardly flexed just posterior of the outer-lateral process (plate 5, fig. 2). On many specimens a slight extension of the inner side of the platform is evident just to the posterior of the junction of the outer process. This may represent the incipient development of an inner-lateral process. The basal cavity is deep and tapers distally along the anterior, posterior and outer-lateral processes, terminating before the process tip.

Pb element. Angulate or pastinate; laterally compressed and arched. A prominent posteriorly inclined cusp lies posterior of the midpoint. The anterior process is straight and bears up to eight almost completely fused denticles. The posterior process is shorter and lower than the anterior process; it bears three to four denticles. A short inner-lateral process may be developed beneath the anterior edge of the cusp. This process bears one or two rudimentary denticles. The basal cavity is narrowly flared beneath the cusp, tapering rapidly to form a narrow groove beneath the anterior and posterior processes, extending to their tips. A broader groove extends to the tip of the inner-lateral process.

M element. Modified alate to tertiope date (rarely) subpyramidal element. The short cusp is round in cross section and posteriorly recurved. Beneath the cusp the element is deep, broadly flared and triangular in cross section. The lateral edges of the cusp are denticulate, the inner bears four almost completely fused denticles, the outer has only three. The base is extended posteriorly to form a sharp adenticulate process; the postero-lateral faces of the base are slightly concave. The entire lower surface is deeply excavated. In large collections asymmetrical examples of this element are present; these forms have the inner-lateral process situated and directed further towards the posterior.

Sa element. Alate, cusp prominent and lenticular in cross section; long deep lateral processes extend from its edges symmetrically, forming an arch of 120° between the lower edges of the processes. Each process bears up to eight compressed, tall denticles which are fused almost to their tips. Occasionally in large specimens (plate 5, fig. 8) a short triangular projection is directed posteriorly and downwards beneath the cusp.

The basal cavity is shallowly excavated, restricted to beneath the cusp and oval in lower outline.

Sb element. Asymmetrically arched, modified alate element. The small cusp is lenticular in cross section and inclined towards the commonly shorter inner-lateral process. In posterior view the processes form an asymmetrical arch of about 80° between their lower edges, the outer process is more steeply inclined than the inner. Both processes bear up to seven compressed denticles, the most proximal of these are fused, the most distal are generally discrete. The basal cavity is restricted to beneath the cusp and is deeply excavated with its anterior and posterior tips expanded slightly.

Sc element. Bipennate with a deep, slightly inwardly curved anterior process. The cusp is broad, posteriorly inclined and lenticular in cross section. The anterior process is approximately twice as deep as the posterior process, bearing up to eight almost completely fused denticles. The anterior process is downturned forming an angle of about 110° with the posterior process. The posterior process bears up to eight denticles, the most proximal is larger than the rest and is completely fused to the cusp. The basal cavity is deeply excavated, expanded beneath the cusp extending as an extremely narrow groove almost to the tips of the unit.

Remarks. Ramiform elements figured by Schönlaub (1971) are here included in the apparatus of *A. irregularis irregularis*, on the basis of samples from Greenland, figured material from Schönlaub's samples Seewarte 194/3 and 194/4, and additional material from Seewarte collected by R. J. Aldridge. The inclusion of '*Rhynchognathus*' n. sp. Schönlaub (1971) as the M element was first suggested by Klapper & Murphy (1975). Bischoff (1986) emended the generic diagnosis based upon partial reconstruction of *A. irregularis*; this has been expanded for the septimembrate plan herein. Over & Chatterton (1987) illustrated a partial reconstruction of the apparatus of *A. irregularis*. They in-

cluded two dissimilar Pb elements in the apparatus, but this cannot be confirmed in the collections studied.

Occurrence. Particularly common in the *P. celloni* Biozone of Washington Land.

Astropentagnathus irregularis n. ssp.

Plate 5, figs 11–15

Description. Pa₁ element. Indistinguishable from that of *A. irregularis irregularis*.

Pa₂ element. Stelliplanate with anteriorly directed lateral processes, juxtaposed centrally, each inserted at an angle of 45° to the main carina. The anterior and posterior processes are of equal length; the central carina is straight and becomes poorly denticulated to the anterior of the lateral processes. The two most anterior denticles are approximately twice as high as the others. Centrally the carina forms a low, rounded, adenticulate ridge, and posteriorly it curves inwards and downwards following the posterior process, bearing up to ten poorly formed, fused, nodose denticles. The entire element is surrounded by a narrow ledge-like platform which is upturned marginally. Beneath the platform the element narrows slightly and has an excavated cavity. This is completely infilled with basal material in all specimens.

M element. Modified tertioepdate, subpyramidal element, the short posteriorly recurved cusp has a circular cross section. The lateral edges of the triangular base are denticulate and extend downwards to form short processes, each bears up to ten poorly formed tooth-like denticles. Posteriorly the base of the cusp is extended downwards terminating as a short adenticulate process; the postero-lateral faces of the element are flat to slightly concave. The entire lower surface is deeply excavated.

Sa element. Alate with a slight posterior swelling at the base of the cusp. A large antero-posteriorly com-

Plate 5

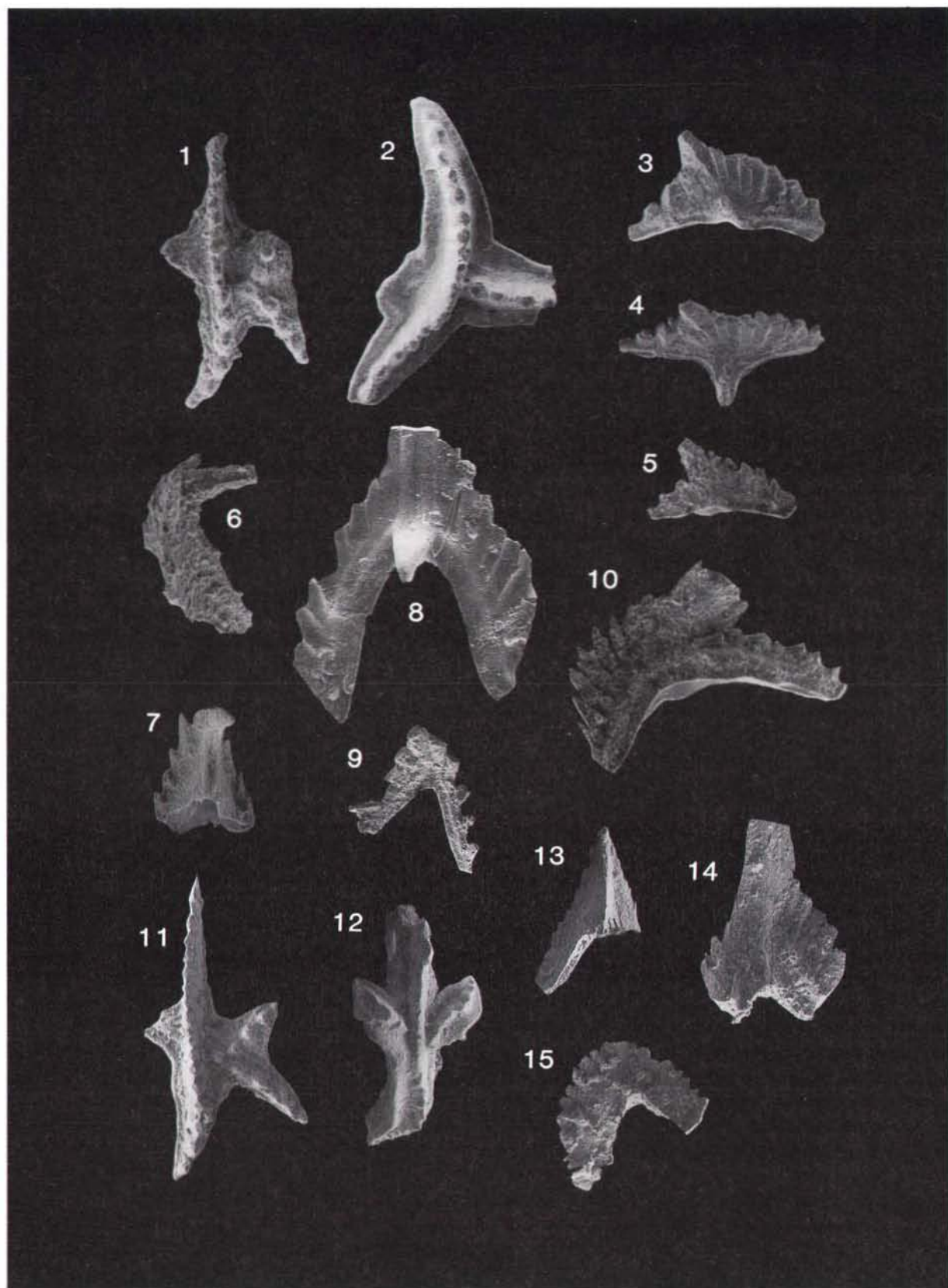
Figs 1–10. *Astropentagnathus irregularis irregularis* Mostler. All specimens from GGU 216809, unless otherwise stated.

- 1, upper view of Pa₁ element, × 60; MGUH 17.632.
- 2, upper view of Pa₂ element, × 40; MGUH 17.633.
- 3, 4, inner-lateral and oblique lateral views of Pb element, × 60; MGUH 17.634.
- 5, inner-lateral view of Pb element, × 60; MGUH 17.666.
- 6, lateral view of M element, × 60; MGUH 17.636.
- 7, posterior view of M element, × 60; MGUH 17.635.
- 8, posterior view of Sa element, × 60; MGUH 17.637 from GGU 256360.

- 9, posterior view of Sb element, × 60; MGUH 17.638.
- 10, posterior view of Sc element, × 60; MGUH 17.639.

Figs 11–15. *Astropentagnathus irregularis* n. ssp. All specimens from GGU 197564.

- 11, upper view of Pa₁ element, × 60; MGUH 19.329.
- 12, upper view of Pa₂ element, × 20; MGUH 19.330.
- 13, posterior view of M element, × 60; MGUH 19.331.
- 14, posterior view of Sa element, × 60; MGUH 19.332.
- 15, posterior view of Sb element, × 60; MGUH 19.333.



pressed cusp dominates the deep lateral processes; the inner process is usually the shallower of the two. Each process bears laterally compressed, outwardly inclined, fused denticles. The basal cavity is oval in lower outline, shallowly excavated, extending as a groove only a short distance along the processes.

Sb element. Only poorly preserved specimens are present. This element is an asymmetrical version of the Sa element with the cusp inclined towards the shorter inner-lateral process. Smaller, fewer denticles are situated on the inner-lateral process.

Remarks. The major difference between this and the nominate subspecies lies in the morphology of the Pa₂ element. Minor differences do occur between the other elements. The M element of *A. irregularis* n. ssp. has a broader, more steeply triangular base to the cusp and short lateral processes which extend below the basal margin of the posterior process. The S elements in this new subspecies have deeper lateral processes and more prominent cusps.

Occurrence. Found only in GGU 197564.

Genus *Aulacognathus* Mostler, 1967

1967 *Aulacognathus* Mostler, p. 300.

1969 *Neospathognathodus* Nicoll & Rexroad, p. 42.

Type species. *Aulacognathus kuehni* Mostler, 1967, p. 300; from the Llandoverly of Westendorf, Kitzbühel Alps, Austria.

Emended diagnosis. Apparatus seximembrate characterised by a highly variable stelliscaphate (Pa) element which has irregularly nodose or ridged inner and outer-lateral processes. Anteriorly the carina is free, posteriorly it is inwardly bent and occasionally thickened. The anguliscaphate (Pb) element occasionally develops

a short inner-lateral process beneath the cusp. Tertioedate (M) element has a reduced posterior process; the alate (Sa) element, asymmetrical modified alate (Sb) and bipennate (Sc) elements have a small oval basal cavity restricted to beneath the cusp.

Remarks. Klapper & Murphy (1975, p. 25) placed *Aulacognathus* and *Neospathognathodus* Nicoll & Rexroad, 1969, in synonymy based on the similarity of the Pa elements in their constituent type species. As noted by Aldridge (1979, p. 10) the recognition of almost identical Pb elements in *A. kuehni*, *A. bullatus* and *A. latus* strengthens this synonymy. Bischoff (1986) considered the apparatus of *Aulacognathus* to be bimembrate. He also separated five new species of *Aulacognathus* based upon upper surface ornament and the disposition of the anterolateral and posterior processes. The former character appears very variable in Greenland species and insufficient specimens are available to judge intraspecific variability. M, Sa, Sb and Sc elements have been included based on collections of *A. bullatus* from Greenland and Illitsch Hof 12 (fig. 31).

Aulacognathus bullatus (Nicoll & Rexroad, 1969)

Plate 6, figs 1-2, 4-7

- v1964 *Spathognathodus* sp. ex. aff. *Spathognathodus celloni* Walliser; Walliser, p. 74, pl. 14, figs 17, 18.
- v*1969 *Neospathognathodus bullatus* p. 44, pl. 1, figs 5-7.
- 1971 *Neospathognathodus bullatus*; Rexroad & Nicoll, pl. 1, fig. 7.
- 1971 *Neospathognathodus ceratoides*; Rexroad & Nicoll, pl. 1, fig. 6.
- v1972 *Neospathognathodus bullatus*; Aldridge, p. 126, pl. 3, fig. 15.
- 1975 *Aulacognathus bullatus*; Klapper & Murphy, p. 26, pl. 2, figs 15-20.
- ?1975 *Aulacognathus ceratoides*; Klapper & Murphy, p. 26, pl. 1, figs 4, 5, 8-14.

Plate 6

Figs 1, 2, 4-7. *Aulacognathus bullatus* (Nicoll & Rexroad).

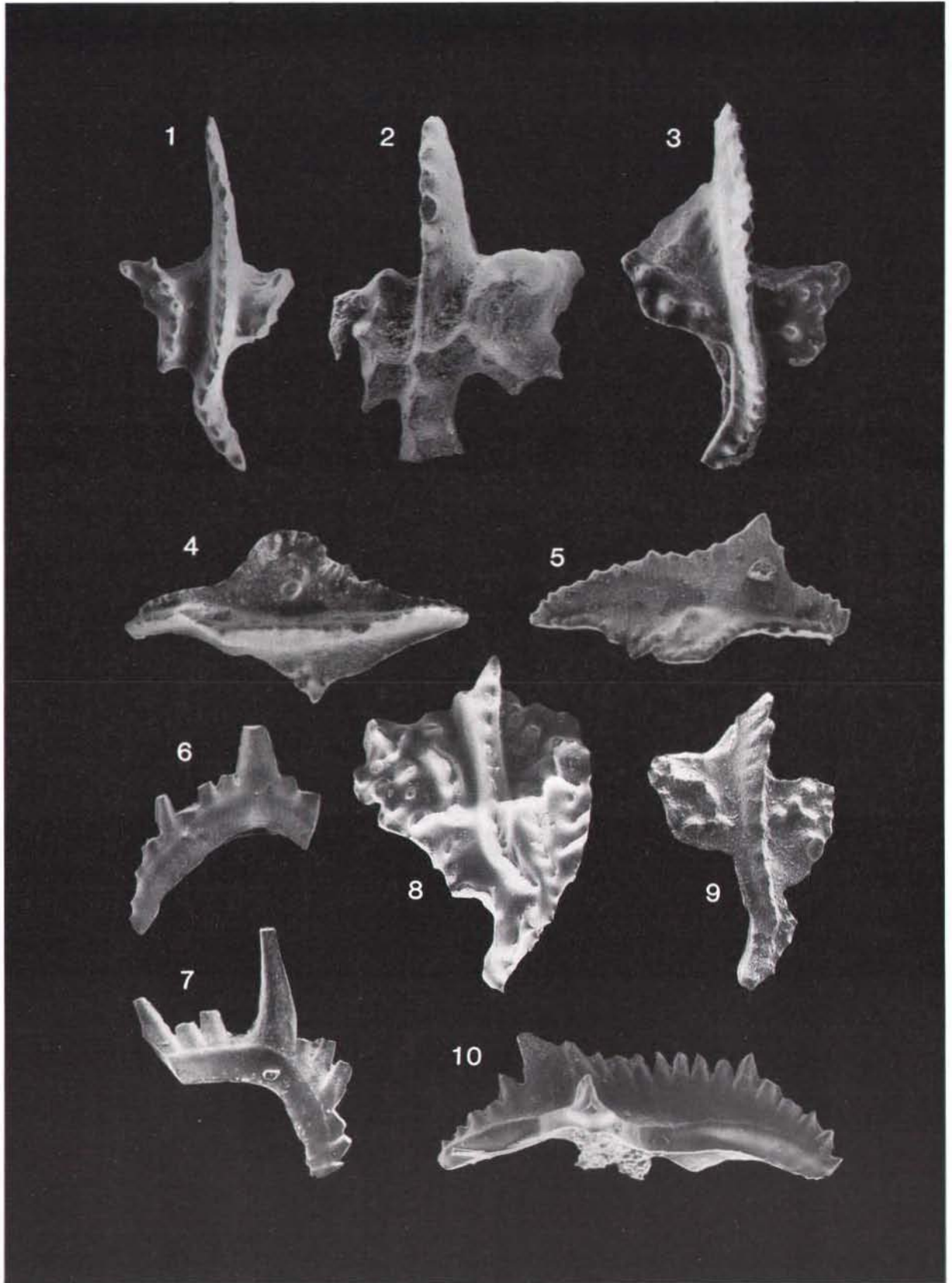
- 1, upper view of Pa element, × 60; MGUH 17.667 from GGU 216773.
- 2, upper view of Pa element, × 60; MGUH 17.668 from GGU 274770.
- 4, 5, upper side and inner-lateral views of Pb element, × 40; MGUH 17.669 from GGU 274770.
- 6, posterior view of Sa element, × 60; MGUH 17.670 from GGU 229037.
- 7, inner-lateral view of Sc element, × 60; MGUH 17.671 from GGU 229037.

Figs 3, 8, 9. *Aulacognathus latus* (Nicoll & Rexroad).

- 3, upper view of Pa element, × 60; MGUH 17.672 from GGU 216773.
- 8, upper view of Pa element, × 40; MGUH 17.673 from GGU 275048.
- 9, upper view of Pa element, × 40; MGUH 14.037 from GGU 184125.

Fig. 10. *Aulacognathus* sp.

- 10, lateral view of Pb element, × 40; MGUH 17.674 from GGU 229037.



- 1975a *Neospathognathodus bullatus*; Schönlaub, p. 59, pl. 1, fig. 6.
 1978 *Neospathognathodus latus*; Pickett, pl. 1, fig. 31.
 v1979 *Aulacognathus bullatus*; Aldridge, pl. 11, figs 1, 6, 7.
 1979 *Aulacognathus bullatus*; Murphy, Dunham, Berry & Matti, fig. 19, no. 3.
 p1981 *Aulacognathus bullatus*; Nowlan, pl. 5, figs 20, 24; non 23.
 1983 *Aulacognathus bullatus*; Nowlan, figs 4E, 40, 4P.
 1987 *Aulacognathus bullatus*; Over & Chatterton, pl. 3, figs 1, 2, 6.

Holotype. *Neospathognathodus bullatus* Nicoll & Rexroad, 1969, p. 44, pl. 1, fig. 5; from sample M-Z II, Lee Creek Member of the Brassfield Limestone, Indiana.

Emended diagnosis. Apparatus seximembrate; diagnostic stelliscaphate (Pa) element with limited platform development and a long carina which is free to the anterior and posterior of the platform. Inner and outer, anteriorly directed, lateral processes are broad and bear an ornament of irregular coalescing nodes or low sinuous ridges.

Description. *Pa element.* A highly variable stelliscaphate element comprising a long blade-like carina and broad anteriorly directed inner and outer processes. The carina bears up to 24, partially fused nodose denticles and is sharply incurved at approximately two-thirds the length from the anterior tip, a secondary denticle may be developed here. The ornament of the lateral processes is highly variable from coalescing nodes to

irregular sinuous and bifurcating ridges. The inner process commonly develops into two ornamented lobes. Both lateral processes are broad and form the narrow platform of this element. The entire lower surface is shallowly excavated.

Pb element. Anguliscaphate with a prominent apical denticle, long anterior process and short posterior process. The anterior process bears up to 15 almost completely fused denticles, the posterior process only five or six denticles. Laterally extended basally, the element may develop a narrow platform (plate 6, figs 4, 5) or may be narrow and blade-like, only slightly thickened (see Aldridge, 1979, pl. 1, figs 2, 3). In the platform specimens a small indistinct anteriorly directed inner-lateral process may be developed beneath the apical denticle; the platform margin may also bear discrete nodes or ridges. The entire lower surface is excavated.

M element (from Illitsch Hof 12; fig. 31). Pyramidal, modified teriopede element, with prominent compressed cusp. The inner-lateral process is longer than the outer and bears up to five partially fused denticles, the outer process commonly only has two or three small, rudimentary peg-like denticles. The posterior process is commonly reduced to a slight swelling beneath the cusp and rarely develops into a short denticulate process. The basal cavity is broad beneath the cusp and tapers rapidly along the lateral processes, terminating before their tips.

Sa element. Broadly arched alate element with a slight posterior swelling beneath the base of the cusp. Cusp erect, tall, antero-posteriorly compressed, lenticulate in cross section. Long, deep lateral processes extend from its base, each bearing up to eight, compressed, partially fused denticles. Both processes are slightly thickened below the denticle row. The basal cavity is only slightly expanded beneath the cusp, extending as a rapidly narrowing groove terminating beneath the first proximal denticle on each lateral process.

Sb element (from Illitsch Hof; fig. 31). Modified teriopede element, lacking a posterior process. The cusp is lenticular in cross section and inclined towards the inner-lateral process. The lateral processes form an angle of approximately 120° between their lower edges. The inner process is the longer and less steeply inclined, bearing up to 11, partially fused, compressed denticles; the outer process bears only four denticles. The basal cavity forms a narrow groove which terminates before the midlength of the lateral processes.

Sc element. Bipennate with tall, laterally compressed, posteriorly inclined cusp. The anterior process is steeply downwards inclined forming an angle of approximately 110° with the base of the posterior process. The anterior process bears up to six compressed, partially fused den-

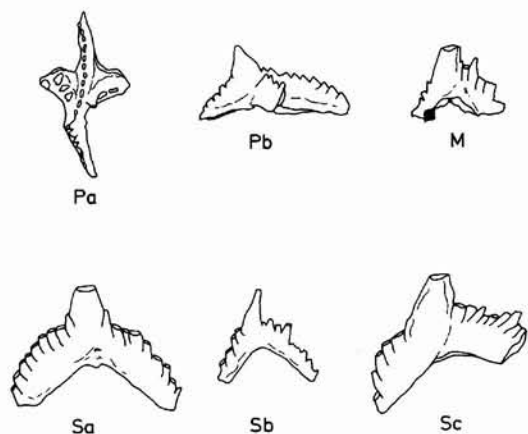


Fig. 31. The apparatus of *Aulacognathus bullatus* (Nichol & Rexroad). All the specimens are from Illitsch 12. Total specimens in the sample: Pa, 24; Pb, 15; M, 10; Sa, 16; Sb, 4; Sc, 3. Specimens kindly provided by R. J. Aldridge. Camera lucida drawings: Pa, MGUH 17.790 × 20; Pb, MGUH 17.924 × 20; M, MGUH 17.930 × 28; Sa, MGUH 17.866 × 28; Sb, MGUH 19.310 × 28; Sc, MGUH 19.311 × 20.

ticles. The posterior process is slightly longer than the anterior, more or less horizontal and bears 10–15 partially fused denticles. Both processes are slightly thickened beneath the denticle row. The basal cavity is only slightly expanded beneath the cusp and extends as a narrow groove, only a short distance along the process.

Remarks. The apparatus recognised here is reconstructed from the Greenland collection with the help of additional material from the research collections of R. J. Aldridge, particularly from sample 'Illitsch Hof 12', collected by J. Barrick from Schönlaub's locality 12 (Sweet & Schönlaub, 1975; Schönlaub, 1975a). This sample contains abundant elements representing the complete apparatus of *A. bullatus* (fig. 31), all specimens are thermally mature and white matter is not visible. The reconstruction presented is in agreement with that present in slides sorted by Aldridge.

Aldridge (1979, p. 11) discussed fully the difficulty in assigning a Pb element to this apparatus. *A. bullatus* is the most common *Aulacognathus* species in the Greenland collection, and Pb elements are assigned to this species unless *A. latus* occurs in the samples.

Nowlan (1981, pl. 5, figs 2, 3) included an M element in his illustrations of *A. bullatus*. This specimen is morphologically distinct from that included here, resembling the morphology of an *Ozarkodina* M element. Rare specimens (plate 6, fig 2) approach the morphology of *A. bullatus* n. ssp. A Over & Chatterton (1987, p. 20, pl. 3, fig. 3). Due to the highly variable nature of the Pa element these may fall within the morphological range of *A. bullatus*. Insufficient specimens are available in the Greenland collection to confirm this separation.

Occurrence. In eastern Peary Land this species occurs in just pre-*P. celloni* Biozone strata, elsewhere it occurs infrequently in *P. celloni* Biozone strata. Outside Greenland *A. bullatus* has been recorded from *P. celloni* Biozone strata of Australia, Canada, Europe and North America. On Anticosti Island this species also occurs before the first appearance of *Pterospodus celloni* (Walliser), though restricted to the lower Telychian (Uyeno & Barnes, 1983).

Aulacognathus latus (Nicoll & Rexroad, 1969)

Plate 6, figs 3, 8–9

- v*1969 *Neospathognathodus latus*, p. 46, pl. 1, figs 8–11.
- 1972 *Neospathognathodus latus*; Rexroad & Nicoll, pl. 2, fig. 41.
- 1975 *Aulacognathus latus*; Klapper & Murphy, p. 26, pl. 1, figs 6, 7.

- 1977a *Aulacognathus latus*; Cooper, p. 1063, pl. 2, figs 2, 10.
- ?1977a *Aulacognathus latus*; Cooper, p. 1063, pl. 2, figs 1, 5.
- v1979 *Aulacognathus latus*; Aldridge, p. 12, pl. 1, figs 4, 5.

Holotype. *Neospathognathodus latus* Nicoll & Rexroad, 1969, p. 46, pl. 1, fig. 11; from the Lee Creek Member of the Brassfield Limestone, Kentucky.

Remarks. Known in Greenland only from rare specimens of the Pa element. These differ little from those described by Nicoll & Rexroad (1969, p. 46). This species differs from that of *A. bullatus* in having a Pa element with a low, broad platform, which has an ornament of well developed nodes. GGU 275048 contains an atypical Pa element whose platform ornament consists of high, sinuous branching ridges (plate 6, fig. 8). Insufficient complete specimens are available to make a taxonomic separation of this form.

Occurrence. *A. latus* Pa elements are found in upper *P. celloni* Biozone strata of North Greenland. Cooper (1977a, p. 1063) recorded the range of this species as lower *P. celloni* Biozone to lower *P. amorphognathoides* Biozone.

Genus *Belodella* Ethington, 1959

Type species. *Belodus devonicus* Stauffer, 1940, p. 420.

Diagnosis. Refer to Barrick, 1977, p. 49.

Remarks. *Belodella* has been recorded from the early Ordovician to late Devonian (Cooper, 1974 for a review). The *B. jemtlandica* apparatus figured by Löfgren (1978, p. 46, fig. 24, following Carnes, 1975) from the Lower Ordovician contains a denticulate, triangular sym. p element, a denticulate aq, an adenticulate sq and an oistodiform r element. *B. erecta* Rhodes & Dineley *sensu* Löfgren (1978, fig. 24, E-H) from the upper Ordovician has a similar apparatus structure, but differs in having a denticulate sq element. Serpagli (1967) described specimens from the upper Ordovician strata of the Carnic Alps, which he identified as *B. devonica* and *B. erecta* Rhodes & Dineley (1953) but did not combine in a single apparatus. Cooper (1974, 1976) interpreted the apparatus of *Belodella* from the Upper Silurian to consist of two element types, both with denticulate upper edges, one has a triangular cross section, the other has a lenticular cross section. These elements conform to the general morphology of the specimens referred to *B. triangularis* and *B. devonicus* by Stauffer (1940).

Ethington & Clark (1982) reported large collections of *Belodella* from the Tor limestone (Toquima Range, central Nevada) which overwhelmingly supported Cooper's reconstruction of the apparatus. Klapper & Philip (1972, p. 104) and Barrick (1977, p. 49) have suggested the inclusion of an adenticulate element in the apparatus of middle Silurian *Belodella*. Elements conforming to their descriptions have been reported from Devonian samples (Bultynck, 1970; Seddon, 1970), but such adenticulate elements have neither been recognised in the collections of Cooper (1974, 1976) and Ethington & Clark (1982) nor from Greenland.

The apparatus reconstruction as proposed herein has constituent elements similar to those of *Walliserodus* Serpagli, exhibiting similar basal cavity outline, microstriation and element curvature; a close morphological relationship obviously exists between these two genera. Elements conforming to the adenticulate morphotype may have been misidentified, but I think this is unlikely in the three separate collections described above.

Thus it appears that the Ordovician, Silurian and Upper Silurian through Devonian apparatuses referred to *Belodella* have different structures, and it is necessary to reconsider the relationship between them.

Two hypotheses regarding the origin of Silurian *Belodella* have been proposed and are summarised by Cooper (1974, 1975). Cooper did not consider the lower Ordovician species of *Belodella* as ancestors since they had not been fully described at that time. The apparatus of *Belodella cooperi* n. sp. differ only from that of *B. erecta* Serpagli as reconstructed by Löfgren (1978) by the lack of the oistodiform element. The evolution of Upper Silurian *B. devonicus* may have occurred by the loss of the sq element from the *B. cooperi* apparatus.

With the available data the Silurian *Belodella* lineage is thought to be a continuation from the Ordovician rather than representing a split from the *Walliserodus* lineage as proposed by Cooper (1974).

Belodella cooperi n. sp.

Plate 7, figs 1-6

Holotype. Specimen MGUH 17.883, plate 16, fig. 5, an sq element from GGU 216849 within the upper *P. celtoni* Biozone at Kap Schuchert, Washington Land, western North Greenland.

Diagnosis. A species of *Belodella* with a trimembrate apparatus. All elements are laterally compressed and bear upper-edge denticles.

Description. *sym. p element*. Indistinguishable from that described as *Belodus triangularis* Stauffer (1940, p. 417, pl. 59, fig. 49).

aq element. Indistinguishable from that described as *Belodus devonicus* Stauffer (1940, p. 417, figs 47, 48).

sq element. Highly compressed, bilaterally symmetrical element. The cusp is proclined and long; the base is short and has posteriorly curved upper and lower margins; the postero-basal corner is extended posteriorly. The upper margin of the base is extended by tall, needle-like, fused denticles; the posterior margin of the cusp is very rarely denticulate. The anterior margin of the cusp and lower margin of the base are narrow and rounded, and short oblique striations are located along it. The lateral faces are flat and divided just above midheight by a step-like costa on each side. The costae

Plate 7

Figs 1-6. *Belodella cooperi* n. sp. (Stauffer).
All specimens from GGU 216849, × 60.

- 1, lateral view of sym. p element; MGUH 17.879.
- 2, lateral view of sym. p element; MGUH 17.880.
- 3, lateral view of aq element; MGUH 17.881.
- 4, lateral view of aq element; MGUH 17.882.
- 5, lateral view of sq element; MGUH 17.883 (holotype).
- 6, lateral view of sq element; MGUH 17.884.

Figs 7-12. *Dapsilodus obliquicostatus* (Branson & Mehl).
All specimens from GGU 216842, × 60.

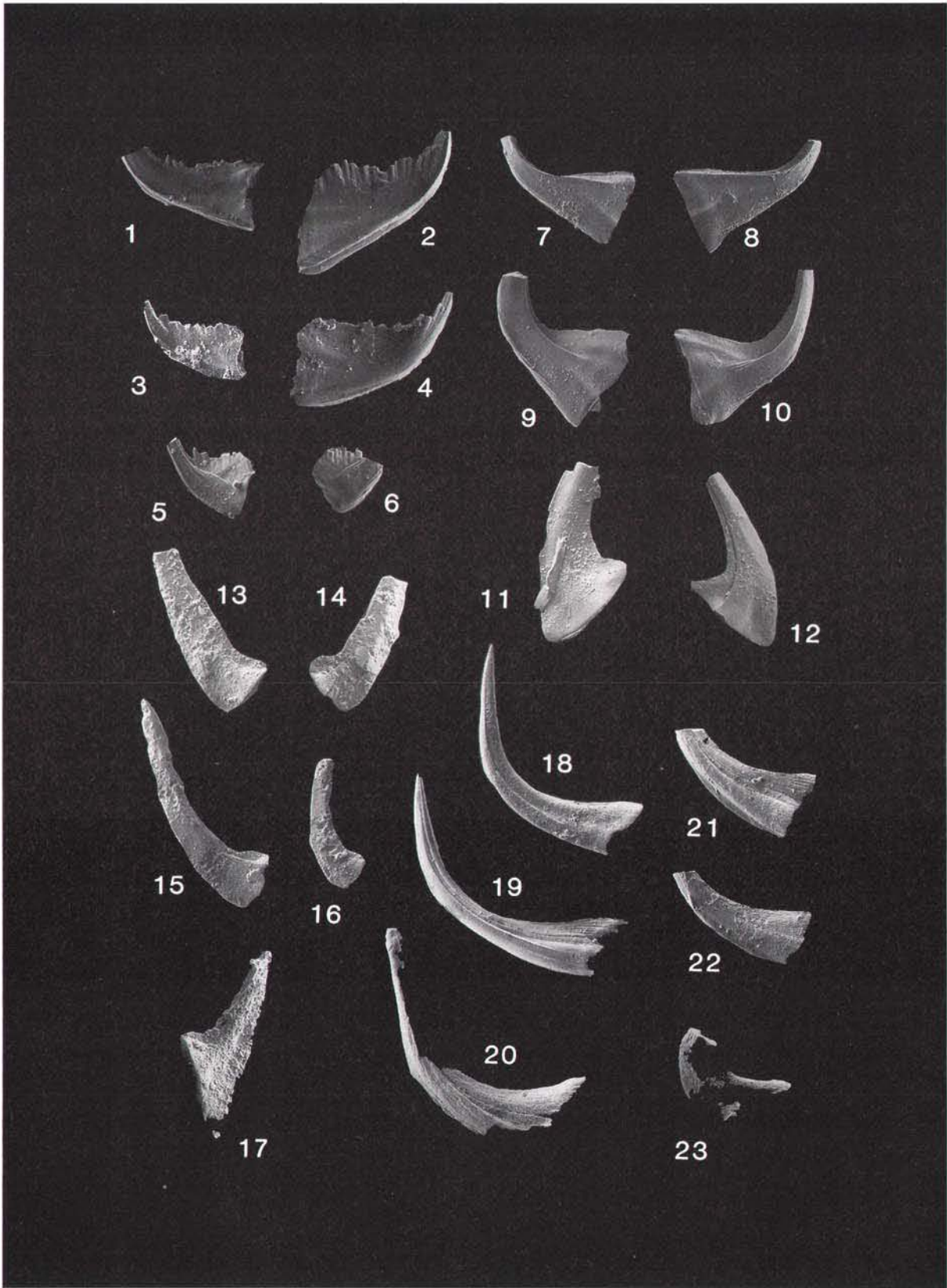
- 7, lateral view of sym. p element; MGUH 17.885.
- 8, lateral view of sym. p element; MGUH 17.886.
- 9, lateral view of sq element; MGUH 17.887.
- 10, lateral view of sq element; MGUH 17.888.
- 11, lateral view of r element; MGUH 17.889.
- 12, lateral view of r element; MGUH 17.890.

Figs 13-17. *Decoriconus fragilis* (Branson & Mehl).
All specimens from GGU 216809, × 60.

- 13, lateral view of sym. p element; MGUH 17.891.
- 14, lateral view of sym. p element; MGUH 17.892.
- 15, lateral view of sq element; MGUH 17.893.
- 16, lateral view of sq element; MGUH 17.894.
- 17, lateral view of r element; MGUH 17.895.

Figs 18-23. *Panderodus* aff. *P. greenlandensis*.
All specimens from GGU 216719, × 60.

- 18, outer-lateral view of sym. p element; MGUH 17.896.
- 19, inner-lateral view of sym. p element; MGUH 17.897.
- 20, inner-lateral view of aq element; MGUH 17.898.
- 21, 22, inner and outer-lateral view of sq element; MGUH 17.899.
- 23, inner-lateral view of r element; MGUH 17.900.



originate near the midlength of the base and pass apically migrating towards the upper edge of the cusp. One or two oblique secondary costae may extend downwards from a point on the primary costa, just below the base of the cusp. The basal margin is straight; excavated from the lower basal corner to the base of the denticles. In lateral view the basal cavity is short and tapers rapidly upwards, its lower margin is upwardly curved and its upper margin is more or less straight. White matter, as in the sym. p element, fills the denticles and cusp, passing down to the apex of the basal cavity.

Remarks. The apparatus of *B. devonicus* differs in lacking an sq element. *Belodella cooperi* differs from *Belodella* sp. cf. *B. devonica sensu* Cooper (1976) in being shorter longitudinally and having a broader basal margin. The aq element has a tendency to develop rudimentary denticles along the anterior edge of the cusp; this character is also found in the lenticular element of *B. anomalis* Cooper (1974), the apparatus of which has no sq element.

Occurrence. Found in all sections except for those in northern Peary Land and Kronprins Christian Land; ranges from the *P. celloni* Biozone into the upper (?) Wenlock.

Genus *Carniodus* Walliser, 1964

Type species. *Carniodus carnulus* Walliser, 1964, p. 30.

Emended diagnosis. Apparatus containing a complex of morphologically inter-related elements, the most commonly recurrent members of which are: an arched carminiplanate (carinthiaciform) element; a suite of anguliplanate (carnuliform) elements, characterised by a tall prominent cusp and short denticulate processes; a dolabrate (neoprioniodontan) element; an alate (latialati-form) element; an asymmetrically arched modified dolabrate (carniform element) and a dolaborate (subcarniform) element. All the elements are characterised by a narrow groove-like basal cavity and short fused denticles. In lateral view white matter is diffuse and fills each denticle above the midheight of the processes.

Remarks. The application of locational nomenclature obscures the complexity of the morphological transitions between the elements of *C. carnulus* and leads to an oversimplified picture of the apparatus structure. In view of this an informal terminology is applied here.

Carniodus carnulus Walliser, 1964

Plate 4, figs 14–29; plate 8, figs 1–4

- v1964 ?*Carniodus carinthiacus* Walliser, p. 31, pl. 6, fig. 8; pl. 27, figs 20–26; text fig. 4n.
- v*1964 *Carniodus carnulus*, p. 32, pl. 6, fig. 10; pl. 10, figs 20, 21; pl. 27, figs 27–38; pl. 28, fig. 1; text figs 4a–f.
- v1964 *Carniodus carnicus* Walliser, p. 32, pl. 6, fig. 11; pl. 28, figs 8–11.
- v1964 *Neoprioniodus subcarnus* Walliser, p. 51, pl. 5, fig. 7; pl. 28, figs 12–18.
- v1964 *Roundya latialata* Walliser, p. 71, pl. 6, fig. 15; pl. 31, figs 11–14.
- v1964 *Carniodus carnis* Walliser, p. 34, pl. 5, fig. 3; pl. 10, fig. 13, pl. 28, fig 2; text figs 4y–z.
- 1966 ?*Carniodus carinthiacus*; Spasov & Filipović, p. 38, pl. 1, fig. 3.
- 1966 *Carniodus carnulus*; Spasov & Filipović, p. 39, pl. 1, fig. 15.
- 1966 *Carniodus carnicus*; Spasov & Filipović, p. 38, pl. 1, fig. 16.
- 1966 *Roundya brevialata*; Spasov & Filipović, p. 49, pl. 1, fig. 14.
- 1966 *Carniodus carnis*; Spasov & Filipović, p. 40, pl. 1, figs 12, 13.
- 1966 *Neoprioniodus subcarnus*; Spasov & Filipović, p. 42, pl. 1, figs 8, 9.
- 1966 *Carniodus carinthiacus*; Spasov, pl. 1, fig. 3.
- 1967? *Carniodus carinthiacus*; Flajs, pl. 4, figs 2, 3.
- 1967 *Carniodus carnicus*; Flajs, pl. 4, fig. 4.
- ?1968 *Carniodus carinthiacus*; Igo & Koike, p. 8, pl. 3, figs 2, 3.
- 1969 *Carniodus carinthiacus*; Nicoll & Rexroad, p. 24, pl. 5, figs 1, 2.
- v1969 *Carniodus carnulus*; Nicoll & Rexroad, p. 25, pl. 5, figs 4, 5.
- pv1969 *Carniodus carnis*; Nicoll & Rexroad, p. 26, pl. 5, figs 6, 8 only.
- v1969 *Neoprioniodus subcarnus*; Nicoll & Rexroad, p. 41, pl. 5, fig. 10.
- 1969? *Carniodus carinthiacus*; Schönlaub, pl. 1, fig. 12.
- 1969 *Carniodus carnulus*; Schönlaub, pl. 1, fig. 5.
- 1969b *Carniodus? carinthiacus*; Drygant, p. 54, pl. 1, fig. 5.
- 1969b *Neoprioniodus subcarnus*; Drygant, p. 53, pl. 1, figs 12–14.
- p1971 *Carniodus carinthiacus*; Schönlaub, p. 46, pl. 3, figs 7–8.
- 1972 *Carniodus carinthiacus*; Rexroad & Nicoll, pl. 2, fig. 1–3.
- 1972 *Carniodus carnicus*; Rexroad & Nicoll, pl. 2, figs 4–5.
- 1972 *Carniodus carnulus*; Rexroad & Nicoll, pl. 1, figs 8–11.
- 1972 *Carniodus carnis*; Rexroad & Nicoll, pl. 1, figs 12, 13.
- 1972 *Neoprioniodus subcarnus*; Rexroad & Nicoll, pl. 2, figs 6, 7.
- v1972 *Carniodus carinthiacus*; Aldridge, p. 168, pl. 5, figs 8–10.
- v1972 *Carniodus carnicus*; Aldridge, p. 168, pl. 5, fig. 11.
- v1972 *Carniodus carnulus*; Aldridge, p. 169, pl. 5, figs 12–14.
- v1972 *Exochognathus latialatus*; Aldridge, p. 179, pl. 7, figs 10, 11.
- v1972 *Carniodus carnis*; Aldridge, p. 169, pl. 5, figs 15, 16.
- v1972 *Neoprioniodus subcarnus*; Aldridge, p. 195, pl. 5, fig. 17.

- 1975 *Carniodus carinthiacus*; Saladžius, pl. 1, figs 5a-b.
 1975 *Neoprioniodus subcarnus*; Saladžius, pl. 1, figs 11a-b.
 1975 *Neoprioniodus triangularis triangularis*; Saladžius, pl. 1, figs 13a-b.
 1975 *Carniodus carnulus*; Aldridge, pl. 1, figs 3, 4, 8, 9.
 1976 *Carniodus carnulus*; Barrick & Klapper, p. 68, pl. 1, figs 1, 2, 6-8, 12-14.
 1977 *Carniodus carinthiacus*; Liebe & Rexroad, pl. 1, fig. 12.
 1977 *Carniodus carnulus*; Liebe & Rexroad, pl. 1, fig. 3.
 1977 *Carniodus carnicus*; Liebe & Rexroad, pl. 1, fig. 4.
 1977 *Neoprioniodus subcarnus*; Liebe & Rexroad, pl. 1, fig. 1.
 1977 *Exochognathus latialatus*; Liebe & Rexroad, pl. 1, fig. 16.
 1977 *Carniodus carnulus*; Viira, p. 181, text fig. 1.
 1977 *Neoprioniodus subcarnus*; Viira, pl. 181, text fig. 1.
 1977? *Carniodus carinthiacus*; Viira, p. 181, text fig. 1.
 1977 *Carniodus carnicus*; Viira, p. 181, text fig. 1.
 1978 Apparatus 'D'; Miller, pl. 1, figs 14-17.
 1980 *Carniodus carnulus*; Helfrich, pl. 1, figs 1-6.
 1981 *Carniodus carnulus*; Nowlan, pl. 7, figs 8-11.
 1981 *Carniodus carnulus*; Uyeno & Barnes, pl. 1, figs 18, 19.
 1982 *Carniodus carnulus*; Aldridge & Mohamed, pl. 2, figs 17-24.
 1983 *Carniodus carnulus*; Uyeno & Barnes, p. 16, pl. 5, figs 1-9.
 v1983 *Carniodus carnulus*; Mabillard & Aldridge, pl. 2, figs 13, 14.
 v1985 *Carniodus carnulus*; Aldridge, p. 84, pl. 3.2, figs 10-18.
 1985 *Carniodus carnulus*; Savage, p. 714, figs 2A-N.
 1986 *Carniodus carnulus*; Bischoff, p. 177, pl. 5, figs 18-34; pl. 6, figs 1-37.
 1987 *Carniodus carnulus*; Over & Chatterton, pl. 6, figs 28-30.

Holotype. *Carniodus carnulus* Walliser, 1964, p. 32, pl. 27, fig. 31. From sample C.12A, *P. amorphognathoides* Biozone of Cellon Mountain, Austria.

Diagnosis. Refer to the generic diagnosis.

Description. *Carinthiaciform element.* Previously described as *C. carinthiacus* (refer to Aldridge, 1972, p. 168). Morphological variation in the size of the apical denticle and the degree of arching produces a range of elements transitional to the carnuliform element in morphology. Rare examples in large collections exhibit a large, posteriorly inclined 'cusp' and a short, inner-lateral process (plate 4, fig. 19). This form displays a similar morphology to the Pb element of *Pterospathodus amorphognathoides* Walliser. *Carnuliform element.* Previously described as *C. carnulus* (refer to Aldridge, 1972, p. 169). Rare examples of this element possess a short, inner-lateral projection at the base of or below the posterior edge of the cusp. Increased posterior inclination of the cusp and reduction in the number of

denticles on the anterior processes result in a transition to the neoprioniodon element morphology; intermediates between the carnuliform and specimens of the neoprioniodontan element are present in large collections.

Neoprioniodontan element. Dolabrate element dominated by a large, laterally compressed, posteriorly inclined cusp, with sharp anterior and posterior edges. The short posterior process bears up to four completely fused denticles, which decrease in size distally. In rare specimens one or two small denticles may be situated on a short inner-lateral process (plate 8, fig. 3). A slightly thickened ledge is present beneath the denticle row around the whole element. The basal cavity is shallowly excavated and expanded laterally beneath the cusp, and extends as a narrow tapering groove to the tip of the posterior process. In lateral view, white matter completely fills the denticles and cusp; its base is coincident with the top of the thickened lateral ledges.

Latialatiform element. The Greenland specimens of this element are identical to those described as *Exochognathus latialatus* (Walliser) by Aldridge (1972, p. 179).

An asymmetrical latialatiform element, rarely present in the Greenland and Welsh Borderland collections, differs from the symmetrical latialatiform element in having a shorter inner-lateral process.

Carniform element. Specimens are identical to those described as *C. carnicus* Walliser by Aldridge (1972, p. 169).

Subcarniform element. Previously described as *Neoprioniodus subcarnus* (refer to Aldridge, 1972, p. 195). In rare specimens the distal third of the posterior process appears to be differentiated into the morphology of a carnuliform element (plate 8, fig. 2).

Remarks. On the basis of Greenland material and large collections of the species from the Welsh Borderland housed in the micropalaeontological collection at the University of Nottingham, the apparatus structure appears to be considerably more complicated than that proposed by Barrick & Klapper (1976). The Pa (carinthiaciform), M (neoprioniodontan), Sa (latialatiform) and Sc (subcarniform) elements can be readily homologised. Several lines of circumstantial evidence suggest that some specimens described as the carnuliform element may represent the Sb element. Specimens (e.g. plate 4, fig. 27) have on their inner or posterior side, a short, lateral thickening beneath the cusp, a prominent cusp and asymmetrically distributed denticles on the processes. Also rare specimens of the latialatiform and subcarniform elements occur, for example those illustrated by Walliser (1964, p. 5, pl. 28, figs 15, 17) and herein (plate 8, fig. 2), in which one of the processes

appears to be distally differentiated into a carnuliform element. These specimens may represent partially fused, juxtaposed elements within the apparatus, or 'mutant' specimens from an apparatus in which the Sb and Sc elements have not been fully separated during ontogeny. It is also interesting to note that in large collections the carnuliform element is by far the most common numerically (e.g. GGU 82687 contains 20 carinthiaciform and 69 carnuliform elements) and therefore the carnuliform element may have occupied more than one position in the apparatus or existed as multiple pairs within a single apparatus. If the carnuliform element is equivalent to an Sb element, possible candidates for the Pb element include examples of the carinthiaciform element, particularly the specimens with a prominent cusp (plate 4, fig. 16–18). These also occasionally develop a short inner-lateral process (plate 4, fig. 19) and approach the morphology of a *Pterospathodus* Pb element. Carnuliform elements (e.g. plate 4, fig. 20) might also be homologised as the Pb element. The element previously referred to *C. carnicus* is difficult to homologise; it is not found in the Greenland collection and occurs only rarely in the Welsh Borderland; it may be a mutation of the carnuliform element, or, as suspected from its scaphate basal cavity, may not be a *C. carnulus* element.

Within large collections of *C. carnulus* rare elements assignable to the categories described develop an additional, short, denticulate, inner-lateral process (plate 8, figs 3, 4). These specimens are most commonly of the carnuliform to neoproniodontan transitional morphology and may be the expression of a recessive character found only in large populations; otherwise, they may be gerontic individuals or extreme members of the symmetry transition series of specimens displaying dimorphic characteristics. In all but the first category they would be expected to occur much more commonly than they do.

Carniodus, as perceived herein has a modified Type IVa apparatus plan (Barnes *et al.*, 1979); the relationships between, and the homologies of, the elements, particularly in the first transition series, are complex. *Occurrence*. Found abundantly in *Pterospathodus celloi* and *P. amorphognathoides* Biozone strata throughout Greenland.

Genus *Dapsilodus* Cooper, 1976

Type species. *Distacodus obliquicostatus* Branson & Mehl, 1933a, p. 41.

Emended diagnosis. Apparatus trimembrate comprising laterally compressed elements. The sym. p element with

straight upper and lower edges, the former extended laterally by two low costae. The sq element possesses a central costa on each lateral face, the acostate r element has a longer cusp than base.

Dapsilodus obliquicostatus (Branson & Mehl, 1933a)

Plate 7, figs 7–12

- *1933 *Distacodus obliquicostatus*, p. 41, pl. 3, fig. 2.
- 1962 *Acodus inornatus*; Ethington & Furnish, p. 1259
- 1962 *Distacodus procerus*; Ethington & Furnish, p. 1265.
- ?1966 *Distacodus procerus*; Clark & Ethington, p. 678, pl. 82, fig. 4.
- v1969 *Distacodus obliquicostatus*; Nicoll & Rexroad, p. 31, pl. 7, figs 1–4.
- v1969 *Distacodus?* n. sp. Nicoll & Rexroad, p. 32, pl. 7, figs 5–7.
- v1969 *Acodus* cf. *A. inornatus*; Nicoll & Rexroad, p. 23, pl. 7, figs 8–10.
- ?1970 *Acontiodus obliquicostatus*; Serpagli, p. 82, pl. 23, figs 1–10, pl. 24, figs 1–6.
- 1971 *Acodus inornatus*; Rexroad & Craig, p. 687, pl. 81, figs 11–15.
- 1971 *Distacodus obliquicostatus*; Rexroad & Craig, p. 688, pl. 81, figs 5–10.
- 1971 *Distacodus postercostatus* Rexroad & Craig, p. 689, pl. 82, figs 1–4.
- v1972 *Distacodus obliquicostatus*; Aldridge, p. 171, pl. 9, fig. 4.
- 1972 *Distacodus obliquicostatus*; Miller, p. 359, pl. 1, fig. 5.
- ?1972 *Distacodus procerus*; Link & Druce, p. 32, pl. 2, figs 26–29.
- ?1974c *Acontiodus obliquicostatus*; Drygant, pl. 1, figs 32, 33.
- 1976 *Dapsilodus obliquicostatus*; Cooper, p. 211, pl. 2, figs 10–13, 18–20.
- 1977 *Dapsilodus obliquicostatus*; Barrick, p. 50, pl. 2, figs 6, 10, 13.
- 1977 *Distacodus obliquicostatus*; Liebe & Rexroad, pl. 2, fig. 10, 11.
- 1977 *Distacodus postercostatus*; Liebe & Rexroad, pl. 2, fig. 12.
- 1977 *Acodus inornatus*; Liebe & Rexroad, pl. 2, fig. 13.
- 1978 *Distacodus obliquicostatus*; Rexroad, Noland & Pollock, p. 4, pl. 1, fig. 9.
- 1981 *Dapsilodus obliquicostatus*; Aldridge, Dorning & Siveter, pl. 2, figs 3–5.
- 1983 *Dapsilodus obliquicostatus*; Uyeno & Barnes, p. 16, pl. 9, figs 11, 12.
- 1983 *Dapsilodus obliquicostatus*; Wang & Ziegler, fig. 3, no. 8.
- 1987 *Dapsilodus obliquicostatus*; Over & Chatterton, pl. 6, figs 1–2.

Holotype. *Distacodus obliquicostatus* Branson & Mehl 1933a, p. 41, pl. 3, fig. 2. From the Bainbridge Formation (middle Silurian), Lithium, Missouri.

Diagnosis. Refer to generic diagnosis.

Description. *Sym. p element:* Refer to the description of the symmetrical distacodiform element of *D. obliquicostatus* in Cooper (1976, p. 211).

sq element. Refer to the description of the asymmetrical distacodiform element of *D. obliquicostatus* in Cooper (1976, p. 211).

r element. Refer to the description of the acodontiform element of *D. obliquicostatus* in Cooper (1976, p. 211).

Remarks. Serpagli (1970) reconstructed the apparatus of *Acontiodus obliquicostatus* as bimembrate consisting of elements herein designated sq and r. Cooper (1976) transferred the species to a new genus *Dapsilodus* and described an additional element (sym. p). The apparatus of the type species of *Acodus*, *Acontiodus* and *Distacodus* (the genera under which the elements of *Dapsilodus* have been previously described) are unknown (Löfgren, 1978, pp. 43–46) and their relationship to *Dapsilodus* cannot be demonstrated. Barrick (1977, p. 50) emended the diagnosis of *Dapsilodus* applying the nomenclatural terminology of Sweet & Schönlaub (1975) to the elements. He recognised M (equivalent to the r element herein), Sa (equivalent to the sym. p element) and Sb and Sc elements, separated by the degree of twisting. It appears from his descriptions that this character is found only in *D. praecipuus* Barrick and *D. sparsus* Barrick, but he did not illustrate these as separate elements.

Occurrence. Found in strata from lower-middle Llandovery to upper Llandovery in age, from central Peary Land to Washington Land. Outside Greenland Cooper (1976) recorded the range of this species as lower Silurian to lower Devonian in Europe, North America, North Africa and Australia.

This species occurs in large numbers in samples from Kap Schuchert (Washington Land, fig. 21). Mabillard & Aldridge (1985, p. 95) also noted the rapid increase in abundance of *D. obliquicostatus* in offshore environments.

Genus *Decoriconus* Cooper, 1975

Type species. *Paltodus costulatus* Rexroad, 1967, p. 40.

Diagnosis. Refer to Cooper (1976, p. 212).

Remarks. The apparatus structure of *Decoriconus* appears to comprise a transition series from the sym. p to sq elements with a distinctive r element. This suggests a relationship between this genus and *Drepanoistodus*

Lindström. If the trimembrate apparatus structure of *Decoriconus costulatus* proposed by McCracken & Barnes (1981, p. 75, pl. 2, figs 24–27) can be confirmed it is likely that *Decoriconus* diverged from a *Drepanoistodus* stock during the Upper Ordovician.

Decoriconus fragilis Branson & Mehl, 1933a Plate 7, figs 13–17

- *1933 *Paltodus fragilis*, p. 43, pl. 3, fig. 3.
- v1969 *Drepanodus aduncus*; Nicoll & Rexroad, p. 35, pl. 7, figs 11–15.
- v1969 *Paltodus costulatus*; Nicoll & Rexroad, p. 51, pl. 7, figs 16–18.
- ?1970 *Paltodus costulatus*; Pollock, Rexroad & Nicoll, p. 757, pl. 114, figs 29, 30.
- 1971 *Drepanodus aduncus*; Rexroad & Craig, p. 690, pl. 79, figs 11–14.
- 1971 *Paltodus fragilis*; Rexroad & Craig, p. 694, pl. 79, figs 8, 9, 15–17.
- v1972 *Drepanodus aduncus*; Aldridge, p. 175, pl. 9, fig. 7.
- v1972 *Paltodus costulatus*; Aldridge, p. 202, pl. 9, fig. 21.
- 1972 *Drepanodus aduncus*; Miller, p. 559, pl. 1, figs 8, 9.
- 1972 *Paltodus costulatus*; Miller, p. 562, pl. 1, fig. 6, 7.
- 1972 *Drepanodus aduncus*; Rexroad & Nicoll, pl. 2, figs 36–37.
- 1972 *Paltodus fragilis*; Rexroad & Nicoll, pl. 1, fig. 42–43.
- 1977 *Decoriconus fragilis*; Barrick, p. 53, pl. 2, figs 15, 21–23.
- 1978 *Decoriconus? fragilis*; Rexroad, Noland & Pollock, p. 4, pl. 1, fig. 10.
- 1987 *Decoriconus fragilis*; Over & Chatterton, pl. 6, fig. 3.

Holotype. *Paltodus fragilis* Branson & Mehl, 1933a, p. 43, pl. 3, fig. 6. From the Bainbridge Formation (middle Silurian), Lithium, Missouri.

Emended diagnosis. Trimembrate apparatus comprising small, twisted laterally striate cones with a short base and long cusp. The diagnostic r element has a broad straight basal margin and a steeply proclined cusp; it is triangular when viewed laterally.

Description. Complete symmetry transition occurs between the sym. p element (previously described as *Paltodus costulatus* Rexroad, 1967) and the sq element (previously described as *Paltodus fragilis* Branson & Mehl, 1933a). The end members of this transition differ only in the degree of curvature of the cusp. *r element.* Previously described as *Drepanodus aduncus* Nicoll & Rexroad (1969). A range in morphology of this element is illustrated by the Greenland collections, from the laterally compressed more or less symmetrical element (plate 7, figs 15–16) to the twisted asymmetrical ele-

ments described by Cooper (1976, p. 213, pl. 2, figs 5–8).

Remarks. Cooper (1976, p. 212) proposed the original apparatus reconstruction of *D. fragilis* which was subsequently confirmed by Barrick (1977, p. 53). The apparatus of *Decoriconus* differs from that of *Dapsilodus* in that the sym. p and aq elements are morphologically transitional, a feature more typical of *Drepanoistodus*. *D. fragilis* lacks an aq element and, if descended from a *Drepanoistodus* stock, must have lost this element. A similar evolutionary development may also have occurred in *Belodella*.

Occurrence. Abundant in the Washington Land Group at Kap Schuchert in association with *Aspelundia fluegeli* and *Dapsilodus obliquicostatus*. Outside Greenland this species has been recorded in rocks of *P. celloni* Biozone to Upper Silurian in age (Cooper, 1980, p. 213).

Genus *Dentacodina* Wang, 1980

1980 *Dentacodina* Wang, p. 370.

Type species. *Dentacodina multidentata* Wang, 1980, p. 370.

Remarks. All the elements except the Pa can be homologised with those of *Distomodius* (Branson & Branson) *sensu* Barrick & Klapper (1976). The structure of several elements, particularly the Pa and S elements, suggests their denticles may have formed separately from the main element, later fusing to the base of the cusp (Jeppsson, 1972, p. 57). Intermediate forms in this process may be those illustrated by Walliser (1964, pl. 10, figs 1–7, 10–12 and pl. 1, figs 2, 7–13).

Dentacodina aff. *D. dubia* (Rhodes, 1953)

Plate 20, figs 17–22

aff. 1953 *Cordylodus? dubius* Rhodes, p. 299, pl. 23, figs 221–224.

Description. *Pa element.* A single broad-based cone, antero-posteriorly compressed, oval in midheight cross section. The base flares broadly to the anterior and posterior and slightly laterally; the entire lower surface is deeply excavated.

Pb element. Modified coniform element comprising a long, slightly compressed, highly reclined and inwardly bowed cusp. Its base is broadly flared to form a heart-shaped platform, which is broadest posteriorly and nar-

rows to a point anteriorly. Inwardly, between the cusp and the anterior edge of the platform, the margin is sharply indented. The anterior edge of the cusp possesses a weakly developed costa which increases in height anteriorly, extending to the anterior edge of the platform. The entire lower surface appears to be shallowly excavated, obscured in all specimens by mineral infill.

M element. Laterally compressed, fused group of three coniform elements. These are subequal in size, posteriorly recurved and oval in cross section. The most anterior of the cones is erect, the others are posteriorly inclined. In lateral view the lower edge of the element is strongly arched upwards, the apex lying beneath the posterior edge of the anterior denticle. Commonly a broad zone of basal material occurs beneath the element, its lower edge close to that of the element; the basal material is deeply excavated.

Sa element. Alate element, dominated by a broad, squat cusp which is circular in cross section. Posteriorly and centrally, a single, short denticle projects from just above its base. Antero-laterally the two symmetrically disposed processes consist of two fused, coniform denticles, these also have a circular cross section; are inclined postero-laterally and have a broad base which tapers gradually upwards. The most proximal denticle of each process is fused to the cusp only by its base. The entire lower surface is deeply excavated.

Sb element. Laterally compressed element, again dominated by a squat, circular cross sectioned cusp. This is gently curved towards the posterior. Basally the cusp is expanded posteriorly but lacks the posterior denticle of the Sa element. Laterally the cusp bears one or two separate coniform denticles fused at the edge. Those on the inner face are situated slightly more postero-laterally when compared with those on the outer face of the cusp. The lowest denticle on each side is usually the largest, two to three times the size of the other denticles. The lower surface is infilled with basal material in all specimens.

Sc element. Long, posteriorly recurved cusp with a laterally compressed, broad base; the upper two-thirds of the cusp are almost horizontally directed. Two coniform denticles are fused, one to the posterior basal corner and the other centrally to the inner-lateral edge of the cusp. These are small, circular in cross section and upwardly curved, the posterior denticle is more or less horizontally directed, the inner-lateral denticle lies parallel though separate from the anterior edge of the cusp; the posterior denticle is usually the smaller of the two. The lower surface of this element is infilled with a broad zone of basal material. The white matter distribution in all the elements is very similar. The cusp and

denticles are completely filled with dense white matter, which does not extend into the basal section of any of the elements. Each coniform denticle has a separate basal cavity tip which is marked by the basal outline of the white matter.

Remarks. Elements referred to this species consist characteristically of fused coniform elements, all have similar white matter distribution and basal cavity style. *Distomodus dubius* Jeppsson differs from the Greenland specimens in the style of the denticulation: each denticle is an integral part of an element and does not appear to be superficially fused to it. The cusps of the elements of *D. dubius* are laterally costate, a feature not developed in their counterparts in *R. aff. R. dubia*. *R. aff. R. dubia* Rhodes of Mabillard & Aldridge (1983) has a similar apparatus structure, but differs in containing strongly, laterally compressed elements.

If the specimens discussed prove to be part of the same genus, then the lineage appears to have ranged from Llandovery to at least early Gedinnian. Jeppsson (1972) noted the abundance of similar elements in shallow water faunas from Ludlow strata of Scania.

Occurrence. Found infrequently in *Pterospathodus celoni* Biozone strata.

Genus *Distomodus* Branson & Branson, 1947

- 1947 *Distomodus*, p. 553.
 1964 *Hadrognathus* Walliser, p. 35.
 1970 *Exochognathus* Pollock, Rexroad & Nicoll, p. 751.
 1977 *Johnognathus* Mashkova, p. 127.

Type species. *Distomodus kentuckyensis* Branson & Branson, 1947.

Diagnosis. Refer to Bischoff, 1986, p. 94.

Remarks. *Johnognathus* Pa elements represent broken processes of *D. stauognathoides* Pa and Sa elements (Over & Chatterton, 1987, pl. 2, figs 13–16, 21–25), Savage (1985, fig. 9A) figured a similar specimen which helps substantiate this conclusion.

Distomodus stauognathoides (Walliser, 1964)

Plate 8, figs 6–10; pl. 9, figs 2–3.

- v*1964 *Hadrognathus stauognathoides*, p. 35, pl. 5, fig. 2; pl. 13, figs 6–15.
 v1964 *Roundya caudata* Walliser, p. 70, pl. 5, fig. 9; pl. 31, figs 18, 19.
 v1964 *Roundya detorta* Walliser, p. 70, pl. 5, fig. 8; pl. 31, figs 15–17.

- v1964 *Ligonodina egregia* Walliser, p. 40, pl. 6, fig. 5; pl. 32, figs 3, 4.
 1965 *Hadrognathus stauognathoides*; Brooks & Druce, p. 376, pl. 2, figs 5, 6.
 v1969 *Hadrognathus stauognathoides*; Nicoll & Rexroad, p. 36, pl. 3, figs 12–14.
 v1969 *Trichonodella? expansa* Nicoll & Rexroad, p. 67, pl. 4, figs 19–22.
 v1969 *Distomodus kentuckyensis*; Nicoll & Rexroad, p. 34, pl. 5, figs 24, 25.
 v1969 *Roundya detorta*; Nicoll & Rexroad, p. 58, pl. 6, figs 16–18.
 v1969 *Distomodus? egregia*; Nicoll & Rexroad, p. 33, pl. 5, figs 26–28.
 v1969 *Distomodus? extrorsus*; Nicoll & Rexroad, p. 34, pl. 5, fig. 23.
 1970 *Hadrognathus stauognathoides*; Moskalenko, pl. 1, fig. 8.
 1970 *Ligonodina cf. egregia*; Moskalenko, pl. 1, fig. 2.
 1971 *Hadrognathus stauognathoides*; Schönlaub, p. 44, pl. 1, figs 17, 18.
 1971 *Ambalodus carnicus* Schönlaub, p. 45, pl. 2, figs 18–20.
 1971 *Distomodus kentuckyensis*; Schönlaub, p. 47, pl. 3, fig. 9.
 1971 *Hibbardella caudata*; Schönlaub, p. 47, pl. 3, figs 12, 13.
 1971 *Hibbardella breviaulata*; Schönlaub, p. 47, pl. 3, figs 10, 11.
 ?1972 *Hadrognathus stauognathoides*; Rexroad & Nicoll, pl. 2, fig. 45.
 ?1972 *Exochognathus expansus*; Rexroad & Nicoll, pl. 2, figs 24, 25.
 ?1972 *Distomodus kentuckyensis*; Rexroad & Nicoll, pl. 2, fig. 46.
 ?1972 *Exochognathus brassfieldensis*; Rexroad & Nicoll, pl. 2, fig. 23.
 ?1972 *Exochognathus caudatus*; Rexroad & Nicoll, pl. 1, fig. 14.
 ?1972 *Distomodus egregia*; Rexroad & Nicoll, pl. 2, figs 47, 48.
 ? 1972 *Distomodus extrorsus*; Rexroad & Nicoll, pl. 2, figs 49, 50.
 v1972 *Hadrognathus stauognathoides*; Aldridge, p. 180, pl. 2, figs 8, 10, 11.
 v1972 *Trichonodella? expansa*; Aldridge, p. 218, pl. 7, figs 14a, 14b, 14c.
 v1972 *Distomodus kentuckyensis*; Aldridge, p. 173, pl. 6, figs 5–8, 11.
 pv1972 *Exochognathus detortus*; Aldridge, p. 178, pl. 7, fig. 12, spec. X.672 only.
 v1972 *Exochognathus caudatus*; Aldridge, p. 172, pl. 6, fig. 13.
 v1972 *Distomodus? egregius*; Aldridge, p. 172, pl. 6, figs 3, 4, 9.
 v1975 *Hadrognathus stauognathoides*; Aldridge, pl. 3, fig. 18.
 1975 *Hadrognathus stauognathoides*; Klapper & Murphy, p. 27, pl. 2, figs 21–25.
 1975b *Hadrognathus stauognathoides*; Schönlaub, p. 53, pl. 1, figs 1–4, 17, 20, 23–25; pl. 2, figs 1–10, 12–21.
 1976 *Distomodus stauognathoides*; Barrick & Klapper, p. 71, pl. 1, figs 20–28.
 1977 *Hadrognathus stauognathoides*; Liebe & Rexroad, pl. 1, fig. 36.
 1977 *Exochognathus expansus*; Liebe & Rexroad, pl. 1, fig. 28.
 1977 *Distomodus kentuckyensis*; Liebe & Rexroad, pl. 1, fig. 30.
 1977 *Exochognathus caudatus*; Liebe & Rexroad, pl. 1, figs 32, 33.

- 1977 *Exochognathus brassfieldensis*; Liebe & Rexroad, pl. 1, fig. 34.
- 1977 *Exochognathus detortus*; Liebe & Rexroad, pl. 1, fig. 39.
- 1977 *Distomodus extrorsus*; Liebe & Rexroad, pl. 1, fig. 31.
- 1977 *Distomodus egregia*; Liebe & Rexroad, pl. 1, figs 37, 38.
- 1977a *Hadrognathus stauognathoides*; Cooper, p. 1066, pl. 1, figs 5, 6, 7, 12, 16.
- 1977 *Johnognathus huddlei* Mashkova, p. 129–131, figs 2a–g (Pa element only).
- 1978 *Hadrognathus stauognathoides*; Miller, pl. 4, fig. 26.
- 1979 *Distomodus stauognathoides*; Aldridge, pl. 1, figs 16–17.
- 1981 *Distomodus stauognathoides*; Nowlan, pl. 5, figs 21, 27; pl. 6, fig. 21.
- 1981 *Distomodus stauognathoides*; Uyeno & Barnes, pl. 3, fig. 1–5.
- 1981 *Johnognathus huddlei*; Uyeno & Barnes, pl. 1, fig. 25.
- 1982 *Distomodus stauognathoides*; Aldridge & Mohamed, pl. 2, figs 1–6.
- 1982 *Johnognathus huddlei*; Aldridge & Mohamed, pl. 2, fig. 25.
- ?p1983 *Distomodus stauognathoides*; Nowlan, figs ?4F, 4G, 4H.
- 1983 *Johnognathus huddlei*; Mabillard & Aldridge, pl. 2, figs 11–12.
- v1983 *Distomodus stauognathoides*; Mabillard & Aldridge, pl. 1, figs 15–20.
- 1983 ?*Johnognathus huddlei*; Uyeno & Barnes, pl. 1, fig. 25.
- v1985 *Distomodus stauognathoides*; Aldridge, p. 80, pl. 3.1, figs 12–17.
- 1985 *Distomodus stauognathoides*; Savage, p. 718, figs 9A–L.
- 1985 *Johnognathus huddlei*; Savage, p. 716, figs 6A–K, 7.
- 1986 *Johnognathus huddlei*; Bischoff, p. 227, pl. 12, figs 29–40; pl. 13, figs 1–7.
- 1986 *Distomodus stauognathoides*; Bischoff, p. 106, pl. 10, figs 13–36; pl. 11, figs 1–33; pl. 12, figs 1–28.
- 1987 *Distomodus stauognathoides*; Over & Chatterton, pl. 2, figs 10–25.
- Holotype. Hadrognathus stauognathoides* Walliser, 1964, p. 35, pl. 5, fig. 2; pl. 13, fig. 7. From sample 11c within the *P. celloni* Biozone of the Carnic Alps, Austria.
- Diagnosis.* Refer to that in Bischoff (1986, p. 227).
- Description. Pa element.* Identical to the specimens referred to *H. stauognathoides* Walliser by Aldridge (1972, p. 180). White matter is concentrated into the high ornament of the upper surface.
- Pb element.* Highly arched, stelliscaphate element, comprising a large, basally expanded cusp, short denticulate anterior and posterior processes and adenticulate inner process. The cusp is laterally compressed; has well developed costae along its anterior and posterior edges and centrally down the lateral faces. The base of the cusp is differentially expanded on its inner-lateral side. The anterior process extends antero-basally, and slightly inwards, it bears one or two denticles. The posterior process is tall, extending from the base of the cusp and bearing two partially fused, compressed denticles. A short, adenticulate postero-laterally directed process extends from the inner base of the cusp. White matter fills the cusp and denticles, the base forming a linear trace just below the base of the denticles.
- M element.* The Greenland specimens are similar in overall morphology to those described as *Distomodus kentuckyensis* Branson & Branson by Aldridge (1972, p. 173). They develop slightly more convex lateral faces, are more erect and have a more steeply denticulate outer-lateral process. White matter fills the main body of the cusp and its lateral costae.
- ?*Sa element.* Only cusp fragments of this element are present in association with the Pa element. These bear

Plate 8

Figs 1–4. *Carniodus carnulus* Walliser.
All specimens from GGU 216853.

- 1, microstriations on inner-lateral face of subcarniform element, $\times 215$; MGUH 17.724.
- 2, inner-lateral view of subcarniform element, $\times 60$; MGUH 17.724.
- 3, inner-lateral view of element, $\times 60$; MGUH 17.725.
- 4, inner-lateral view of element, $\times 60$; MGUH 17.726.

Fig. 5. *Carniodus* sp.
From GGU 184125.

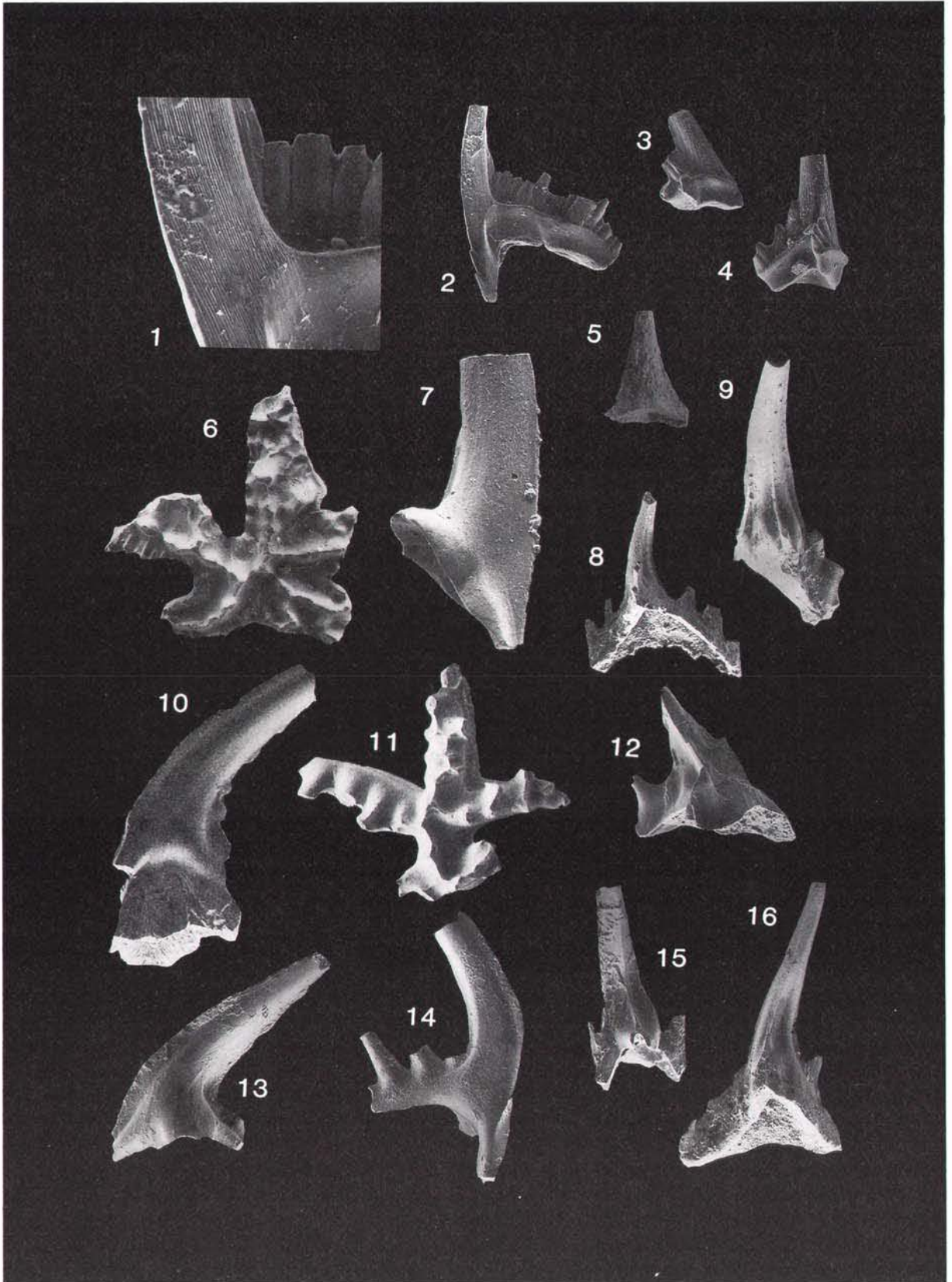
- 5, inner-lateral view of element, $\times 60$; MGUH 17.727.

Figs 6–10. *Distomodus stauognathoides* (Walliser).
All specimens from GGU 216773, unless otherwise stated.

- 6, upper view of Pa element, $\times 60$; MGUH 17.728.
- 7, inner-lateral view of M element, $\times 60$; MGUH 17.729 from GGU 184125.
- 8, posterior view of Sb element, $\times 60$; MGUH 17.730.
- 9, posterior view of Sa element, $\times 40$; MGUH 17.731.
- 10, inner-lateral view of Sc element, $\times 40$; MGUH 17.732.

Figs 11–16. *Distomodus* n. sp.
All specimens from GGU 216837.

- 11, upper view of Pa element, $\times 40$; MGUH 17.733.
- 12, inner-lateral view of Pb element, $\times 60$; MGUH 17.734.
- 13, inner-lateral view of M element, $\times 40$; MGUH 17.735.
- 14, inner-lateral view of Sc element, $\times 40$; MGUH 17.736.
- 15, posterior view of Sa element, $\times 40$; MGUH 17.737.
- 16, posterior view of Sb element, $\times 40$; MGUH 17.738.



the remains of two symmetrically disposed lateral processes and a posterior process. The cusp is rounded in cross section and bears tall costae which are situated centrally on the lateral faces and posteriorly. The basal cavity is deeply excavated extending as a narrow groove along the processes.

Sb element. Previously described as *Exochognathus caudatus* (Walliser). Refer to Aldridge (1972, p. 177–178).

Sc element. Previously described as *Exochognathus brassfieldensis* (Branson & Branson); refer to Aldridge (1972, p. 176–177).

Remarks. The Pb element described from Greenland differs from that recognised by Barrick & Klapper (1976) in lacking a broad, denticulate, posterior process. Barrick & Klapper (1976, p. 71) noted that the development of lateral platform ledges on the posterior process occurs in large robust specimens, and that the morphology exhibited by the Greenland specimens may fall within the range of ontogenetic variation of the Pb element. Where no diagnostic Pa is present in the Greenland samples, elements attributable to *Distomodus* are recorded under *Distomodus* spp.

Occurrence. Rare in upper Aeronian (C₃–C₅ of Jones, 1925) strata throughout North Greenland.

Distomodus n. sp.

Plate 8, figs 11–16

Description. Pa element. Cruciform, stelliscaphate element with narrow processes, the posterior is the shorter of the four. This element is rarely complete, due to the fragile nature of its walls. The anterior and posterior processes are longer than the lateral processes and are slightly curved inwards. The lateral processes diverge anteriorly from a point just posterior of the midlength; they form a variable angle of 45°–90° to the anterior process. Rare specimens occur in which one of the lateral processes diverges at a slightly different angle from the other. The upper surface of all the processes, bears irregular, discrete nodes; larger specimens have a mixed ornament of coalescing nodes, sinuous transverse ridges and discrete denticles. The entire lower surface is deeply excavated, the basal cavity being deeper beneath the junction of the processes. White matter is restricted to the areas of raised ornament on the upper surface.

Pb element. Arched, pastiniscaphate element with a long, compressed, posteriorly inclined cusp, short denticulate posterior process and adenticulate anterior and postero-lateral processes. The base of the cusp is lat-

erally expanded; its edges bear prominent longitudinal costae, which pass downwards into the denticles. These commonly bear only two compressed, discrete denticles, of which the most proximal is completely fused to the cusp. White matter fills the cusp and denticles; its base forms a linear trace at the midheight of the processes.

M element. Modified dolabrata element, with a prominent posteriorly inclined cusp, short posterior process and short anticusp. The cusp is laterally compressed and has tall costae along its anterior and posterior edges, it is lenticular in midheight cross section. Basally the cusp is inflated inwards and extended posteriorly as a short process which may bear one or two denticles. The antero-basal corner of the cusp is extended downwards to form an adenticulate rudimentary anticusp. The basal cavity is deeply excavated, extending as a groove along the posterior process and anticusp. White matter fills the cusp and posterior process denticles; when these are absent, a thin trace of white matter extends along the upper edge of the posterior process.

Sa element. The Greenland specimens of this element are similar to those referred to *Exochognathus caudatus* Walliser by Aldridge (1972, p. 177), differing only in having shorter lateral processes, which bear one or two discrete denticles. In large well preserved specimens each denticle has its own separate basal cavity apex. White matter fills the cusp and denticles, its base defines a sharp linear trace, just above the midheight of the processes.

Sb element. Tertiopedate element, dominated by a tall, erect, laterally twisted cusp, which bears tall longitudinal costae, centrally on the lateral and posterior faces. The base of the cusp is laterally and posteriorly expanded. The costae pass downwards into the denticles of the asymmetrically disposed lateral and posterior processes. The posterior process is shorter than the laterals, each of which bears three to four discrete denticles. The basal cavity is deeply excavated beneath the cusp, extending as a tapering groove along the processes. White matter is distributed as in the Sa element.

Sc element. Specimens are similar to those referred to *Ligonodina? extrorsa* Rexroad (1967) and *Distomodus? extrorsus* (Rexroad) by Nicoll & Rexroad (1969) and Aldridge (1972), differing only in possessing a single denticle on the inner-lateral process and commonly three partially fused denticles on the posterior process. White matter distribution is as described for the Sa element. The single inner-lateral denticle is completely filled with white matter.

Remarks. This species is only present in two reconnaissance samples from Washington Land and conforms

closely to that of *D. kentuckyensis*. *Distomodus* n. sp. is characterised by the Pa element, most specimens of which are fragmentary. They bear irregular though discrete nodes and resemble *Icriodina stenolaphata* Rexroad (1967). Several large, robust specimens are similar to the Pa element of *D. kentuckyensis*. Rare specimens approach *Icriodina* sp. Aldridge (1972, p. 87, pl. 2, fig. 2). This variation may be ontogenetic or represent morphologically distinct Pa elements within a single apparatus. The Pb element of *Distomodus* n. sp. is more closely comparable with that of *D. staurogathoides* than that of *D. kentuckyensis*. Murphy *et al.* (1979, p. 29, figs 1, 4) illustrated two cruciform Pa elements with only a single row of nodes on the carina, which may represent juvenile Pa elements of *Distomodus* n. sp.

Occurrence. Found in samples GGU 216837 and 216838 (fig. 21).

?*Distomodus* sp.

Plate 9, fig. 1

Description. ?Pa element. A single specimen, oval in upper outline, slightly broader anteriorly, bears an upper ornament of two transverse ridges, each slightly raised laterally. The entire lower surface is deeply excavated.

Remarks. This may be a juvenile specimen of a *Distomodus* species.

Genus *Kockelella* Walliser, 1964

Type species. *Kockelella variabilis* Walliser, 1957, p. 35.

Diagnosis. Refer to Barrick & Klapper (1976, p. 72).

Remarks. The apparatus structure of *Kockelella* is similar to that of *Ozarkodina*, but the genus differs in the morphology of the Pa element and the wide spacing of the denticles on the Pb, M and S elements.

Kockelella manitoulinensis (Pollock, Rexroad & Nicoll, 1970)

Plate 9, figs 4-14

- v* 1970 *Spathognathodus manitoulinensis*, p. 761, pl. 111, figs 17-19.
 1977 *Spathognathodus manitoulinensis*; Liebe & Rexroad, pl. 1, fig. 26.
 1981 *Spathognathodus manitoulinensis*; McCracken & Barnes, p. 90, pl. 7, fig. 19.

Holotype. *Spathognathodus manitoulinensis* Pollock, Rexroad & Nicoll, 1970, p. 761, pl. 111, figs 19a, 19c. Sample 5-1, from the Manitoulin Dolomite, Michigan.

Emended diagnosis. A species of *Kockelella* with a carminiscaphate (Pa) element displaying an inwardly deflected posterior process. All elements except the Pa element have a small laterally restricted basal cavity and widely spaced, compressed, pointed denticles.

Description. Pa element. Carminiscaphate, with two blade-like processes. The anterior process is straight to slightly sigmoidal and is twice as high as the posterior process. An inconspicuous apical denticle is situated at the junction of the processes. Up to fourteen denticles are present on the anterior process and only five on the posterior; the denticles are small, compressed and triangular in lateral view, in large specimens they are variable in size with those on the posterior process smaller than those on the anterior. The posterior process is inwardly deflected, at an angle of 150°-170° to the anterior process, this angle varies randomly through the stratigraphical range of the species. The basal cavity is laterally flared beneath the apical denticle; the outer lip is usually more strongly developed than the inner lip. In rare, small specimens the basal cavity is hardly flared. In lower view the basal cavity outline is broadly oval, extending on the tips of the processes as a tapering groove. Posteriorly the lower edge of the process is commonly slightly flared, producing a broader groove beneath this process.

Pb element. Angulate, laterally compressed element. The cusp is tall, compressed and inclined slightly towards the posterior. Anteriorly the process is straight and may be directed downwards forming an angle of up to 160° with the lower edge of the almost horizontal posterior process. The anterior bears three to four discrete, pointed denticles, the posterior process only two or three smaller denticles. Basally, the shallowly excavated cavity is slightly flared beneath the cusp; it is oval in lower view, extending to the tips of the processes as a narrow, tapering groove.

M element. Dolabrate, with a small, erect, compressed cusp and long posterior process extending downwards from the lower edge of the cusp. The process bears up to five pointed, discrete denticles which are separated by narrow 'v-shaped' spaces. Antero-basally the cusp may develop a short, rudimentary, denticulate process. The basal cavity is broadly expanded beneath the inner edge of the cusp, extending to the tip of the posterior process as a narrow, tapering groove.

Sa element. Alate, the cusp is erect, laterally compressed, oval in midheight cross section, bearing a costa

on each edge. The lateral processes are equal in length and form an angle of approximately 120° between their lower edges. Each bears three or four compressed, widely spaced, slender, outwardly inclined denticles. The shallowly excavated basal cavity is posteriorly expanded beneath the cusp, extending as a rapidly tapering groove to the tips of the processes.

Sb element. Tertiopedate, with the posterior process reduced to a slight swelling at the base of the cusp. The cusp is laterally compressed, its edges are costate. The lateral processes form an angle of 110° – 130° between their lower edges and are slightly, posteriorly, bowed; the inner is less steeply inclined and shallower than the outer, both bear three or four compressed, peg-like denticles. The posterior tip of the basal cavity is slightly flared, the cavity extending as a narrow groove to the tips of the processes.

Sc element. Bipennate, the anterior process is sharply downturned and only slightly inwardly bowed, its lower edge forming an angle of 110° with that of the posterior process. The anterior process bears three widely spaced, anteriorly inclined denticles, the most proximal of which is situated close to the cusp. Posteriorly, the process is broken in all specimens, it is only slightly downturned and bears similar denticles to those on the anterior process, they appear to be less widely spaced. The basal cavity is only slightly expanded beneath the cusp and shallowly excavated, extending to the tips of the processes as a narrow groove.

Remarks. The Pa element is the most commonly recorded. The deflection on the Pa element of the post-

erior processes and the denticulation, basal cavity morphology and white matter distribution of the P, M and S elements are almost identical to those in comparable elements of *Kockellella ranuliformis* (see Barrick & Klapper, 1976).

Aldridge (1972) described *Spathognathodus abruptus* and considered it distinct from *S. manitoulinensis* in the angle of deflection of the posterior process, the shorter posterior process and the increased inner-lateral development of the basal cavity. Study of the holotypes of both these species shows them to have closely similar denticulation, white matter distribution and basal cavity style. Topotype collections of *S. abruptus* stored at the University of Nottingham contain rare ramiform elements similar to those of *K. manitoulinensis*, but no Pb elements. The morphological differences described by Aldridge (1972) between the Pa elements of these two species fall within the range of morphologies displayed by paratype specimens of *K. manitoulinensis* figured by Pollock *et al.* (1970, pl. 111, figs 17–19). McCracken & Barnes (1981, p. 90) considered *S. abruptus* to be a junior synonym of *O. manitoulinensis*, but until the complete *S. abruptus* apparatus is known this synonymy is premature. McCracken & Barnes (1981, p. 84) also recorded specimens of *Ozarkodina oldhamensis* with a bowed posterior process and suggested that these were transitional to *K. manitoulinensis*. The morphological differences displayed by the other elements of *O. oldhamensis* suggest this similarity is purely coincidental.

The Pa element of *K. manitoulinensis* is closely similar in process orientation, basal cavity morphology and white matter distribution to its counterpart in the appa-

Plate 9

Fig. 1. ?*Distomodus* sp.

1, upper view of Pa fragment, $\times 60$; MGUH 17.739 from GGU 216887.

Figs 2, 3. *Distomodus staurognathoides* (Walliser). Specimens from GGU 275048, $\times 40$.

2, upper view of Pa lateral process; MGUH 17.740.
3, inner-lateral view of Pb element; MGUH 17.741.

Figs 4–14. *Kockellella manitoulinensis* (Pollock, Rexroad & Nicoll). All specimens $\times 60$.

4, inner-lateral view of Pa element; MGUH 17.742 from GGU 256381.
5, inner-lateral view of Pa element; MGUH 17.743 from GGU 256387.
6, inner-lateral view of Pa element; MGUH 17.744 from GGU 228905.
7, inner-lateral view of Pa element; MGUH 17.745 from GGU 228958.

8, upper view of Pa element, MGUH 17.746 from GGU 256387.

9, inner-lateral view of Pb element, MGUH 17.747 from GGU 256381.

10, inner-lateral view of Pb element; MGUH 17.748 from GGU 256387.

11, inner-lateral view of M element; MGUH 17.749 from GGU 256381.

12, posterior view of Sa element; MGUH 17.750 from GGU 256387.

13, posterior view of Sb element; MGUH 17.751 from GGU 256387.

14, inner-lateral view of Sc element; MGUH 17.752 from GGU 256387.

Figs 15–19. *Kockellella* cf. *K. ranuliformis* (Walliser). All specimens from GGU 228978, $\times 40$.

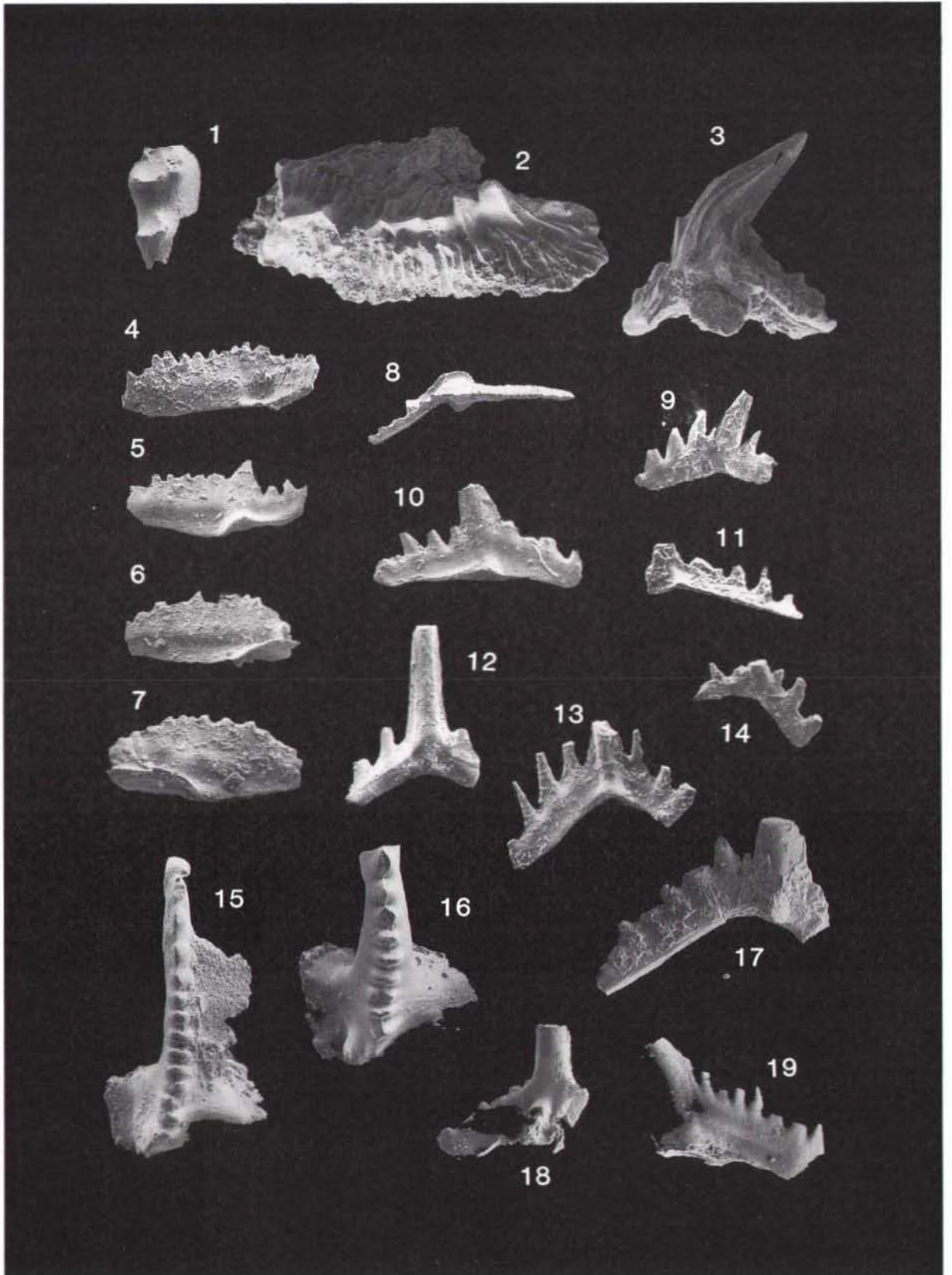
15, upper view of Pa element; MGUH 17.753.

16, upper view of Pa element; MGUH 17.754.

17, inner-lateral view of M element; MGUH 17.755.

18, posterior view of Sa element; MGUH 17.756.

19, inner-lateral view of Pb element; MGUH 17.757.



ratus of *Ozarkodina? pseudofissilis* Lindström, 1959. Orchard (1980, p. 22, pl. 6, figs 26, 28, 31) included an angulate (Pb) element, with completely fused denticles in the apparatus of *O.? pseudofissilis*, which seems to distinguish it from *K. manitoulinensis*. The two Pa elements may be homeomorphs.

Occurrence. The lowest record is 25 m above the last unequivocal Richmondian fauna in the middle part of the Turesø Formation, and the species ranges into the upper part of the Odins Fjord Formation. It occurs abundantly in Peary Land and is commonly the only ramiform apparatus present in samples from the lower Odins Fjord Formation. In Washington Land this species has only been recorded at Bessels Fjord in strata indicative of shallow shelf environments.

Outside Greenland this species has been documented from lowest Silurian to the *P. amorthognathoides* Biozone (Barnes *et al.*, 1978, p. 69).

Kockelella cf. *K. ranuliformis* (Walliser) Barrick & Klapper, 1976

Plate 9, figs 15–19

- v* cf. 1964 *Spathognathodus ranuliformis* Walliser, p. 82, pl. 6, fig. 9; pl. 22, figs 5–7.
cf. 1976 *Kockelella ranuliformis*; Barrick & Klapper, p. 76, pl. 2, figs 1–11.

Description. Pa element. Segminiscaphate, with an inwardly bowed carina and small, posteriorly situated

platform. The carina is free for most of its length, bears twelve to fifteen denticles, which in large specimens have a tendency to split centrally (plate 9, figs 15, 16); the most posterior denticle situated at the margin of the platform, is slightly inwardly offset. In upper view the platform is quadrate in outline, its outer lateral development forms two-thirds of its width. The upper surface of the platform is steeply inclined downwards, its margin is flat. The entire under surface of the platform is shallowly excavated, the basal cavity extending along the carina as a narrow groove.

The specimens are thermally mature and white matter is not visible. The remaining elements are identical to those figured by Barrick & Klapper (1976, p. 76, pl. 2, figs 1–11).

Remarks. *Kockelella* cf. *K. ranuliformis* differs from *K. ranuliformis* in the asymmetrical and posteriorly restricted development of the platform in the Pa element. This character is also shown by *K. walliseri* (Helfrich) (see Barrick & Klapper, 1976, p. 78, pl. 2, figs 24, 25) which additionally displays an outer, antero-lateral process. The Greenland specimens may represent a variant of *K. ranuliformis*.

Specimens of the Sc element of *K. cf. K. ranuliformis* are fragmented and unsuitable for illustration.

Occurrence. Found only in the Wulff Land Formation of central Peary Land and Kronprins Christian Land. Outside Greenland *K. ranuliformis* is recorded from the *P.*

Plate 10

Fig. 1. *Kockelella* aff. *K. patula* Walliser.
From GGU 256351.

1, upper view of Pa element, × 40; MGUH 17.758.

Figs 2–5. *Oulodus* sp. A.
All specimens × 40.

2, inner-lateral view of M element; MGUH 17.759 from GGU 216842.

3, posterior view of Sa element; MGUH 17.760 from GGU 216837.

4, inner-lateral view of Pa element; MGUH 17.761 from GGU 216842.

5, oblique upper-posterior view of Sb element; MGUH 17.762 from GGU 216842.

Figs 6–10. *Oulodus* sp. B.
All specimens from GGU 274721, × 60.

6, inner-lateral view of Pa element; MGUH 17.763.

7, inner-lateral view of M element; MGUH 17.764.

8, posterior view of Sa element; MGUH 17.765.

9, posterior view of Sb element; MGUH 17.766.

10, inner-lateral view of Sc element; MGUH 17.767.

Figs 11–16. *Oulodus* sp. A. Aldridge.
All specimens × 60.

11, lower view of Pb element; MGUH 17.768 from GGU 228970.

12, inner-lateral view of ?Pa element; MGUH 14.068 from GGU 184125.

13, posterior view of Sa element; MGUH 14.070 from GGU 184125.

14, inner-lateral view of M element; MGUH 17.769 from GGU 228970.

15, posterior view of Sb element; MGUH 14071 from GGU 184125.

16, inner-lateral view of Sc element; MGUH 17.770 from GGU 228970.

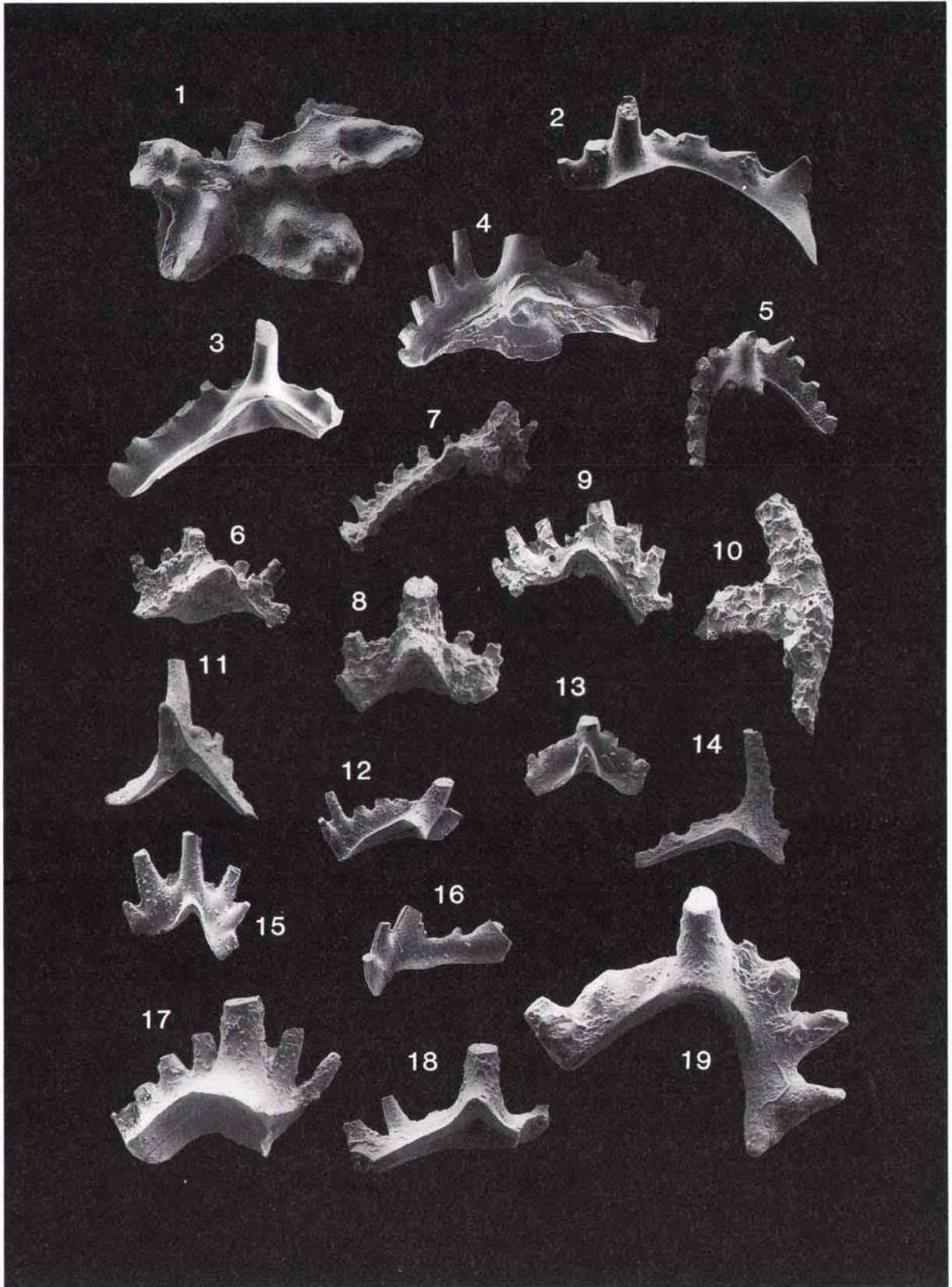
Fig. 17. *Oulodus* sp. indet. group 1.

17, inner-lateral view of P element, × 40; MGUH 17.771 from GGU 256375.

Figs 18, 19. *Oulodus* spp. indet. group 2.
Specimens from GGU 274754, × 60.

18, posterior view of Sa element; MGUH 17.772.

19, posterior view of Sb element; MGUH 17.773.



celloni and *P. amorphognathoides* Biozones of Europe and North America.

Kockelella aff. *K. patula* (Walliser) Barrick & Klapper, 1976
Plate 10, fig. 1

v* aff. 1964 *Kockelella patula* Walliser, p. 39, pl. 7, fig. 2; pl. 15, fig. 16.

Description. *Pa* element. A scaphate platform fragment consisting of four lancolate processes, each bearing a series of tall, irregular nodes, or coalescing nodes to high sinuous ridges. The ornament is irregularly arranged along the centre of the processes. The entire surface is shallowly excavated, broad grooves extend beneath the processes and become shallow distally.

Remarks. A single, incomplete specimen is present in GGU sample 256351 (fig. 3), the only conodont from this reconnaissance sample. Morphologically it is similar to *K. patula* Walliser (1964) and Barrick & Klapper (1976), but differs in having an upper ornament of irregular nodes.

Genus *Oulodus* Branson & Mehl, 1933b

- 1933b *Oulodus* Branson & Mehl, p. 116.
1935a *Gyrognathus* Stauffer, p. 144.
1935b *Barbarodina* Stauffer, p. 602.
1969 *Ligonodina* Jeppsson, p. 19.
1971 *Delotaxis* Klapper & Philip, p. 446.

Type species. *Cordylodus serratus* Stauffer, 1930, p. 124; from the Ordovician, Decorah Shale of Minnesota. Senior subjective synonym of *Oulodus mediocris* Branson & Mehl (1933b, p. 116), the originally designated type species, by subsequent designation of Sweet & Schönlaub (1975, p. 45).

Diagnosis. Refer to Sweet & Schönlaub (1975, p. 45).

Remarks. Within the Greenland collections the apparatuses of three *Oulodus* species have been reconstructed, but remain in open nomenclature due to low specimen numbers and/or poor preservation. A further eight indeterminate species groups contain individual *Oulodus* specimens, occurring within a single or closely related samples. These include new taxa, but cannot be confidently grouped into apparatuses. Thus they are illustrated and described informally.

Oulodus sp. A Aldridge, 1979
Plate 10, figs 11–16

v 1979 *Oulodus* sp. A Aldridge, p. 13, pl. 2, figs 13–16.

Description. ?*Pa* element. Described as the M element of *Oulodus* sp. A by Aldridge (1979, p. 13).

Pb element. Digyrate, with asymmetrically arched antero-lateral processes and strongly, posteriorly inclined cusp. The lateral processes are subequal in length and develop an angle of approximately 160° between their inner faces; the inner process is bowed posteriorly and bears two to four compressed, discrete denticles, the most distal of which is commonly smaller than the others. The outer process bears four or five, posteriorly inclined denticles which are oval in cross section, closely packed and separated by narrow 'v-shaped' spaces. The basal cavity is posteriorly extended beneath the cusp, as a broad tapering groove and has a narrower groove along the processes. It is deeply excavated beneath the cusp, extending beneath the processes as narrow grooves.

M element. Dolabrate with a tall cusp, long posterior process and short anticusp; the cusp is gently inwardly recurved and occasionally slightly inclined posteriorly. The short, anteriorly inclined anticusp bears one or two discrete, peg-like denticles. A straight posterior process extends from the base of the cusp at an angle of approximately 80°, its upper edge is twisted outwards, and bears up to five compressed, closely packed denticles, oval in cross section and separated by tight 'u-shaped' spaces; the most proximal denticle is smaller than the others. The inner margin of the basal cavity is expanded laterally beneath the posterior edge of the cusp, the cavity tapers rapidly, extending to the tips of the posterior process and anticusp as a narrow groove.

Sa, Sb, and Sc elements. As described by Aldridge (1979, p. 13).

Remarks. Aldridge (1979, p. 13) described elements of *Oulodus* sp. A. Aldridge from GGU 184125, Odins Fjord Formation, Peary Land. His reconstruction of its apparatus is extended to include ?*Pa*, *Pb* and M elements, with his M element questionably reassigned to the *Pa* position. Aldridge (1979, p. 13, pl. 2, fig. 12) referred a single neoprioniodontan (M) element to *Oulodus* sp. B Cooper which is morphologically similar to the newly described M element of *Oulodus* sp. A Aldridge. The P, Sa and Sb elements of *Oulodus* sp. B Cooper (1975, pl. 2, figs 18, 19, 21) are morphologically distinct from their counterparts in *Oulodus* sp. A Aldridge. The *Pb* element of *Oulodus jeannae* is similar to that of *Oulodus* sp. A Aldridge. Study of the specimen

figured by Sweet & Schönlaub (1975, pl. 1, fig. 14) shows it to have a shorter, more triangular, basal cavity extension beneath the cusp. Nowlan (1981, p. 264, fig. 4) figured M and Sb elements which are similar to those of *Oulodus* sp. A. Aldridge, but his specimens were pre-*P. celloni* Biozone in age, and may be from an older apparatus. All the Greenland specimens are thermally mature (C.A.I. 3–4) and no white matter is visible.

Occurrence. Found only in *Pterospirifer celloni* Biozone strata of Peary Land and Kronprins Christian Land.

Oulodus sp. A

Plate 10, figs 2–5

Description. Only a single well-preserved specimen of each element has been recovered. Pa element modified digyrate with more or less horizontally directed lateral processes. The cusp is slightly offset posteriorly from the plane of the process denticulation. The inner process is shorter than the outer, posteriorly bowed with upper edge anteriorly twisted. M element digyrate, the outer process much longer than the inner, is inwardly bowed; the inner process is bowed inwardly and directed antero-laterally. Sa element alate; Sb tertiope-date with posteriorly twisted lateral processes and short posterior process.

Remarks. The elements of *Oulodus* sp. A are similar to those of *Oulodus? kentuckyensis* McCracken & Barnes (1981, p. 80, pl. 1, figs 12, 13, 15) in the distribution of white matter and the lower surface morphology of the elements. Until more specimens become available and a complete apparatus structure can be elucidated, it is difficult to assess whether *Oulodus* sp. A is synonymous with *O.? kentuckyensis*. The Pa and Sb elements of *Oulodus* sp. A also bear a similarity to those described by Sweet & Schönlaub (1975, p. 49, pl. 1, figs 19–24) in the apparatus of *Oulodus jeannae*. Study of their figured M element shows it to differ in having a more steeply inclined outer-lateral process and lacks an inner-lateral process.

Occurrence. Found only in GGU 216837 and 216842 of mid Llandovery (fig. 21).

Oulodus sp. B

Plate 10, figs 6–10

Description. Pa element digyrate with a broadly expanded lower surface and short inwardly bowed antero-

lateral processes. The cusp is curved posteriorly, oval in cross-section and basally expanded. The inner process is shorter than the outer. A deep basal pit is located beneath the cusp. M element digyrate with a short inner process. Sa element alate, the basal cavity is expanded posteriorly beneath the cusp and its edge is upturned into a broad symmetrical arch. The cavity narrows rapidly, extending as a groove which terminates close to the tip of the inner process. Sb element tertiope-date lacking a well developed posterior process. The basal cavity is similar to that in the Sa, maximum expansion occurring beneath the inner edge of the cusp, the cavity only extends to the midlength of the lateral processes. Sc element bipennate, the basal cavity extends to the tips of the processes as two narrow grooves. All S elements possess a basal pit beneath the cusp.

Remarks. This apparatus reconstruction is based on *Oulodus* elements in sample GGU 274720, with additional specimens from GGU 274721 and 274738. *Oulodus* sp. nov. A Aldridge & Mohamed (1982, pl. 1, figs 34–39) has similar Pa and S elements but differs in the morphology of the M element.

Occurrence. Found only in middle Llandovery strata of Kronprins Christian Land (fig. 8).

Oulodus sp. indet. group 1

Plate 10, fig. 17

Remarks. This group is represented by two separate occurrences of incomplete, large, robust, *Oulodus* P elements with broad expanded basal cavities. They are found in GGU 256375 and 274722 (figs 6, 8) and represent the only upper Ordovician species of *Oulodus* recorded from North Greenland. These specimens bear little resemblance to other Ordovician species of *Oulodus* and probably represent a new species.

Oulodus spp. indet. group 2

Plate 10, figs 18–19; plate 11, fig. 1

Remarks. This group of elements is found only in GGU 274754 (fig. 8), and probably contains representatives of more than one apparatus. Elements are assigned to Sa, Sb and Sc positions; the Sb is distinctive in having a broadly arched, posterior lip to the basal cavity, and it may be part of an apparatus including elements from *Oulodus* spp. indet. groups 3 and 4 (plate 11, figs 2–5). A similar element was referred by McCracken & Barnes (1981, pl. 6, fig. 14) to the apparatus of *Oulodus? kentuckyensis*.

Oulodus spp. indet. group 3

Plate 11, figs 2-3

Remarks. Two large robust elements from GGU 274747 (fig. 8) are assigned to Pb and Sa positions. Both have broad, upwardly arched, lower posterior margins to the basal cavity and a deep basal pit beneath the cusp, which extends laterally as two deep grooves. The lateral processes of the Sa element (plate 11, fig. 2) are twisted upwards at a quarter of their length, to form an angle of 90° with the posterior edge of the cusp. The Pb element differs from that referred to *Oulodus jeannae* by Sweet & Schönlaub (1975) in having a less steeply upturned lower posterior margin to the basal cavity.

Oulodus spp. indet. group 4

Plate 11, figs 4-5

Remarks. This group contains Pb and Sa elements found in GGU 256388 (fig. 6). The Pb element is similar to that in *Oulodus* spp. indet. group 3, but its inner-lateral process is not as steeply inclined downwards and the cusp of this specimen is posteriorly offset from the plane of the process. The Sa element has a similarly offset cusp. These specimens are similar to those in *Oulodus* spp. indet. group 2 and may be part of the same apparatus.

Oulodus spp. indet. group 5

Plate 11, figs 6-8

Remarks. Pb, Sa and Sb elements found in GGU 228901 (fig. 6) are probably referable to two apparatuses. The

Sb element (plate 11, fig. 6) has peg-like denticles and a short cusp, with a circular cross section. The Pb and Sb elements (plate 11, figs 7, 8) bear compressed denticles and have a posteriorly restricted basal cavity expansion. These elements are similar to their counterparts in *Oulodus jeannae* Sweet & Schönlaub (1975, pl. 1, figs 20, 21), but the inner-lateral basal cavity in the Greenland Pb element is much broader, and the lateral processes of the Sb element are more tightly arched and posteriorly recurved.

Oulodus spp. indet. group 6

Plate 11, figs 9-10

Remarks. Includes a Pb and an M element from GGU 274758 (figs 8, 9). The M element differs from that in *Oulodus jeannae* Sweet & Schönlaub (1975) in having a narrow, groove-like, basal cavity and an adenticulate inner-lateral process.

Oulodus spp. indet. group 7

Plate 11, figs 11-13

Remarks. This group includes the *Oulodus* elements in GGU 242890 and 242894 (fig. 16). All have peg-like denticulation and deep lateral processes of which one is highly twisted towards the posterior. The ?P element (plate 11, fig. 12) is broken, but appears to have consisted of an extremely broad cusp and two lateral processes, the outer posteriorly recurved and directed downwards. An element with similar morphology was referred to *Oulodus? annianus* by Schönlaub (1975b, p.

Plate 11Fig. 1. *Oulodus* spp. indet. group 2.

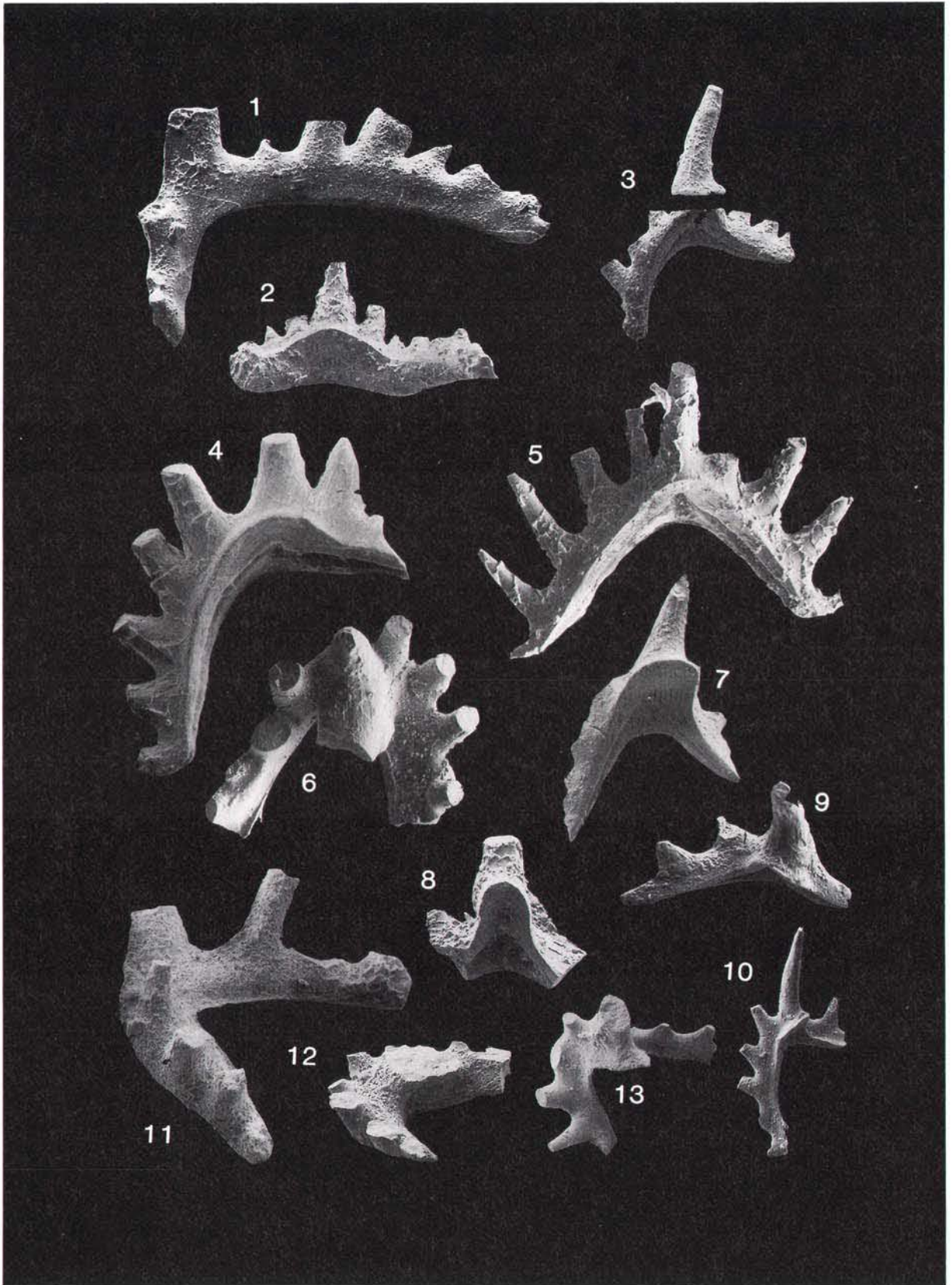
1. inner-lateral view of Sc element, × 40; MGUH 17.774 from GGU 274754.

Figs 2, 3. *Oulodus* spp. indet. group 3.
Specimens from GGU 274747, × 40.2. posterior view of S element; MGUH 17.775.
3. lower view of Pb element; MGUH 17.776.Figs 4, 5. *Oulodus* spp. indet. group 4.
Specimens from GGU 256388, × 40.4. inner-lateral view of P element; MGUH 17.777.
5. posterior view of Sa element; MGUH 17.778.Figs 6-8. *Oulodus* spp. indet. group 5.
Specimens from GGU 228901, × 40.6. oblique upper view of Sb element; MGUH 17.779.
7. lower view of Pb element; MGUH 17.780.
8. posterior view of Sa element; MGUH 17.781.Figs 9, 10. *Oulodus* spp. indet. group 6.
Specimens from GGU 274758, × 60.9. inner-lateral view of M element; MGUH 17.782.
10. oblique lateral view of Pb element; MGUH 17.783.Figs 11-13. *Oulodus* spp. indet. group 7.

11. inner-lateral view of Sc element, × 40; MGUH 17.784 from GGU 242890.

12. oblique inner-lateral view of ?P element, × 60; MGUH 17.785 from GGU 242894.

13. oblique posterior view of ?Sb element, × 60; MGUH 17.786 from GGU 242890.



51, pl. 1, fig. 16). The ?Sb element (plate 11, fig. 13) is similar; its outer-lateral process is steeply directed downwards, with the denticles directed almost horizontally outwards. The inner process of the Sc element (plate 11, fig. 11) diverges from the antero-lateral edge of the cusp and is steeply inclined downwards forming an angle with its lower edge of approximately 50° to that of the posterior process. This specimen approaches the morphology exhibited by the Sc element of *Oulodus petila* (Nicoll & Rexroad, 1969) *sensu* Barrick & Klapper (1976, pl. 4, fig. 33).

Oulodus spp. indet. group 8

Plate 12, figs 1-3

Remarks. GGU 216729 (fig. 16) contains three *Oulodus* elements. The M element (plate 12, fig. 2) is dolabrate and is similar to that of *Aspelundia fluegeli* (Walliser). It differs in having a less laterally compressed cusp and the inner lower margin of the basal cavity is arched upwards and expanded inwards beneath the posterior edge of the cusp. The posteriorly inclined denticles on the arched posterior process are circular in cross section and closely packed. The ?Sb element (plate 12, fig. 3) approaches the morphology of its counterpart in the apparatus of *Oulodus* sp. B Cooper (1975, p. 997, plate 2, fig. 20).

Genus *Ozarkodina* Branson & Mehl, 1933a

- 1933a *Ozarkodina* p. 51.
 1933a *Plectospathodus* p. 47.
 1933a *Spathodus* p. 46 (*non* Boulenger, 1900).
 1941 *Spathognathodus*, p. 98.
 1969 *Hindeodella*; Jeppsson, p. 13.
 1970 *Ozarkodina*; Lindström, p. 439.

Diagnosis. Refer to Barrick & Klapper (1976, p. 78).

Type species. *Ozarkodina typica*, by original designation of Branson & Mehl (1933a, p. 51); from the Silurian, Bainbridge Formation of Missouri. A junior subjective synonym of *Ozarkodina confluens* (Branson & Mehl, 1933a).

Remarks. Twelve species of *Ozarkodina* are present in the Greenland collections; these can be referred to three distinct groups based upon M element morphology and the white matter distribution in the Pa elements. The groups include those species similar to *O. confluens* Branson & Mehl (such as *O. broenlundii* Aldridge), species similar to *O. excavata excavata*, (for example *Ozarkodina* n. sp. C and *O. excavata* from Greenland) and species similar to *O. polinclinata* Nicoll & Rexroad (such as *O. pirata* Uyeno & Barnes). The last group has an M element similar to *Aspelundia fluegeli*. Kuwano (1982) suggested that the apparatus of *O. excavata excavata* contained two morphologically dis-

Plate 12

Figs 1-3. *Oulodus* spp. indet. group 8.
 All specimens from GGU 216729, × 60.

- 1, posterior view of Sb element; MGUH 17.787.
- 2, inner-lateral view of M element, MGUH 17.788.
- 3, oblique posterior view of ?Sb element; MGUH 17.789.

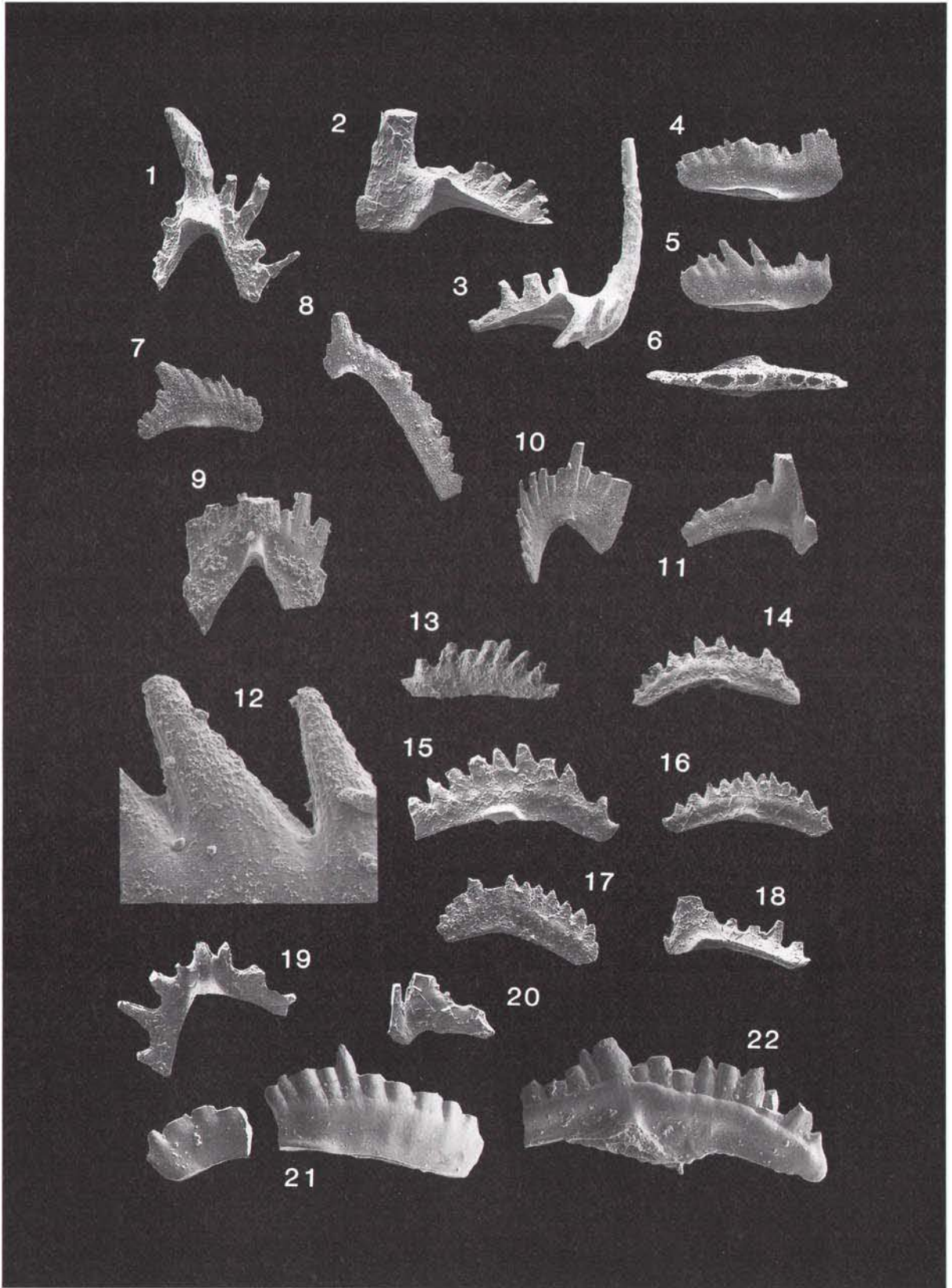
Figs 4-12. *Ozarkodina broenlundii* Aldridge.
 All specimens from GGU 184125, × 60 unless otherwise stated.

- 4, lateral view of Pa element; MGUH 14.408 (Aldridge, 1979, pl. 1, fig. 18).
- 5, lateral view of Pa element; MGUH 14.049 (holotype) (Aldridge, 1979, pl. 1, fig. 19).
- 6, upper view of Pa element; MGUH 14.051 (Aldridge, 1979, pl. 1, fig. 21).
- 7, inner-lateral view of Pb element; MGUH 14.050 (Aldridge, 1979, pl. 1, fig. 20).
- 8, inner-lateral view of M element; MGUH 14.052 (Aldridge, 1979, pl. 1, fig. 22).
- 9, posterior view of Sa element; MGUH 14.054.
- 10, posterior view of Sb element; MGUH 14.055 (Aldridge, 1979, pl. 1, fig. 25).
- 11, inner-lateral view of Sc element; MGUH 14.053 (Aldridge, 1979, pl. 1, fig. 23).

12, microstriations on the denticles of Pa element, × 360; MGUH 14.049.

Figs 13-22. *Ozarkodina excavata* (Branson & Mehl).
 All specimens × 60.

- 13, lateral view of Pa element; MGUH 17.791 from GGU 256379.
- 14, lateral view of Pa element; MGUH 17.792 from GGU 256382.
- 15, lateral view of Pa element; MGUH 17.793 from GGU 256388.
- 16, lateral view of Pa element; MGUH 17.794 from GGU 256383.
- 17, inner-lateral view of Pb element; MGUH 17.795 from GGU 274721.
- 18, inner-lateral view of the M element; MGUH 17.796 from GGU 256383.
- 19, posterior view of ?Sb element; MGUH 17.797 from GGU 256383.
- 20, inner-lateral view of ?Sc element; MGUH 17.798 from GGU 256384.
- 21, lateral view of Pa element; MGUH 17.799 from GGU 228978.
- 22, lateral view of Pa element; MGUH 17.800 from GGU 216772.



tinct pairs of Sb elements, which provides further evidence for the separation of this and related species from *O. confluens*. If the informal groups can be confirmed as separate lineages, then *Ozarkodina* is separable into at least three subgenera.

Ozarkodina broenlundii Aldridge, 1979

Plate 12, figs 4–12

- v1979 *Ozarkodina broenlundii* Aldridge, p. 16, pl. 1, figs 18–25.

Holotype. MGUH 14049, Aldridge, 1979, pl. 1, fig. 19; Pa element from sample GGU 184125, upper part of the Odins Fjord Formation at Børglum Elv, Peary Land, in eastern North Greenland.

Diagnosis. Refer to Aldridge (1979, p. 16).

Description. Refer to Aldridge (1979, pp. 16–17).

Remarks. This species is distinguished from *O. confluens* Branson & Mehl by its variable height and irregularly, but well spaced, denticles, shallow groove-like basal cavity and lack of a posterior extension of the cusp in the Sa and Sb elements. The Pa element of *O. broenlundii* has a similar basal cavity and high central denticles to its counterpart in *O. pirata*, but is distinguished by the high anterior denticles.

Occurrence. Found in *Pterospathodus celloni* Biozone faunas of Peary Land, Kronprins Christian Land, Wulff Land and Washington Land.

Ozarkodina excavata (Branson & Mehl, 1933a)

Plate 12, figs 13–22; plate 13, fig. 1

- v1933a *Prioniodus excavatus*, p. 45, pl. 3, figs 7, 8.
 v1933a *Ozarkodina simplex*, p. 52, pl. 3 figs 46, 47.
 v1933a *Trichognathus excavata*, p. 51, pl. 3, figs 35, 36.
 v1953 *Prioniodella inclinata* Rhodes, p. 324, pl. 23, figs 233–235.
 1953 *Trichonodella aboraflexa* Rhodes, p. 312, pl. 23, figs 231, 241, 242.
 1953 *Plectospathodus extensus* Rhodes, p. 323, pl. 23, figs 236–240.
 v1957 *Spathognathodus inclinatus*; Walliser, p. 47, pl. 1, figs 16–20.
 v1957 *Ozarkodina media* Walliser, p. 40, pl. 1, figs 21–25.
 v1957 *Prioniodina bicurvata*; Walliser, p. 46, pl. 2, figs 18, 19.
 v1957 *Trichonodella excavata*; Walliser, p. 48, pl. 3, figs 3, 4, 6, 9.
 v1957 *Plectospathodus extensus*; Walliser, p. 43, pl. 3, figs 1, 2; fig. 3.

- v1957 *Hindeodella equidentata*; Walliser, p. 34, pl. 2, fig. 23.
 v1964 *Spathognathodus inclinatus inclinatus*; Walliser, p. 76, pl. 8, fig. 6; pl. 9, fig. 9; pl. 19, figs 6–16.
 v1964 *Ozarkodina media*; Walliser, p. 58, pl. 8, fig. 5; pl. 9, fig. 8; pl. 26, figs 19–25, 27–34.
 v1964 *Neopriioniodus excavatus*; Walliser, p. 49, pl. 8, fig. 4; pl. 9, fig. 7; pl. 9, fig. 7; pl. 29, fig. 2b; text fig. 5c.
 v1964 *Trichonodella excavata*; Walliser, p. 89, pl. 31, fig. 26.
 v1964 *Plectospathodus extensus*; Walliser, p. 64, pl. 8, fig. 1; pl. 9, fig. 4; pl. 30, figs 13, 14.
 v1964 *Hindeodella equidentata*; Walliser, p. 36, pl. 8, fig. 3; pl. 9, fig. 6; pl. 32, fig. 11.
 1969 *Hindeodella excavata*; Jeppsson, p. 18, figs 1 G–L; fig. 3.
 v1971 *Ozarkodina simplex*; Rexroad & Craig, p. 693, pl. 80, figs 26–31.
 v1971 *Prioniodella inclinata*; Rexroad & Craig, pl. 80, fig. 25.
 v1971 *Ozarkodina media*; Rexroad & Craig, pl. 80, figs 24, 25.
 v1971 *Neopriioniodus excavatus*; Rexroad & Craig, p. 692, pl. 80, figs 6–9.
 v1971 *Plectospathodus extensus*; Rexroad & Craig, p. 698, pl. 82, figs 1, 2.
 1972 *Hindeodella excavata*; Jeppsson, p. 61, pl. 1, fig. 30; text fig. 1A.
 v1972 *Spathognathodus inclinatus*; Aldridge, p. 213, pl. 4, figs 15, 16.
 v1972 *Plectospathodus extensus*; Aldridge, p. 207, pl. 7, figs 21, 22.
 1974 *Hindeodella excavata*; Jeppsson, pl. 4, figs 1–17 (see for further synonymy).
 p1975 *Ozarkodina plana*; Sweet & Schönlaub, pl. 52, pl. 1, figs 2, ?5, only.
 p1975 *Spathognathodus inclinatus inclinatus*; Schönlaub & Zezula, pl. 2, figs 10a–b only.
 v1975 *Ozarkodina excavata*; Aldridge, pl. 2, figs 9–14.
 1975 *Ozarkodina protoexcavata* Cooper, p. 1106, pl. 3, figs 1–6.
 1976 *Ozarkodina excavata excavata*; Barrick & Klapper, p. 78, pl. 4, figs 13–23, 26.
 1976 *Ozarkodina excavata*; Cooper, p. 215, pl. 2, figs 1–4, 6, 7.
 ?1976 *Spathognathodus inclinatus*; Miller, pl. 8, figs 1, 32.
 ?1976 *Ozarkodina media*; Miller, pl. 8, figs 21, 35, 36.
 ?1976 *Ozarkodina simplex*; Miller, pl. 8, figs 34.
 ?1976 *Trichonodella excavata?*; Miller, pl. 8, fig. 13.
 1976 *Ozarkodina excavata*; Cooper, p. 188, pl. 16, figs 8–15.
 1978 *Ozarkodina excavata excavata*; Rexroad, Noland & Pollock, p. 9, pl. 1, figs 17–22.
 1978 *Ozarkodina excavata*; Helfrich, pl. 2, figs 1–7.
 1980 *Ozarkodina excavata excavata*; Mayr, Uyeno, Tipnis & Branes, pl. 32.1, figs 28, 32.
 1980 *Ozarkodina excavata*; Helfrich, pl. 2, figs 31–38.
 1981 *Ozarkodina excavata excavata*; Nowlan, pl. 6, figs 10–16, 18.
 1982 *Ozarkodina excavata*; Aldridge & Mohamed, pl. 1, figs 16–17.
 v1983 *Ozarkodina excavata*; Mabillard & Aldridge, pl. 3, figs 1–6.
 1985 *Ozarkodina excavata excavata*; Savage, p. 722, figs 14A–L.
 1986 *Ozarkodina excavata excavata*; Bischoff, p. 134, pl. 25, figs 35–40; pl. 26, figs 1–40.

Neotype. *Neoprioniodus excavata* Branson & Mehl; Rexroad & Craig, p. 692, pl. 80, fig. 7. From sample 2, Bainbridge Formation, Lithium, Missouri.

Diagnosis. Refer to Jeppsson (1974, p. 29).

Description. All elements of *O. excavata* have been adequately described and reference should be made to the works cited in the synonymy. Specimens of the Pa element from *P. celloni* Biozone samples have a conspicuous cusp situated just to the posterior of the mid-length of the element.

Remarks. *Ozarkodina excavata* from Greenland differs only slightly from Upper Silurian *O. excavata excavata* in the morphology of its M and ?Sb elements; all known elements have a more oval basal cavity when viewed from beneath. White matter is not visible in the Greenland specimens.

Ozarkodina n. sp. C has an arched, blade-like Pa element similar to that of *O. excavata*, but differs in having larger denticles to the posterior of the apical denticle and an asymmetrically developed, narrowly flaring basal cavity. The other elements in the apparatus are similar to their counterparts in *O. excavata*. *Ozarkodina* n. sp. C appears in the lowermost Silurian of Wulff Land and may be a stratigraphical or geographical variant of *O. excavata*.

Occurrence. Found infrequently in Llandovery samples; most commonly in Peary Land.

Ozarkodina aff. *O. gulletensis*? (Aldridge, 1972)
Plate 13, figs 2, 3

- ?v aff. 1972 *Spathognathodus gulletensis* Aldridge, p. 212,
pl. 4, figs 9-12.
?v aff. 1979b *Hindeodella gulletensis*; Jeppsson, p. 224,
pl. 72, figs 14-22.

Description. Pa element. A single specimen of a carminate element with an arched denticulate upper edge and straight lower edge. A posteriorly inclined, prominent apical denticle is situated to the posterior of the mid-length. The anterior process is approximately twice as high as the posterior process and bears seven squat, triangular denticles. The denticles on both processes are fused almost to their apices. The posterior process is much shorter than the anterior, bearing three denticles which are subequal in height. The basal cavity is situated beneath the apical denticle and has asymmetrically flared lips; it extends to the tips of the processes as a tapering groove. The inner lip is situated slightly post-

erior of the outer lip and bears a single peg-like denticle. In lateral view, white matter completely fills each denticle; its base defines a sharp linear trace which is deepest beneath the apical denticle and is inclined upwardly along the processes. The two denticles at the end of the anterior process contain white matter only at their tips.

Pb element. Angulate, strongly arched upper edge and straight lower edge. The cusp is posteriorly inclined, flattened lenticular in cross section; it is approximately twice as broad, but only marginally taller than the largest denticles. The anterior process is approximately twice as high as the posterior process and bears four compressed denticles. These are almost fused to their apices and decrease in height (but not width) distally; the most proximal denticle is fused almost completely to the edge of the cusp. The posterior process is short and slightly inwardly bowed bearing only a single, broad, compressed denticle. The basal cavity is expanded almost symmetrically beneath the cusp; its inner edge is upturned beneath the cusp, forming a broad arch. The basal cavity tapers anteriorly and posteriorly, extending to the tips of the element as an extremely narrow groove. In lateral view, white matter is seen to fill each denticle completely above its base; white matter does not extend downwards into the processes.

Remarks. The white matter distribution in the Pa element is similar to that in its counterpart in the apparatus of *O. gulletensis* Aldridge. The former element, however, has an arched upper edge, fewer denticles and an asymmetrically expanded basal cavity which develops a denticle on its inner lip. Study of the holotype and paratype specimens of *O. gulletensis* shows the number and height of the denticles to be intraspecifically variable. The basal cavity expansion and white matter distribution do not vary between specimens. The Pb element of *O. aff. O. gulletensis*? is smaller than that referred to *H. gulletensis* by Jeppsson (1979b, pl. 2, fig. 17). The Greenland specimen is probably a juvenile, and it has a white matter distribution similar to juvenile specimens of the Pb element of *H. confluens* (Jeppsson, 1979b, pl. 6, fig. 1). The asymmetrical basal cavity development of *O. aff. O. gulletensis*? is probably sufficient to separate it as a new species.

Occurrence. Found only in samples of *Pterospododus celloni* Biozone age from Washington Land and Wulff Land.

Ozarkodina cf. *O. hadra* (Nicoll & Rexroad, 1969)

Plate 13, figs 4-9

v. cf. 1969 *Spathognathodus hadros* Nicoll & Rexroad, p. 59, pl. 5, figs 17, 18.

Description. *Pa* element. Carminate, shallowly arched, element with subparallel upper and lower edges. A small, though prominent, apical denticle is situated just to the posterior of midlength; it is compressed and posteriorly inclined. The deeper and longer anterior process bears seven compressed, almost completely fused denticles; erect to slightly posteriorly inclined, the three distal denticles are larger than the others. The posterior process bears five to six posteriorly inclined denticles, the two most proximal of these are slightly smaller than the others, which tend to increase in size towards the centre of the process. The basal cavity is situated beneath the apical denticle and is slightly asymmetrically expanded; its inner flare is situated just to the anterior of the outer flare. Several specimens have a slightly less well developed inner expansion of cavity. The basal cavity is shallowly excavated beneath the apical denticle, extending as an extremely narrow groove, terminating at approximately the midlength of the anterior process; there is no groove beneath the posterior process.

Pb element. Strongly arched, angulate element, the cusp is lenticular in cross section with costate anterior and posterior edges; the outer face of the cusp is weakly microstriated. The inwardly bowed anterior process forms an angle of 100°-120° to the anterior edge of the cusp; this bears three laterally triangular, broad, basally fused denticles, of which the most proximal is smaller than the others. The posterior process is broken in the majority of specimens, bearing five broadly spaced denticles similar in shape and size to those on the anterior process. One specimen possesses a slightly outwardly directed posterior process. The basal cavity is flared beneath the cusp, has a circular lower outline and extends only a short distance beneath the anterior and posterior processes, terminating beneath the first proximal denticle of each process.

M element. Modified teritiopede with a short inner and strongly arched outer process, lacks a posterior process, anterior process reduced. The cusp is broad, lenticular in midlength cross section. The inner process bears one or two discrete, peg-like denticles; the outer process is occasionally inwardly bowed, bearing seven partially fused denticles with oval cross sections. The most proximal denticle is commonly much shorter than the others. The lower edge of the basal cavity is expanded and broadly upturned beneath the cusp. The cavity tapers rapidly to a narrow groove beneath the posterior process, terminating at approximately the

Plate 13

Fig. 1. *Ozarkodina excavata* (Branson & Mehl).

1, ?inner-lateral view of *Pb* element, × 60; MGUH 17.801 from GGU 228978.

Figs 2, 3. *Ozarkodina* aff. *O. gulletensis* (Aldridge). Specimens from GGU 216772, × 60.

2, inner-lateral view of *Pa* element; MGUH 17.802.

3, inner-lateral view of *Pb* element; MGUH 17.803.

Figs 4-9. *Ozarkodina* cf. *O. hadra* (Nicoll & Rexroad). All specimens from GGU 82687, × 40.

4, inner-lateral view of *Pa* element; MGUH 17.804.

5, posterior view of *Sa* element; MGUH 17.805.

6, inner-lateral view of *Pb* element; MGUH 17.806.

7, inner-lateral view of *M* element; MGUH 17.807.

8, posterior view of *Sb* element; MGUH 17.808.

9, inner-lateral view of *Sc* element; MGUH 17.809.

Figs 10-16. *Ozarkodina hassi* (Pollock, Rexroad & Nicoll). All specimens × 60.

10, inner-lateral view of *Pa* element; MGUH 17.810 from GGU 274721.

11, inner-lateral view of *Pa* element; MGUH 17.811 from GGU 198806.

12, inner-lateral view of *Pb* element; MGUH 17.812 from GGU 274721.

13, inner-lateral view of *M* element; MGUH 17.813 from GGU 274721.

14, posterior view of *Sa* element; MGUH 17.814 from GGU 254883.

15, posterior view of *Sb* element; MGUH 17.815 from GGU 274721.

16, inner-lateral view of *Sc* element; MGUH 17.816 from GGU 254883.

Figs 17-19. *Ozarkodina* aff. *O. hassi* (Pollock, Rexroad & Nicoll).

All specimens from GGU 274747, × 60.

17, inner-lateral view of *Pa* element; MGUH 17.817.

18, inner-lateral view of ?*Pb* element; MGUH 17.818.

19, inner-lateral view of ?*M* element; MGUH 17.819.

Figs 20-23. *Ozarkodina pirata* Uyeno & Barnes.

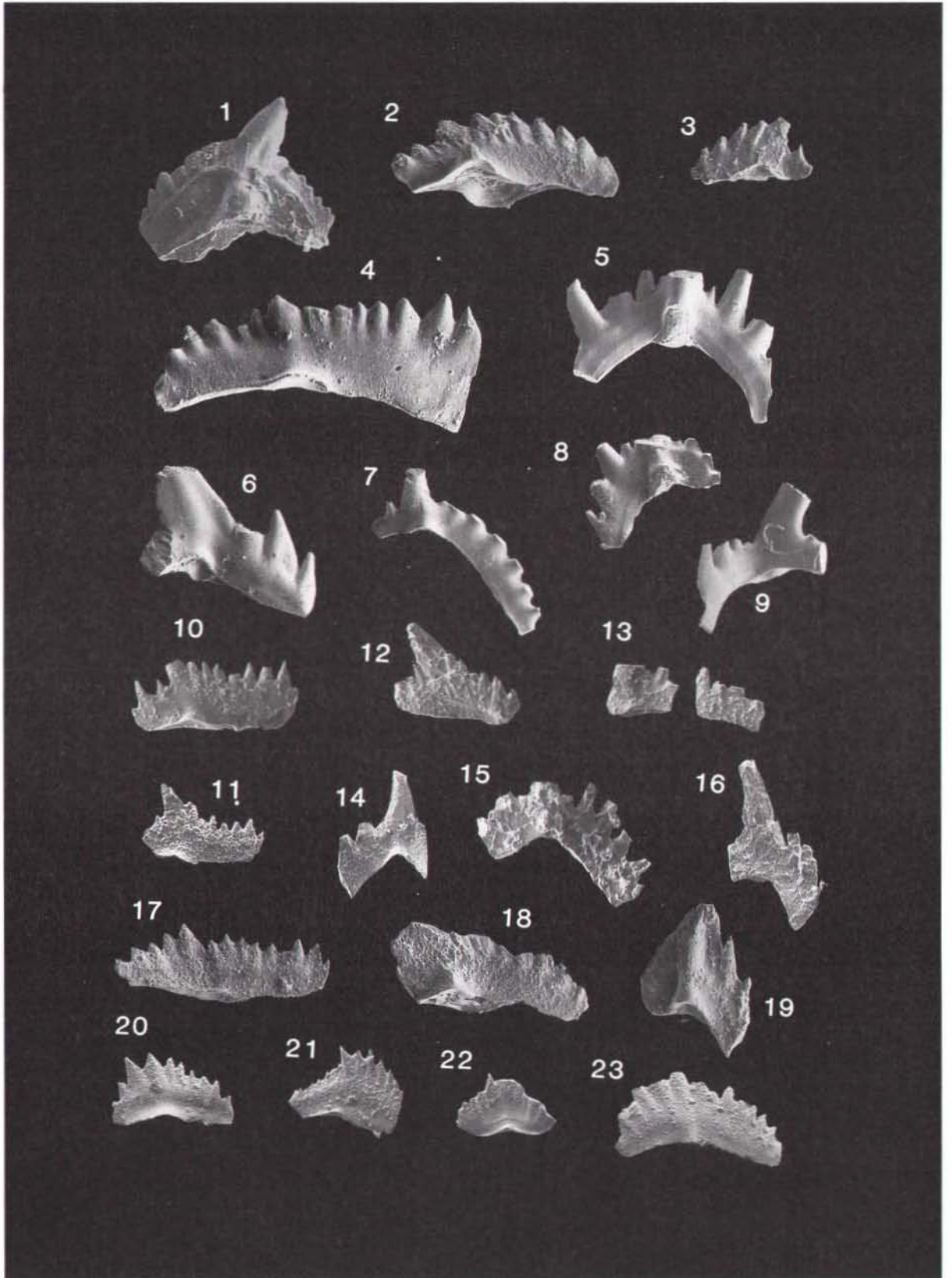
All specimens from GGU 274766, × 60.

20, inner-lateral view of *Pa* element; MGUH 17.820.

21, inner-lateral view of *Pb* element; MGUH 17.821.

22, posterior view of *Sa* element; MGUH 17.822.

23, inner-lateral view of *Pa* element; MGUH 17.823.



midlength of the process. The basal cavity does not extend beneath the anterior process.

Sa element. Alate with a tall, laterally compressed cusp. The lateral edges of the cusp are costate, its anterior face broadly convex, its posterior face shallowly expanded. The lateral processes form an angle of approximately 160° between their lower edges; the processes are equal in length bearing four to five compressed denticles which are basally fused, tall and separated by broad 'v-shaped' spaces; the most proximal on each process is smaller than the others. In large specimens the faces of the processes may be slightly thickened. The basal cavity extends posteriorly beneath the cusp, it is deeply excavated and narrows laterally terminating beneath the first proximal denticle on each process.

Sb element. Modified tertiopede element lacking a well developed posterior process. The cusp is broad and erect, its posterior face expanded only slightly. The lateral processes develop an angle of approximately 120° between their lower edges; the inner is shorter and extends almost horizontally, it is posteriorly bowed and bears four closely packed, basally fused, compressed denticles. The outer process bears four large denticles, of which the central two are slightly larger than the others. The basal cavity, commonly filled with sediment, is extended posteriorly beneath the cusp where it is deeply excavated. Laterally the cavity tapers rapidly, to a narrow groove which extends to beneath the first proximal denticle on each lateral process.

Sc element. Bipennate with strongly inwardly curved anterior process. The cusp is tall, posteriorly inclined and oval in cross section; the anterior edge is weakly costate, the posterior more rounded. The anterior process forms an angle of 160° between its lower edge and that of the posterior process; it bears four compressed denticles which increase in size distally, the most proximal denticle is partially fused to the cusp. The posterior process is broken in all specimens, extends horizontally from the cusp and bears compressed denticles similar to those on the anterior process. The basal cavity is expanded almost symmetrically beneath the cusp, tapering rapidly to a narrow groove which extends for only a short distance beneath the processes. Anteriorly the basal groove terminates beneath the first or second proximal denticle.

Remarks. The elements are typically large, with similar denticulation and basal cavity expansion. The Pa element differs from that of *O. hadra* in having three large, anterior, distal denticles and a prominent apical denticle. Klapper & Murphy (1975, p. 37) illustrated similar specimens such as *O. confluens* delta morphotype, but these differ in having a nearly symmetrical, narrower,

more posteriorly situated basal cavity. The Pa element of *O. gulletensis* Aldridge (1972) has a similar basal cavity, but lacks the high anterior distal denticles and arched lower edge. The Sa and Sb elements of its apparatus appear to lack the posterior extension of the cusp. (Jeppsson, 1979b, pl. 72, figs 14–22).

The Greenland specimens of *O. cf. O. hadra* are thermally mature, and it is difficult to see white matter. The high anterior denticles on the Pa element and morphology of the M and S elements suggest a close morphological affinity with *O. confluens*.

Occurrence. Found in the *Pterospathodus celloni* Biozone of Peary Land and Washington Land. GGU 82687 contains the most abundant specimens.

Ozarkodina hassi (Pollock, Rexroad & Nicoll, 1970)

Plate 13, figs 10–16

- v1967 *Spathognathodus* cf. *S. oldhamensis* Rexroad, p. 49, pl. 3, fig. 3.
- v1967 *Ozarkodina edithae*; Rexroad, p. 40, pl. 2, fig. 6.
- v1967 *Synprioniodina* cf. *Prioniodus bicurvatus*; Rexroad, p. 50, pl. 3, figs 9, 10.
- v*1970 *Spathognathodus hassi*; p. 760, pl. 111, figs 8–12.
- 1970 *Ozarkodina* cf. *O. edithae*; Pollock, Rexroad & Nicoll, p. 756, pl. 111, figs 3, 4.
- 1970 *Synprioniodina bicurvata*; Pollock, Rexroad & Nicoll, p. 762, pl. 114, figs 16, 17.
- 1970 *Trichonodella* n. sp. Pollock, Rexroad & Nicoll, p. 763, pl. 113, fig. 21.
- p1970 *Plectospathodus flexuosus*; Pollock, Rexroad & Nicoll, p. 758, pl. 113, fig. 20; non fig. 19.
- 1970 *Ligonodina? variabilis*; Pollock, Rexroad & Nicoll, p. 755, pl. 114, figs 11, 12.
- v1972 *Spathognathodus hassi*; Aldridge, p. 213, pl. 4, figs 2, 3.
- v1972 *Ozarkodina* cf. *O. edithae*; Aldridge, p. 199, pl. 4, fig. 17.
- v1972 *Synprioniodina bicurvata*; Aldridge, p. 216, pl. 5, fig. 28.
- v1972 *Plectospathodus flexuosus*; Aldridge, p. 208, pl. 7, fig. 24.
- v1972 *Ligonodina? variabilis*; Aldridge, p. 189, pl. 8, fig. 14.
- v1975 *Ozarkodina hassi*; Aldridge, pl. 2, fig. 22.
- 1975 *Ozarkodina hassi*; Cooper, p. 1005, pl. 3, figs 1–12.
- 1977 *Spathognathodus hassi*; Liebe & Rexroad, pl. 1, figs 20, 21.
- 1977 *Ozarkodina* aff. *O. edithae*; Liebe & Rexroad, pl. 1, fig. 22.
- 1977 *Synprioniodina bicurvata*; Liebe & Rexroad, pl. 1, fig. 6.
- ?1977 *Plectospathodus flexuosus*; Liebe & Rexroad, pl. 2, fig. 34.
- 1977 *Ligonodina variabilis*; Liebe & Rexroad, pl. 1, fig. 14.
- 1981 *Ozarkodina hassi*; McCracken & Barnes, p. 83, pl. 7, figs 1, 2, 4, 6–13.
- 1981 *Ozarkodina hassi*; Nowlan, pl. 5, figs 1, 2, 5, 6.
- 1981 *Ozarkodina hassi*; Fähræus & Barnes, pl. 1, fig. 8.

- 1982 *Ozarkodina hassi*; Aldridge & Mohamed, pl. 1, fig. 21.
 v1985 *Ozarkodina hassi*; Aldridge, p. 78, pl. 3-1, fig. 4.
 1987 *Ozarkodina hassi*; Over & Chatterton, pl. 1, figs 1-2.

Holotype. *Spathognathodus hassi* Pollock, Rexroad & Nicoll, 1970, p. 760, pl. 111, fig. 9. Sample 7-2, p. 747, from the lower Llandoverly of Manitoulin Island, Ontario.

Emended diagnosis. Elements Pa, Pb, M, Sa, Sb, Sc all with shallow, laterally expanded basal cavities. The carminisclerite (Pa) element is characterised by a prominent apical denticle and denticles of unequal height along the anterior process, almost completely fused. Denticles along the posterior process are shorter than those on the anterior in both the Pa and angulate Pb elements.

Description. *Pa element.* Refer to that of *Spathognathodus hassi* Pollock, *et al.* (1970, p. 760). This element shows ontogenetic variation in the Greenland specimens, larger forms having a more broadly flared basal cavity than smaller specimens. The youngest representatives of this species, from Bessels Fjord (plate 13, fig. 11) are more robust with a larger apical denticle and anterior process denticles. The processes of these specimens are thickened slightly beneath the denticle row.

Pb element. Refer to the description of *Ozarkodina cf. O. edithae* Walliser by Pollock *et al.* (1970, p. 756).

M element. Compressed, dolabrate element comprising an erect cusp and arched, downwardly directed posterior process, bearing five compressed, fused denticles. The antero-basal corner of the cusp is slightly extended. The inner margin of the basal cavity is upturned and slightly expanded beneath the posterior edge of the cusp, extending as a slit-like groove to the tip of the posterior process.

Sa element. Alate element, the cusp is compressed and broad, slightly posteriorly inflated at its base. The lateral processes form an angle of approximately 100° between their lower edges. Each process bears three or four compressed, partially fused denticles; these are tall and free from approximately midlength. The posterior edge of the basal cavity is upturned and slightly posteriorly flared beneath the cusp, extending as a tapering, shallow groove almost to the tips of the lateral processes.

Sb element. Refer to that of *Plectospathodus flexuosus* Branson & Mehl by Aldridge (1972, p. 208).

Sc element. Bipennate compressed element; the cusp is lenticular in cross section. The anterior process is

downturned and only slightly inwardly bowed, its upper edge forming an angle of 160°-170° with the anterior edge of the cusp, and bears up to four compressed, partially fused denticles. The posterior process is straight and horizontally directed from the base of the cusp, this process is broken in all specimens but bears compressed, posteriorly inclined, partially fused denticles. The basal cavity is excavated beneath the cusp, but only slightly laterally expanded, extending as a shallow groove almost to the tips of the processes.

Remarks. The apparatus of *O. hassi* present in the Greenland collection differs from that proposed by Cooper (1975) in the morphology of the M element. The Greenland specimens have a much reduced anterior process and a shallowly arched posterior process; they compare more closely with the M element proposed by McCracken & Barnes (1981, p. 83) and confirmed by the topotype collections stored at the University of Nottingham. The M element designated by Cooper (1975, pl. 3, fig. 11) has a long inner-lateral process bearing four compressed denticles and a deep outer process with tall denticles. On the basis of process orientation it is suspected that this represents an Sb element of a different *Ozarkodina* species.

Previous synonymies of *O. hassi* have included *Trichonodella* sp. B Rexroad (1967, p. 53, pl. 3, fig. 17). Study of the figured specimen shows it to be incomplete; it is absent from the topotype sample and the Greenland collection and is not included in synonymy. *Plectospathodus flexuosus* Branson & Mehl *sensu* Liebe & Rexroad (1977) is tentatively included; it occurs in association with the Pa element, but the illustration is of insufficient quality to allow a firm decision.

O. hassi is distinct from *O. oldhamensis* Rexroad which has a Pa element with a much broader basal cavity, lacks a prominent apical denticle and has anterior denticles that are equal in height forming an almost straight upper edge to the anterior process.

Study of the holotypes of *O. hassi*, *O. comptus* (Pollock, Rexroad & Nicoll) and *O. oldhamensis* (all Pa elements) shows them to have similar white matter distribution. Thus, diffuse as opposed to dense opaque white matter completely fills the denticles and has a sharply defined base which follows the outline of the lower edge of the element at approximately the mid-height of the carina. These three species appear to be closely related.

Occurrence. Found in samples from central and eastern Peary Land, Kronprins Christian Land, J. P. Koch Fjord, Wulff Land and Bessels Fjord.

On Anticosti Island the first occurrence of *O. hassi*

and/or *O. oldhamensis* is thought by McCracken & Barnes (1981, p. 72) to be indicative of the Ordovician–Silurian boundary. *O. hassi* has been documented from Aeronian and lower Telychian strata of the Welsh Borderland (Aldridge, 1972, 1975).

Ozarkodina aff. *O. hassi* (Pollock, Rexroad & Nicoll, 1970)

Plate 13, figs 17–19

Description. *Pa element.* A single, complete, carminate, inwardly bowed element with a more or less straight lower edge. The anterior process is longer and deeper than the posterior, both decrease in height distally. A tall, compressed apical denticle is situated posterior of midlength; it is lenticular in cross section and slightly posteriorly inclined. The anterior process bears eight compressed, irregularly spaced, basally fused denticles, of variable height; all are erect except the two most proximal. The posterior process bears four posteriorly inclined denticles which are fused to midheight and decrease in height distally. The basal cavity is symmetrically expanded beneath the apical denticle; in lower view it is lenticular in outline, broadest beneath the anterior edge of the apical denticle. The cavity terminates anteriorly and posteriorly beneath the third denticle on each process; posteriorly the cavity tapers gradually.

?Pb element. Two extremely poorly preserved fragments occur with the *Pa* element and may represent the *Pb* element of this apparatus. The most complete is figured; this is angulate and comprises a broad based cusp remnant and an anterior process that is inclined downwards. This process bears the fused remnants of eight compressed denticles. The basal cavity is broadly expanded beneath the cusp; its inner flare is situated slightly posterior of the outer; deeply excavated beneath the anterior edge of the cusp, the cavity tapers rapidly both anteriorly and posteriorly, terminating beneath the third denticle on the anterior process.

?M element. A poorly preserved fragment of a dolabrate element occurs with the elements above and may represent the *M* element of this apparatus. The cusp is erect and has costate anterior and posterior edges; medially on the inner side the cusp is strongly inflated. A deep, steeply inclined, posterior process remnant extends from the base of the cusp bearing two tall, partially fused, pointed denticles. The antero-basal corner of the cusp is compressed and extended slightly downwards and anteriorly. The anteriorly rounded basal cavity is expanded inwards beneath the cusp, ex-

tending only a short distance beneath the posterior process.

Remarks. A single sample, GGU 274747, from the middle of the Turesø Formation of Kronsprins Christian Land contains these poorly preserved and thermally altered elements. The *Pa* element differs from that of *O. excavata*, which is broadly arched and has a basal cavity which extends to the tips of the processes. The irregularity of the denticles on the anterior process, prominent apical denticle and a restricted basal cavity suggest a closer affinity to *Ozarkodina hassi* which occurs in samples above and below.

Ozarkodina pirata Uyeno & Barnes, 1983

Plate 13, figs 20–23; plate 14, figs 1–8

- v1979 *Ozarkodina* aff. *O. polinclinata* (Nicoll & Rexroad); Aldridge, p. 17, pl. 2, figs 1–5.
 1981 *Ozarkodina* n. sp. Uyeno & Barnes, pl. 1, fig. 2.
 p1983 *Ozarkodina pirata* Uyeno & Barnes, p. 21, figs 16, 21–25 pl. 2, figs 12, 13, 19–28, non pl. 1, fig. 17, ?pl. 2, fig. 19.

Holotype. Specimen number GSC 64831 a *Pa* element from GSC locality C-92669: figured in Uyeno & Barnes (1983, pl. 2, fig. 12). From member I, Jupiter Formation, Anticosti Island.

Emended diagnosis. Elements with shallow restricted basal cavities. The *Pa* element is characterised by tall, fused denticles posterior of midlength; denticles decrease in height anteriorly and posteriorly; the basal cavity is narrow and groove-like. In lateral view closely packed but separate rectangular blocks of white matter fill the denticles of each element, their lower edges forming a sharply defined, downwardly convex trace.

Description. Refer to the description of the *Pa*, *Pb*, *M*, *Sa* and *Sb* elements of *O.* aff. *O. polinclinata* Nicoll & Rexroad; Aldridge (1979, pp. 17–18). *Sc element.* Bipennate compressed element; the narrow cusp is lenticular in cross section. The anterior process projects vertically downwards from the antero-basal corner of the cusp; its upper edge is twisted slightly towards the posterior; is long and bears four or five inwardly inclined, compressed denticles. The posterior process is broken in all specimens but bears compressed, partially fused denticles.

Remarks. The basal cavity is a narrow groove extending the length of the element. The high central denticles and lack of two or three tall denticles at the tip of the anterior process remain constant features throughout

the range of this species (mid to late Llandovery in Greenland). Stratigraphically older forms (plate 13, figs 20–23) have a straight lower edge and slight lateral inflation occurs beneath the denticle row. Specimens from the *P. celloni* Biozone of Greenland most closely resemble those from Anticosti Island (Uyeno & Barnes, 1983).

The Pb element of *O. pirata* from Greenland is more strongly arched and has a deeper anterior process than that of *O. pirata* by Uyeno & Barnes (1983, pl. 1, fig. 17; pl. 2, fig. 19); the latter approach that of Uyeno & Barnes (1983, pl. 1, fig. 17; pl. 2, fig. 19).

The M element of *O. pirata* and *Aspelundia fluegeli* are indistinguishable; that of *O. polinclinata* differs in having a much wider separation of the cusp from the denticles and a more broadly arched inner edge to the basal cavity. Rexroad & Nicoll (1972, pl. 1, figs 35–38) illustrated specimens which appear to be morphologically intermediate between *O. pirata* and *O. polinclinata*.

Occurrence. Found in middle to upper Llandovery strata in Peary Land, Kronprins Christian Land, Wulff Land and Washington Land.

Ozarkodina n. sp. A

Plate 14, fig. 13

Description. *Pa element.* Carminate element with a straight lower edge and arched upper edge. The anterior process is incomplete in all specimens, deeper than the posterior process and bearing compressed, slender, needle-like, almost completely fused denticles. The apical denticle is inconspicuous, situated above the basal cavity tip. The posterior process bears sixteen to twenty needle-like, posteriorly inclined denticles which are more or less subequal in height; the process decreases in height posteriorly. The basal cavity is long and groove-like; its inner edge is slightly flared and in lower view the cavity is lenticular in outline. The basal cavity terminates just before the tip of the posterior process.

Remarks. The Pa element displays a marked difference in denticulation from other species of *Ozarkodina*.

Occurrence. Found only in the Odins Fjord Formation at Odin Fjord, Peary Land.

Ozarkodina n. sp. B

Plate 14, figs 14–16

Description. *Pa element.* Large, slightly arched, carminate element with a prominent apical denticle, situated just to the posterior of the midpoint. The anterior processes are long and inclined slightly downwards, bearing ten to twelve completely fused, compressed denticles, which are lenticular in cross section and gradually decrease in height distally. The most proximal denticle is almost as tall as the cusp, but not as tall as its counterpart on the posterior process. The upper edge of the anterior process is straight and more steeply inclined downwards than that of the posterior process. The posterior process is shorter, though of similar form to the anterior process, bearing six to eight tall, fused denticles which decrease in height distally. Beneath the denticle row the blade is occasionally slightly inflated laterally. The cavity is only slightly expanded on the inner side and forms a narrow groove beneath the processes. The basal cavity is commonly infilled with basal material.

M element. Dolabrate with a short, denticulate anticusp and longer posterior process. The cusp is broad based and lenticular in midheight cross section. The anticusp bears two to four compressed, fused denticles. The posterior process is broken in all specimens, is directed downwards and forms an angle of approximately 100° with the posterior edge of the cusp. It bears compressed, partially fused denticles. The lower edge of the element is inwardly expanded beneath the cusp and posterior process. The basal cavity is shallow and narrows to a groove beneath the anticusp, terminating just before the tip.

Sa element. Alate; the cusp is broad, erect and compressed. The lateral processes form an angle of approximately 160° between their lower edges. The processes are of equal length and bear five small, outwardly inclined, compressed denticles, which are fused almost to their tips. The basal cavity is slightly expanded beneath the cusp; rounded lenticular in lower view, it tapers rapidly forming an extremely narrow groove beneath the lateral processes. This cavity is shallower beneath the processes and terminates almost at their tips.

Remarks. All the elements have compressed, almost completely fused denticles and a small groove-like basal cavity. The Pa element closely resembles *Ozarkodina* aff. *O. media* Pollock, Rexroad & Nicoll (1970, p. 756, pl. 113, figs 13, 14), but differs in having a more pronounced differentiation of the anterior and posterior processes and a more prominent apical denticle.

Similarities between the Pa elements of *Ozarkodina* n. sp. A, *Ozarkodina* n. sp. B and *O. pirata* suggest

close morphological affinity; the M element of *Ozarkodina* n. sp. B is similar to that of *O. excavata*.

Occurrence. Found only in GGU 228901 from the Odins Fjord Formation in central Peary Land.

Ozarkodina n. sp. C

Plate 14, figs 17–20

Description. *Pa element.* Arched carminate element; the upper edge bears compressed, posteriorly inclined, partially fused denticles, with triangular free apices. The apical denticle is inconspicuous, situated above the basal cavity, slightly anterior of the midlength of the element. The anterior process is more or less horizontal bearing five to eight denticles. The posterior process is slightly downturned bearing six to seven denticles, which are slightly larger than those of the anterior process; the lateral faces of the element are inflated beneath the denticle row. The basal cavity is inwardly expanded, the inner edge of the basal cavity is upturned beneath the apical denticle, the outer edge of the basal cavity projects downwards and slightly outwards below the inner edge. The cavity extends as a shallow groove to the midlength of the anterior process, the posterior process lacks a basal groove.

Pb element. Angulate, compressed element with a straight lower edge and prominent, posteriorly inclined

cusps. The anterior process is approximately twice as deep as the posterior process, bearing five compressed denticles which are fused to midheight; the fourth distal denticle is twice the size of the other denticles. The posterior process bears four much smaller, compressed, peg-like denticles which are discrete, except for the most proximal which is fused to the edge of the cusp; the denticles are separated by narrow, 'u-shaped' spaces. The basal cavity is narrow and groove-like.

Sa element. Alate, compressed element; the cusp is broad and erect, its lateral edges are costate. The lateral processes are inclined slightly downwards, bear short, compressed, almost completely fused denticles. The most proximal denticles are fused to the base of the cusp. The basal cavity is extremely small; its posterior margin is upturned slightly beneath the cusp. The lower edge of the processes is poorly preserved, and it is not possible to see if a basal groove was developed.

?Sb element. A single fragment occurs with four Pa elements in GGU 254879 and may represent the Sb element of this apparatus. It is a compressed, modified teriopede element lacking a well developed posterior process. In posterior view the lower edge of this specimen is almost straight. The inwardly inclined cusp is compressed and is oval in cross section. The inner-lateral process bears three compressed, tall denticles, which are outwardly inclined and fused almost to their tips. The most proximal of these denticles is much smaller than the others. The outer-lateral process is

Plate 14

Figs 1–8. *Ozarkodina pirata* Uyeno & Barnes.
All specimens $\times 60$.

- 1, inner-lateral view of Pa element; MGUH 17.824 from GGU 228970.
- 2, inner-lateral view of Pa element; MGUH 17.825 from GGU 216853.
- 3, inner-lateral view of Pa element (holotype); MGUH 14.056 from GGU 184125.
- 4, inner-lateral view of Pb element; MGUH 14.057 from GGU 184125 (Aldridge, 1979, pl. 2, fig. 2).
- 5, inner-lateral view of M element; MGUH 14.058 from GGU 184125 (Aldridge, 1979, pl. 2, fig. 5).
- 6, inner-lateral view of Sc element; MGUH 17.826 from GGU 228970.
- 7, posterior view of Sa element; MGUH 17.827 from GGU 228970.
- 8, posterior view of Sb element; MGUH 17.828 from GGU 228970.

Figs 9–12. *Ozarkodina* n. sp. E.
All specimens from GGU 256308, $\times 60$.

- 9, inner-lateral view of Pa element; MGUH 17.829.
- 10, inner-lateral view of ?M element; MGUH 17.830.
- 11, posterior view of ?Sb element. MGUH 17.831.
- 12, inner-lateral view of ?Sc element; MGUH 17.832.

Fig. 13. *Ozarkodina* n. sp. A.

13, inner-lateral view of Pa element, $\times 80$; MGUH 17.833 from GGU 254711.

Figs 14–16. *Ozarkodina* n. sp. B.
All specimens from GGU 228901, $\times 40$.

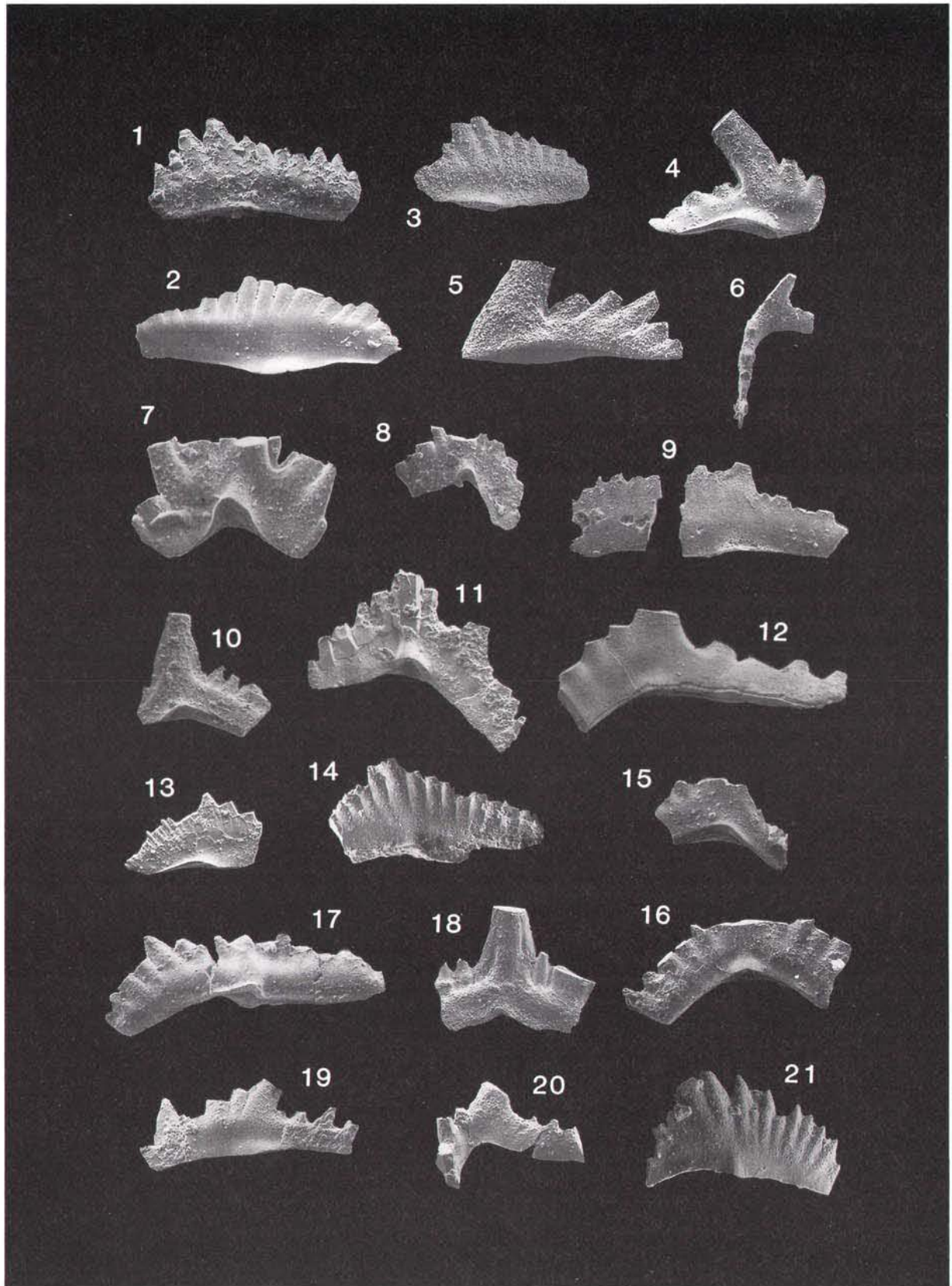
- 14, inner-lateral view of Pa element; MGUH 17.834.
- 15, inner-lateral view of M element; MGUH 17.835.
- 16, posterior view of Sa element; MGUH 17.836.

Figs 17–20. *Ozarkodina* n. sp. C.
All specimens from GGU 254879, $\times 60$.

- 17, inner-lateral view of Pa element; MGUH 17.837.
- 18, posterior view of Sa element; MGUH 17.838.
- 19, inner-lateral view of Pb element; MGUH 17.839.
- 20, inner-lateral view of ?Sc element; MGUH 17.840.

Fig. 21. *Ozarkodina* n. sp. D.

21, inner-lateral view of Pa element, $\times 60$; MGUH 17.841 from GGU 274766.



broken and bears only the fused remnants of two denticles. The posterior lower edge of the basal cavity is upturned beneath the cusp and asymmetrically inclined towards the inner-lateral process. The cavity is shallowly excavated, extending laterally as a tapering groove which terminates just before the tip of the inner process.

Sc element. Bipennate with a strongly, inwardly curved and downwardly directed anterior process. The cusp is lenticular in midheight cross section. The horizontal posterior process bears almost identical denticles to those on the posterior process of the Pb element. The anterior process bears up to four discrete denticles, which are circular in cross section. The basal cavity is only slightly expanded beneath the cusp, extending as a narrow groove to the tips of the processes.

Remarks. Basal cavity shape and posterior process morphology distinguish *Ozarkodina* n. sp. C from *O. excavata*. The apparatus of these species are closely similar in many respects and *Ozarkodina* n. sp. C may be a stratigraphical or geographical variant of *O. excavata*.

Ozarkodina n. sp. D

Plate 14, fig. 21

Description. Pa element. Carminate, slightly inwardly bowed element with an arched, denticulate upper edge. The inconspicuous, apical denticle is situated above the basal cavity, just posterior of midlength. The anterior process bears nine tall, compressed denticles, fused to above midheight and of variable height; the most proximal denticle is larger than the rest which tend to decrease in height distally. The denticles posterior of midlength are posteriorly inclined, those to the anterior are anteriorly inclined. The posterior process bears four denticles; the most proximal is the largest, the remaining denticles are shorter than those of the anterior process and decrease in height posteriorly. The upper edge of the posterior process is steeply inclined downwards, the lower edge less so. The symmetrical basal cavity is slightly expanded, extending to the tips of the processes as a shallowly excavated tapering groove. Inwardly the edge of the cavity beneath the apical denticle is broadly concave upwards, outwardly it is broadly concave downwards. White matter is present in all denticles, not completely filling them, but in blocks that are larger in the larger denticles and are separated by narrow gaps. The base of the white matter defines a sharp linear trace which is broadly upwardly concave at approximately the mid-depth of the blade. The highest point of this trace occurs beneath the apical denticle.

Remarks. Five Pa elements of this species are known from GGU 274766, from the upper Odins Fjord Formation in Kronprins Christian Land. The high central denticles and groove-like basal cavity suggest an affinity with *O. pirata*.

Ozarkodina n. sp. E

Plate 14, figs 9-12

Description. Pa element. Carminate, straight blade with a high anterior process and much lower posterior process. A prominent, though short, erect apical denticle is situated to the posterior of midlength; it has a broad base. The anterior process is approximately twice as high and longer than the posterior, bearing eight tall, erect denticles which are fused almost to their tips. The posterior process bears only four to five much shorter denticles. The basal cavity takes the form of a narrow groove extending the entire length of the element. The inner lower edge of the cavity is flared slightly beneath the cusp; the entire lower surface is shallowly excavated. No white matter is visible due to the thermal alteration of the specimens.

?M element. Dolabrate, with a broad, compressed cusp. The anterior basal corner of the cusp is extended slightly and bears a single denticle. The posterior process is broken in all specimens, but bears triangular, discrete, compressed denticles. The inner, lower edge is upturned beneath the posterior process; it becomes strongly upwardly arched and outwardly flared beneath the posterior edge of the cusp and narrows beneath the anterior basal corner of the cusp. The cavity is deeply excavated where it is posteriorly flared, shallowing beneath the anterior basal corner of the cusp. The basal cavity extends the entire length of the element.

?Sb element. Modified teriopede element lacking a well developed posterior process. The tall cusp is compressed and has sharp lateral edges. The inner-lateral process is the shorter of the two and diverges less steeply than the outer process, an angle of 130° being developed between their lower edges. The inner process bears five compressed, partially fused denticles, of which the most proximal is almost completely fused to the cusp; the denticles decrease in size distally; the outer process bears the remnants of six denticles. The posterior edge of the basal cavity is upturned into a narrow arch beneath the cusp and is also slightly expanded posteriorly, the cavity extends to the tips of the processes as a tapering groove.

?Sc element. Bipennate; anterior process is sharply downturned and inwardly bowed, its upper edge forming an angle of approximately 110° with the edge of the

cusps; this process bears four partially fused denticles. The posterior process diverges horizontally, its upper edge is twisted slightly outwards and bears six posteriorly inclined denticles which are fused only at their base. The basal cavity is slightly expanded beneath the cusp, extending to the tips of the processes as a narrow, shallowly excavated groove.

Remarks. These specimens form part of an *Ozarkodina* apparatus present in GGU 256308 although it is not

certain the ramiform elements are from the same apparatus as the Pa element. The proposed M element, in particular, bears close resemblance to that for early representatives of *O. excavata*. The Pa element has a similar deep anterior process to its counterpart in the apparatus of *O. oldhamensis* Rexroad (1967, p. 49; pl. 3, figs 1, 2).

Occurrence. Found only in the Melville Land Member of eastern Peary Land.

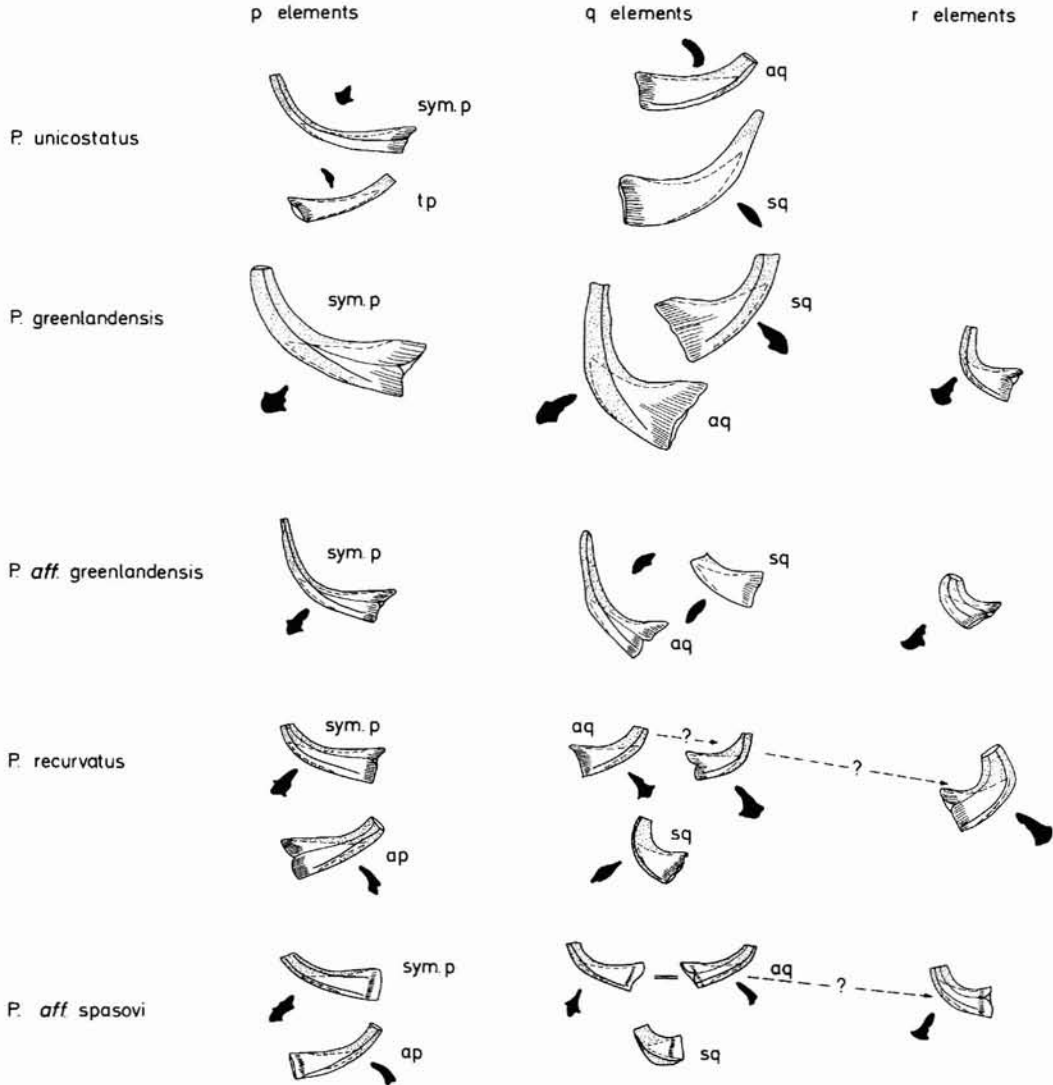


Fig. 32. Species of *Panderodus* illustrating distribution of white matter (stippled), outline of basal cavity and cross-section at midheight. Arrows indicate morphological transition. Camera lucida drawings $\times 25$. *P. unicostatus*, MGUH 14.074 (sym. p), MGUH 19.312 (tp), MGUH 19.313 (aq), MGUH 14.072 (sq). *P. greenlandensis*, MGUH 19.314 (sym. p), MGUH 19.315 (aq), MGUH 19.316 (sq), MGUH 19.317 (r). *P. aff. P. greenlandensis*, MGUH 19.318 (sym. p), MGUH 19.319 (aq), MGUH 19.320 (sq), MGUH 19.32 (r). *P. recurvatus*, MGUH 17.922 (sym. p), MGUH 17.923 (ap), MGUH 19.322 (aq), MGUH 19.323 (sq), MGUH 17.928 (aq), MGUH 17.931 (r). *P. aff. P. spasovi*, MGUH 19.324 (sym. p), MGUH 19.325 (ap), MGUH 17.913 (?tp), MGUH 17.920 (sq), MGUH 17.916 (r), MGUH 17.918 (aq).

Genus *Panderodus* Ethington, 1959

Type species. Paltodus unicostatus Branson & Mehl, 1933a, p. 42.

Diagnosis. Refer to the diagnosis in Sweet (1979, p. 62).

Remarks. Sweet (1979) and Barnes *et al.* (1979) working with Ordovician material have both proposed nomenclatural schemes for the constituent elements of *Panderodus*, and these are summarised in fig. 28. Herein it is recognised to contain a slender sym. p, an aq and a broad, laterally compressed sq element; no r element has been recognised for *P. unicostatus* though one is known in other species. Additional rare elements also occur, such as tp (equivalent to the tortiform element of Sweet, 1979) and a serrate aq element (previously described as *P. unicostatus serratus* of Rexroad, 1967). The latter has recently been considered a minor reiterative variant (Rexroad *et al.*, 1978, p. 11).

L. Jeppsson (Lund, personal communication) is currently reviewing *Panderodus* and consequently this genus is dealt with only briefly herein. Element homologies are summarised in fig. 32.

Panderodus cf. *P. feulneri* (Glenister, 1957)

Plate 15, figs 9–14

- cf. v 1957 *Paltodus feulneri* Glenister, p. 728, pl. 85, fig. 11.
cf. 1979 *Panderodus feulneri* (Glenister); Sweet, p. 64, pl. 7, figs 1, 8, 11–14, 17, 18, 22.

Description. sym. p element. Squat, broad-based cone with a short base and long, erect cusp. The basal margin is straight, and centrally notched on both sides. Both lateral faces are inflated below the furrow, which ex-

tends to the apex of the cusp; the inner furrow bears a narrow groove centrally. The lower edge of both furrows is costate, the costae extending from the basal margin to the apex. A zone of faint basal wrinkles passes around the base of the cone, and the entire basal surface is excavated; the basal cavity terminates at the base of the cusp, close to the lower margin. White matter is concentrated into the tip of the cusp, diffuse white matter may, in larger specimens, extend a short distance along the upper and lower margins of the base.

ap element. Differs from the sym. p element only in the asymmetrical disposition of the inner lower-lateral costa.

sq element. Laterally compressed, the base is long and broad, the keeled upper and narrower lower margins are evenly recurved; the basal margin is straight and more or less flat, with a centrally situated, prominent, basal notch on either side. The inner furrow bears a deep, narrow groove just above the midline of the furrow; this is absent in the outer furrow. A prominent costa originates just apical of the basal wrinkles, at the midpoint of the lower face; apically it migrates upwards, forming the lower edge of the furrow, from base mid-height. A zone of coarse, basal wrinkles passes around the base; the entire basal surface is excavated, and basal cavity outline and white matter distribution are similar to those of the sym. p element.

r element. Squat, strongly recurved cone, with a broad base and a narrow, short cusp. This element is bilaterally symmetrical in all features except the development of the furrow. The narrow upper and broadly rounded, lower margins are strongly curved apically, the upper extending basally as a short heel. Both lateral faces bear a prominent costa close to, and parallel with, the lower margin; these originate at the apical edge of the basal wrinkles and extend to the apex. A narrow furrow extends to the apex on the inner face. The basal

Plate 15

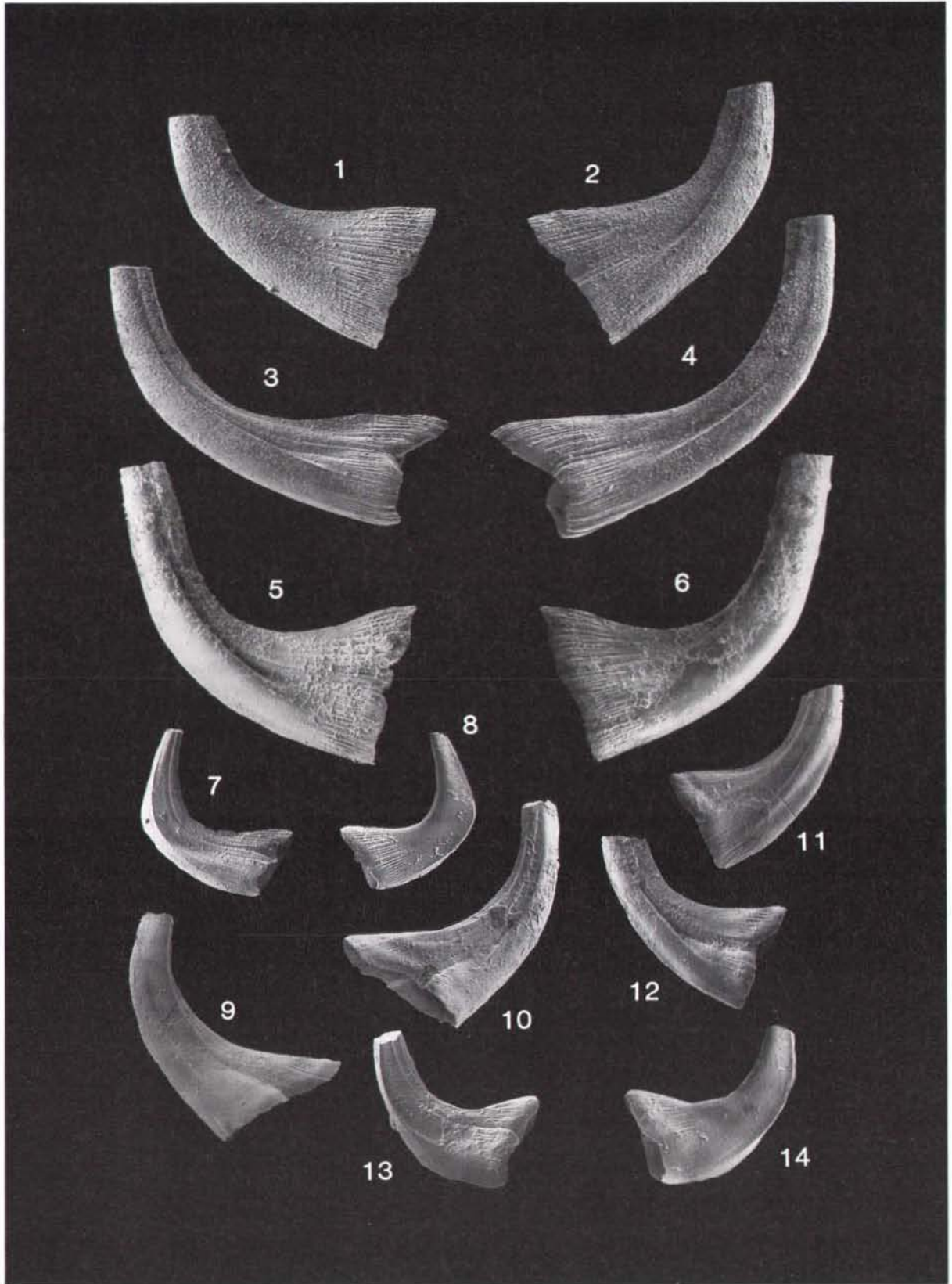
Figs 1–8. *Panderodus greenlandensis* n. sp.
All specimens from GGU 184125, $\times 60$.

- 1, outer-lateral view of ?sq element; MGUH 14.077 (Aldridge, 1979, pl. 2, fig. 21).
- 2, inner-lateral view of ?sq element; MGUH 14.077 (Aldridge, 1979, pl. 2, fig. 26).
- 3, inner-lateral view of sym. p element; MGUH 14.075 (Aldridge, 1979, pl. 2, fig. 23).
- 4, outer-lateral view of sym. p element; MGUH 14.075 (Aldridge, 1979, pl. 2, fig. 28).
- 5, inner-lateral view of aq element; MGUH 14.076 (Aldridge, 1979, pl. 2, fig. 24).
- 6, outer-lateral view of aq element; MGUH 14.076 (Aldridge, 1979, pl. 2, fig. 27).

- 7, inner-lateral view of r element; MGUH 14.078 (Aldridge, 1979, pl. 2, fig. 29).
- 8, outer-lateral view of r element; MGUH 14.078 (Aldridge, 1979, pl. 2, fig. 30).

Figs 9–14. *Panderodus* cf. *P. feulneri* (Glenister).
All specimens from GGU 216835; $\times 40$.

- 9, 10, outer and inner-lateral view of sym. p element; MGUH 17.901.
- 11, 12, outer and inner-lateral view of sq element; MGUH 17.902.
- 13, 14, inner and outer-lateral view of r element; MGUH 17.903.



margin is straight bearing a prominent central basal notch on the inner face. A zone of basal wrinkles passes around the base; the entire basal surface is deeply excavated. The basal cavity and white matter distribution are as described for the other elements.

Remarks. This apparatus contains stout, broad based cones with prominent lateral costae. The sym. p and r elements compare closely with the costate falciform and the arcuatiform elements of *P. feulneri sensu* Sweet (1979). The latter differ in being taller and more slender. The *P. feulneri* apparatus contains no apparent sq element.

Occurrence. Found rarely in lower-middle Llandovery strata in Peary Land, Washington Land, Wulff Land and J. P. Koch Fjord.

Panderodus greenlandensis n. sp.

Fig. 33; plate 15, figs 1-8

- vp1972 *Panderodus* cf. *p. gracilis* (Branson & Mehl);
Aldridge, p. 203, pl. 9, fig. 13; non fig. 12.
1977 *Panderodus recurvatus*; Liebe & Rexroad, pl. 2,
fig. 22.
p1978 *Panderodus serratus*; Miller, pl. 1, figs 5, 8 only.
1979 *Panderodus* spp. Aldridge, pl. 2, figs 23-30.

Name derivation. After Greenland.

Type material. Specimens from the Lower Visby Beds, Gotland. Locality Nyhamn 1 (CK 4639 0582, in Laufeld, 1974), sample G79-217b LJ from approximately 2.5 m above sea level and 4 m from the shore line (fig. 33).

Diagnosis. Elements sym. p, aq, sq and r are all typically robust, broad and have well developed, broadly rounded lateral costae and a deep prominent furrow, white matter is restricted to the base of the cusp and does not extend to the apex.

Description. sym. p element. Robust, bilaterally symmetrical cone with a broad base and cusp, approximately equal in length. The cusp is steeply proclined to erect and curved from its base. The keeled upper margin extends basally forming a flattened heel. The basal margin is straight beneath the lower-lateral faces and inclined beneath the heel. A prominent basal notch is situated centrally on the inner margin of the base. Both lateral faces are inflated and each bears a single costa, which originates at a central point close to the apical edge of the basal wrinkles, both extend to the apex though migrate slightly towards the upper margin. The inner costa forms the steep lower face of the furrow between midheight of the base and the point of maximum curvature of the upper margin. The furrow tapers apically, terminating at the base of the cusp. Within the furrow is a deep narrow groove with slightly raised edges, this extends from the basal notch to the apex. Above the furrow the inner face of the keel may bear fine, longitudinal microstriations. The outer face of the element bears a shallow furrow, this lacks the central groove; basally the outer furrow is deeper and narrower than the inner; it terminates in the lower third of the cusp. A zone of basal wrinkles, approximately one-eighth of the height of the element, passes around the base of all elements in this apparatus. This zone may extend apically in the vicinity of the lateral furrows,

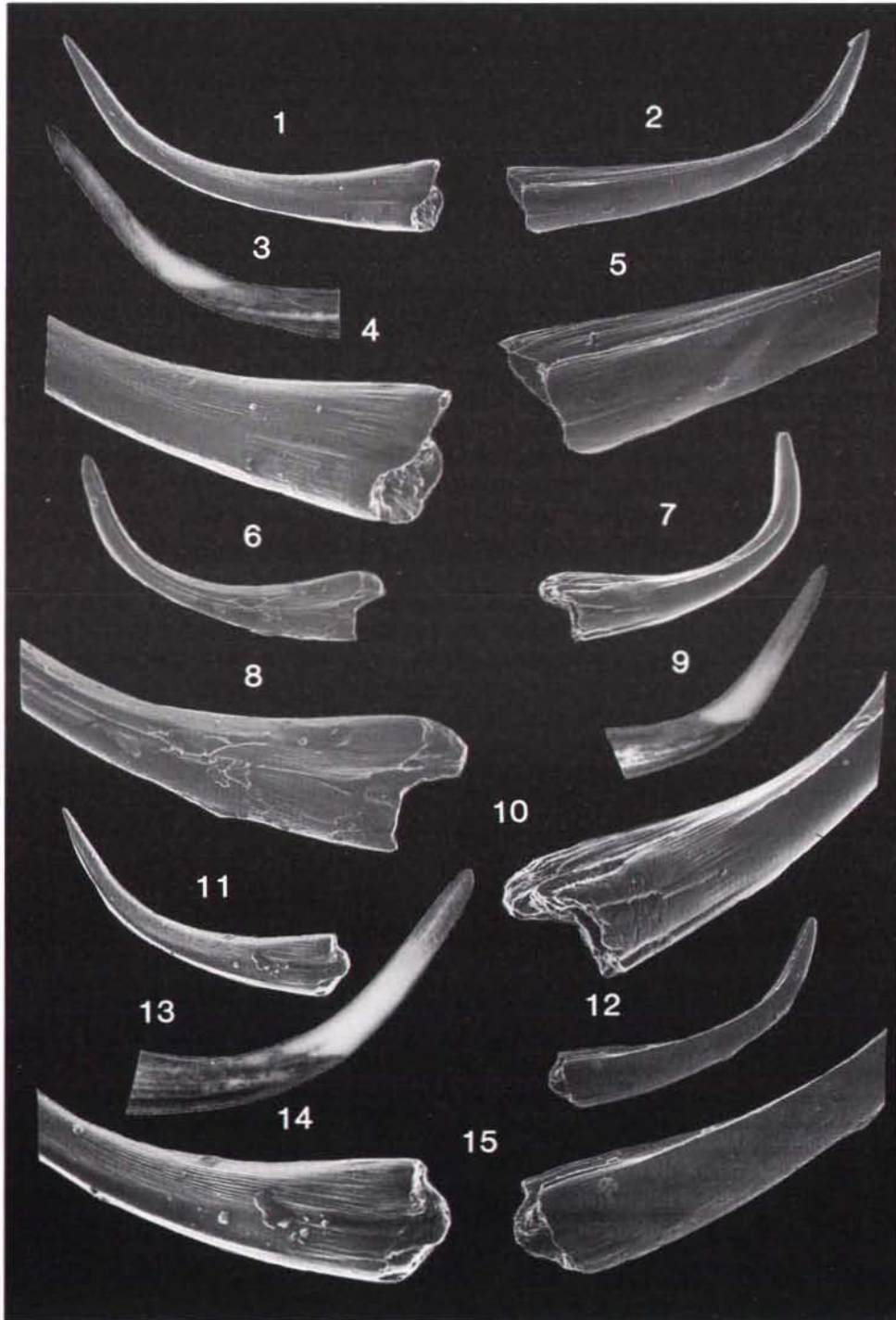
Fig. 33. Type suite of *Panderodus greenlandensis* from the Lower Visby Beds, Gotland, Sweden. Donated by L. Jeppsson (Univ. of Lund) 1-5, paratype MGUH 19.326.

- 1, inner lateral view, $\times 50$ sym. p element;
- 2, outer lateral view, $\times 50$ sym. p element;
- 3, transmitted light showing white matter distribution, $\times 76$;
- 4, lower part of base (inner lateral), $\times 95$;
- 5, lower part of base (outer lateral), $\times 95$;
- 6-10, paratype, 6, MGUH 19.327, inner lateral view, sq element;
- 7, outer lateral view, sq element;
- 8, lower part of base (inner lateral), $\times 95$;
- 9, transmitted light showing white matter distribution, $\times 76$;
- 10, lower part of base (outer lateral), $\times 95$;
- 11-15, holotype, MGUH 19.328;
- 11, inner lateral view, aq element;
- 12, outer lateral view, aq element;
- 13, transmitted light showing white matter distribution $\times 76$;
- 14, lower part of base (inner lateral), $\times 95$;
- 15, lower part of base (outer lateral), $\times 95$.

individual wrinkles vary in height and width randomly. The entire basal surface is completely excavated, basal cavity outline and white matter distribution are illustrated for all the elements in fig. 32.

aq element. Recurved, laterally compressed element, broad-based with a narrow proclined cusp. The inner

face bears a broadly rounded costa close to its lower margin, this extends from the apical edge of the basal wrinkles to the apex. Medially a broad, shallow, apically tapering furrow terminates at the base of the cusp. The outer face is broadly convex and develops a rounded costa and furrow close to its upper margin.



sq element. Broader and more posteriorly curved than the sym. p element. The lower and upper margins are sharp with a low keel occasionally developed along the lower margin. A broadly rounded costa is situated centrally on each lateral face extending from the apical edge of the basal wrinkles to the apex. The basal margin is straight with no heel, a basal notch is barely distinguishable, at the centre of the inner edge. The entire basal surface is excavated.

r element. Short, relatively slender element with a steeply reclined to recurved cusp. Base and cusp are approximately equal in length, the upper margin of the base may be keeled, but is more commonly only sharp, maximum curvature occurring at the base of the cusp. The lower margin of the base is rounded and more or less straight. Inwardly a prominent, sharp costa extends apically from a point just above the base, running close and subparallel to the lower margin; the costa decreases in height apically. Above the costa the remainder of the face is shallowly concave, divided at midline by a shallow furrow with central groove. The furrow terminates at the base of the cusp, its central groove extends along the midline from a basal notch to the apex. The outer face has a prominent longitudinal costa which may be situated as that on the inner face of the aq element or may be positioned slightly towards the midline, in which case it migrates towards the anterior edge of the cusp

from above the maximum curvature. Above the costa the outer face is smooth and shallowly concave with both furrow and basal notch absent. The basal margin is straight.

Remarks. The type locality (and hence the type material for this species) has been selected in Gotland where preservation is far superior to that of the Greenland material and where further material can be collected as required. Lennart Jeppsson (Lund) kindly supplied the type material (fig 33). Several samples from Washington Land (particularly GGU 216719) contain elements similar to those placed in the apparatus of *P. greenlandensis*. They are taller, however, and more slender, developing thin walls to the basal cavity. These elements may represent an ecological or geographical variant of *P. greenlandensis*, and until larger collections are available they are referred to *P. aff. P. greenlandensis* (plate 5, figs 18–23). Many specimens of *P. greenlandensis* are more robust and larger than those from Gotland.

Panderodus recurvatus (Rhodes, 1953)

Plate 16, figs 1–11

- v*1953 *Paltodus recurvatus* Rhodes, p. 297, pl. 23, figs 219, 220.
1977 *Panderodus recurvatus*; Barrick, p. 54, pl. 3, figs 3, 4, 7–12 (see for further synonymy).

Plate 16

Figs 1–11. *Panderodus recurvatus* (Rhodes).

All specimens from GGU 216853, × 60 unless otherwise stated.

- 1, inner-lateral view of sym. p element; MGUH 17.922.
- 2, outer-lateral view of sym. p element; MGUH 17.923.
- 3, microstriations on inner-lateral face of aq element, × 350; MGUH 17.929.
- 4, inner-lateral view of aq element, slender morphotype; MGUH 17.925.
- 5, inner-lateral view of aq element, slender morphotype; MGUH 17.926.
- 6, lateral view of sq element; MGUH 17.927.
- 7, inner-lateral view of aq – r intermediate element; MGUH 17.928.
- 8, lateral view of aq element, broad morphotype; MGUH 17.929.
- 9, microstriations on the inner face of aq element, slender morphotype, × 340; MGUH 17.926.
- 10, inner-lateral view of r element; MGUH 17.931.
- 11, outer-lateral view of r element; MGUH 17.932.

Figs 12–15. *Panderodus* spp. aff. *P. recurvatus* (Rhodes).

All specimens × 60.

- 12, inner-lateral view of aq element; MGUH 17.933 from GGU 216837.
- 13, inner-lateral view of sym. p element; MGUH 17.934 from GGU 216852.

- 14, outer-lateral view of sym. p element; MGUH 17.935 from GGU 82687.
- 15, outer-lateral view of r element; MGUH 17.936 from GGU 216852.

Figs 16–21. *Panderodus* sp. A.

All specimens from GGU 256337 unless otherwise stated, × 60.

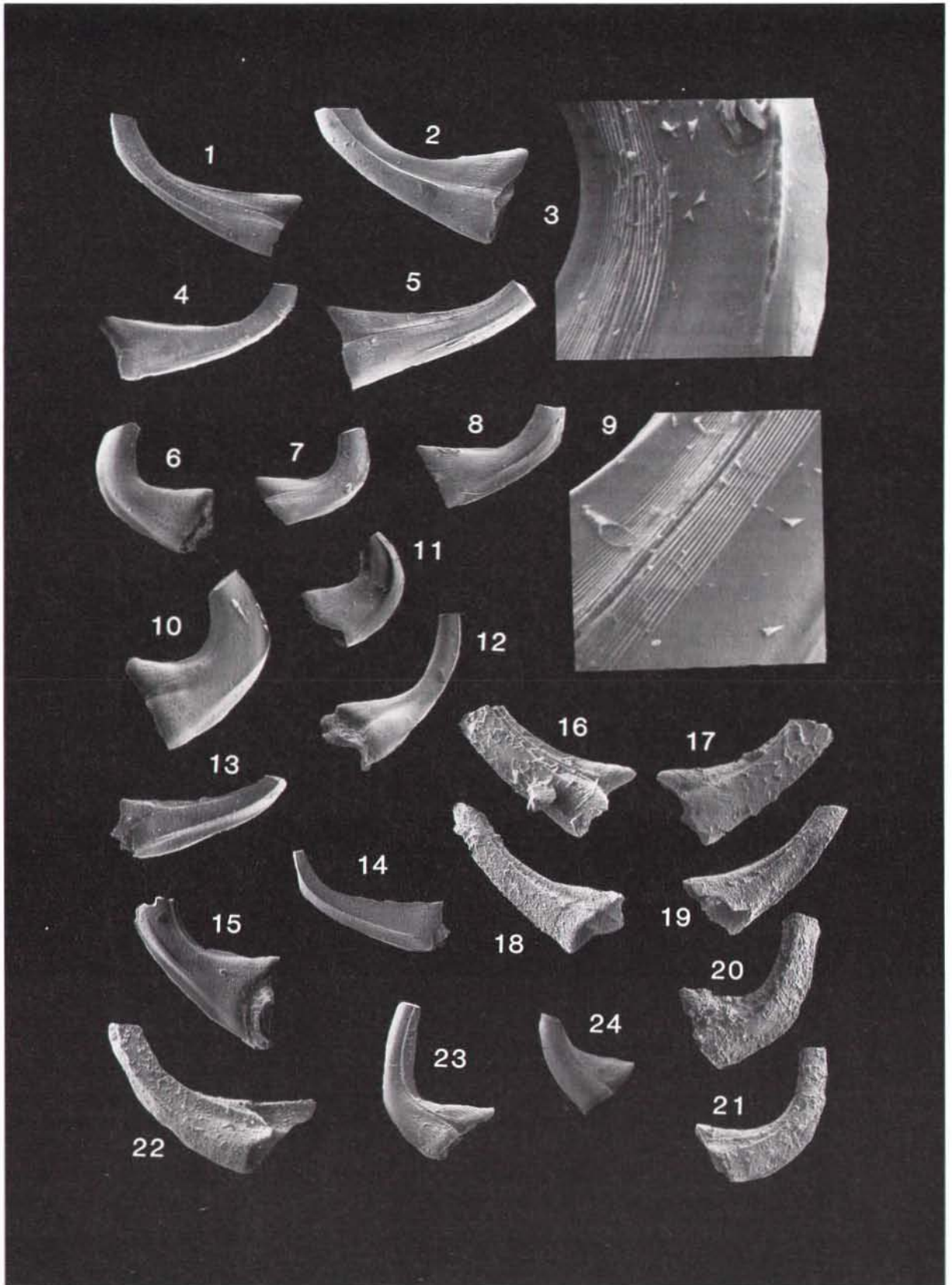
- 16, 17, inner and outer-lateral view of sym. p element; MGUH 17.937.
- 18, outer-lateral view of ap element; MGUH 17.938 from GGU 274724.
- 19, inner-lateral view of ap element; MGUH 17.939 from GGU 274724.
- 20, inner-lateral view of sq element; MGUH 17.940.
- 21, inner-lateral view of sq element; MGUH 17.941.

Fig. 22. *Panderodus* sp. B.

- 22, outer-lateral view of sym. p element, × 60; MGUH 17.942 from GGU 274724.

Figs 23, 24. *Panderodus* sp. C.

- 23, inner-lateral view of r element, × 60; MGUH 17.943 from GGU 82687.
- 24, outer-lateral view of r element, × 60; MGUH 17.944 from GGU 216835.



Holotype. Paltodus recurvatus Rhodes 1953, p. 297.

Emended diagnosis: Apparatus quadrimembrate comprising highly recurved laterally compressed sym. p, aq, sq and r elements.

Description. sym. p element: Refer to Barrick's (1977, p. 54) description of the Sa element; the Greenland specimens differ little. Pre-*P. celloni* Biozone examples are slightly longer and slender with a slightly more rounded cross section.

aq element. As noted by Barrick (1977, p. 55) an unusual symmetry imbalance occurs within this element. The difference occurs in the location of the furrow; the two elements figured (plate 16, figs 4, 5) have the furrow on either the same or the opposite face to the lower lateral costa. Slender to broad, short, asymmetrical, strongly compressed cone. The base is slightly longer than the cusp which is erect to recurved. The upper margin of the base is straight and sharp. Towards the top of the base a low keel is developed, which extends to the apex. The lower margin is keeled and evenly recurved. The basal margin is straight, a prominent basal notch is located on the inner, basal margin, one-third the distance from the upper-basal corner. The inner face bears a prominent costa close to its lower edge; this originates at the base midheight and runs subparallel to the lower margin, migrating to the junction of lateral and upper edges, just above the maximum curvature of the cusp. Above the costa the face is shallowly concave, divided into narrow upper and broad lower faces by a narrow 'v-shaped' groove, which extends from the basal notch to the apex, running subparallel to the midline. The groove is flanked by a narrow zone of oblique microstriations, visible only on the scanning electron microscope (plate 16, figs 3, 9). The outer face is gently convex and may have a short, longitudinal depression close to its centre. The upper and lower keels appear more prominent when viewed from the outer side.

sq element. Highly compressed cone, with keeled upper and lower margins. Base and cusp are subequal in length, the latter erect to recurved. The upper margin of the base is more or less straight with maximum curvature at the base of the cusp; the upper-basal corner is an acute angle. The lower margin is evenly curved from the lower-basal corner, maximum curvature occurring concurrently with that on the upper margin. The lateral faces are virtually identical and may or may not possess a prominent costa just below midlength. This originates at a point one-quarter the distance from the lower-basal corner extending to the apex and running subparallel to the lower margin. The inner face bears a narrow in-

conspicuous groove in a similar position to that on the aq element.

r element. Short, highly curved and commonly inwardly twisted element. The base and cusp are short and subequal in length; the cusp is strongly recurved. The upper margin of the base bears a keel apical of the zone of basal wrinkles. The lower margin is narrowly rounded and evenly curved for two-thirds of its length; above this it is sharply recurved. The basal margin is more or less straight with an inner-basal notch one-third of its length from the upper-basal corner. The area of the basal wrinkles is slightly laterally inflated, and above this the cone is highly compressed. The inner face bears a low costa close to its lower margin, originating at the apical edge of the basal wrinkles, migrating to the junction of lateral and anterior faces at the base of the cusp and extending along this to the apex. Above the costa the face is shallowly concave; a narrow, inconspicuous groove is located close to its upper edge extending from the basal notch to the apex. A shallow furrow may extend obliquely from the basal notch, terminating just above the zone of basal wrinkles. The outer face also bears a prominent costa, close to its lower margin. This is situated above that on the inner face and does not migrate. The remainder of the face is shallowly concave.

Remarks. This apparatus comprises small, strongly compressed, highly recurved elements, which have prominent lateral costae, a shallow furrow, and typically very fine basal wrinkles. A morphological transition occurs from sym. p-aq-r with the elements becoming progressively more asymmetrical, broader, shorter and more recurved. The sq element is strongly compressed, bilaterally symmetrical and is readily homologised with its counterpart in the apparatus of *P. greenlandensis*. In the *P. recurvatus* apparatus this element does not form an integral part of the sym. p-aq-r transition series.

The q and r elements of *P. recurvatus* are similar to their counterparts in the *P. aff. P. spasovi* apparatus, differing in the even upward curvature of the lower edge; the p elements are characteristic in the apparatuses of both species. Barrick (1977) noted that *P. panderi* Stauffer (1940), a Middle Devonian species, was similar to elements within the *P. recurvatus* apparatus. *P. panderi* (Stauffer) described by Sweet (1979) from the upper Ordovician possesses elements which are less markedly recurved and bear more robust, prominent lateral costae.

The phylogeny of *P. recurvatus* is unclear; its apparatus plan has closer affinity to that of *P. greenlandensis* than to *P. unicostatus*.

Occurrence. *P. recurvatus* ranges from mid to late Llandoverly in the majority of Greenland sections. It was previously only recorded in post-*Pterospathodus celloni* Biozone strata (Barrick, 1977).

Panderodus spp. aff. *P. recurvatus* Rhodes, 1953
Plate 16, figs 12-15

Description. A suite of elements within the Greenland collections occur singly or in low numbers and are similar in morphology to *P. recurvatus*. They are typically strongly recurved from the base of the cusp, compressed and bear lateral costae. These elements are from more than one species and the more common representatives are illustrated. Occurrences and element abundances are recorded in Appendix 1.

Panderodus aff. *P. spasovi* Drygant, 1974c
Plate 17, figs 14-24

aff. 1974c *Panderodus spasovi* Drygant, p. 66, pl. 1,
figs 1-3.

Description. *sym. p element.* Strongly compressed, base long, cusp short and steeply proclined. The upper margin of the base is sharp and more or less straight, concave in larger specimens (plate 17, fig. 14). The lower margin is straight and develops a low keel. The inner face bears a longitudinal costa which runs subparallel to the lower margin, extending from close to the lower-basal corner to the apex. The face is shallowly concave from the costa to the upper edge, bearing a shallow, narrow furrow above the midline. The furrow extends apically from an inconspicuous basal notch, and terminates below midheight of the base. A narrow groove passes centrally through the furrow, subparallel to the upper margin to the apex. A narrow zone of oblique microstriations is present adjacent to the groove on the *p* elements, but has not been seen on the other elements. The outer face bears two longitudinal costae situated either side of the midline. Both originate at the apical edge of the basal wrinkles, curve posteriorly upwards and converge gradually. Basal cavity outline, white matter distribution and zone of basal wrinkles are similar for all elements. The basal wrinkles are weakly developed and are separated by deep grooves, they pass around the cone, parallel to, but not extending to the basal margin. The entire basal surface is excavated. White matter is restricted to the tip and basal edges.

?tp element. Extremely rare specimens with a broad base and commonly broken cusp. The upper margin of the base is sharp and slightly concave downwards; bas-

ally extended as a short, acute angled heel. The lower margin is more or less straight, with a low keel. The basal margin is concave apically with an inconspicuous basal notch situated close to the midpoint on the inner side. The inner face is shallowly concave and bears a narrow median furrow which extends from the basal notch to the apex. A deep narrow groove is divorced from the furrow, situated extremely close to the upper margin of the base. The outer face differs from that of the *ap* element in being slightly more compressed.

aq element. Morphologically transitional from the *sym. p* element. The keeled upper margin and narrowly rounded lower margin recurve sharply at the base of the cusp. The basal margin is broad, equivalent in width to half the height of the base; a basal notch is situated centrally on the inner side. Laterally each face bears a single longitudinal costa close to and running subparallel with the lower margin. On the inner side the costa extends from the base to the apex, on the outer side from a point just above the apical edge of the zone of the basal wrinkles to the apex. The inner face is shallowly concave to the upper edge, a deep narrow groove running from the basal notch, migrating across the base towards the upper edge and continuing close to and subparallel to the posterior margin of the cusp. The outer face is smooth and shallowly concave to its upper margin.

sq element. Small, highly compressed, strongly recurved element. Characterised by a short, broad base and slender cusp. The upper and lower margins are sharp and evenly curved. The lower margin bears a keel which increases in height towards base midheight. The lateral faces are smooth and broadly convex, typically developing a narrow zone of basal wrinkles; the entire basal surface is excavated.

r element. Morphologically transitional from the *aq* element, differing only in being shorter and more recurved; the cusp is more or less erect. The basal margin is narrower and not as sharply concave in the inner inflated section of the basal cavity (plate 17, fig. 19).

Remarks. Elements are distinguished from those of *P. recurvatus* by their lateral compression, basal outline, less sharply recurved cusp, and the band of basal wrinkles which does not extend to the basal margin. The *sym. p* element differs from that figured by Drygant (1974c), the holotype of *P. spasovi*, in the inclination of the lower margin and the ornament of the outer face. The Greenland specimens are similar to those figured by Barrick (1977) as the *Sb* element (particularly specimen SUI 42461, pl. 3, fig. 18). The remaining elements, placed in the apparatus of *P. spasovi*? by Barrick, differ from those from Greenland. Whether Barrick's speci-

mens of *P. spasovi*? and the Greenland specimens represent variants of one species is unknown. The elements figured by Drygant are clearly part of a separate apparatus. The apparatus structure (with generally similar elements and common co-occurrence within the upper *P. celloni* and *P. amorphognathoides* Biozones) suggests a close relationship between *P. recurvatus* and *P. aff. P. spasovi*. *P. recurvatus* is first found in mid Llandoverly strata throughout Greenland, and it is possible that *P. aff. P. spasovi* is a descendant.

Occurrence. In all sections across North Greenland.

Panderodus unicastatus (Branson & Mehl, 1933a)

Plate 17, figs 1–7

- *1933a *Paltodus unicastatus* Branson & Mehl, p. 42, pl. 3, fig. 4.
- 1933a *Paltodus simplex*; Branson & Mehl, p. 42, pl. 3, fig. 3.
- 1953 *Paltodus acostatus*; Rhodes, p. 237, pl. 21, figs 111–112; pl. 22, figs 163–164; pl. 23, figs 212–213.
- p1953 *Paltodus unicastatus*; Rhodes, p. 298, pl. 23, figs 214–216 only.
- 1969 *Panderodus unicastatus unicastatus*; Nicoll & Rexroad, p. 55, pl. 7, figs 29, 30 (see for further synonymy).
- 1969 *Panderodus simplex*; Nicoll & Rexroad, p. 54, pl. 7, fig. 28 (see for further synonymy).
- 1971 *Panderodus simplex*; Rexroad & Craig, p. 697, pl. 81, figs 35–40.
- 1971 *Panderodus gracilis*; Rexroad & Craig, p. 695, pl. 81, figs 28, 29.
- 1971 *Panderodus unicastatus*; Rexroad & Craig, p. 697, pl. 81, figs 30–34.

- 1971 *Panderodus n.sp.* Rexroad & Craig, p. 698, pl. 81, figs 26, 27.
- ?1975 *Panderodus serratus*; Cooper, p. 993, pl. 1, figs 3–5, 7–9, 13, 14, 23.
- 1976 *Panderodus unicastatus*; Cooper, p. 213, pl. 1, figs 1–7, 22 (see for further synonymy).
- 1977 *Panderodus unicastatus*; Barrick, p. 56, pl. 3, figs 1, 2, 5, 6.

Holotype. *Paltodus unicastatus* Branson & Mehl, 1933a, p. 42, pl. 3, fig. 3 from the Brassfield Formation, Lithium, Missouri.

Diagnosis. Refer to Barrick (1977, p. 56).

Description. All the elements of *P. unicastatus* have been described previously except the tp element (see synonymy).

tp element. Slender cone with a long base and short proclined cusp. The keeled upper margin of the base is more or less straight, extended basally as a prominent heel; the lower margin narrow and rounded. Strongly, laterally compressed the cusp is twisted inwardly with respect to the base. On the inner side a narrow furrow extends from close to the upper-basal corner to the base of the cusp, the outer face is shallowly convex lacking a furrow or costae. A low zone of basal wrinkles passes around the element. The basal surface is entirely excavated, white matter is restricted to the apex of the cusp.

Remarks. Few differences can be detected between *P. gracilis* Branson & Mehl as described by McCracken & Barnes (1981) and *P. unicastatus*. The elements of the latter are slightly more recurved, the lateral costae are

Plate 17

Figs 1–7. *Panderodus unicastatus* Branson & Mehl.
All specimens from GGU 184125, × 60.

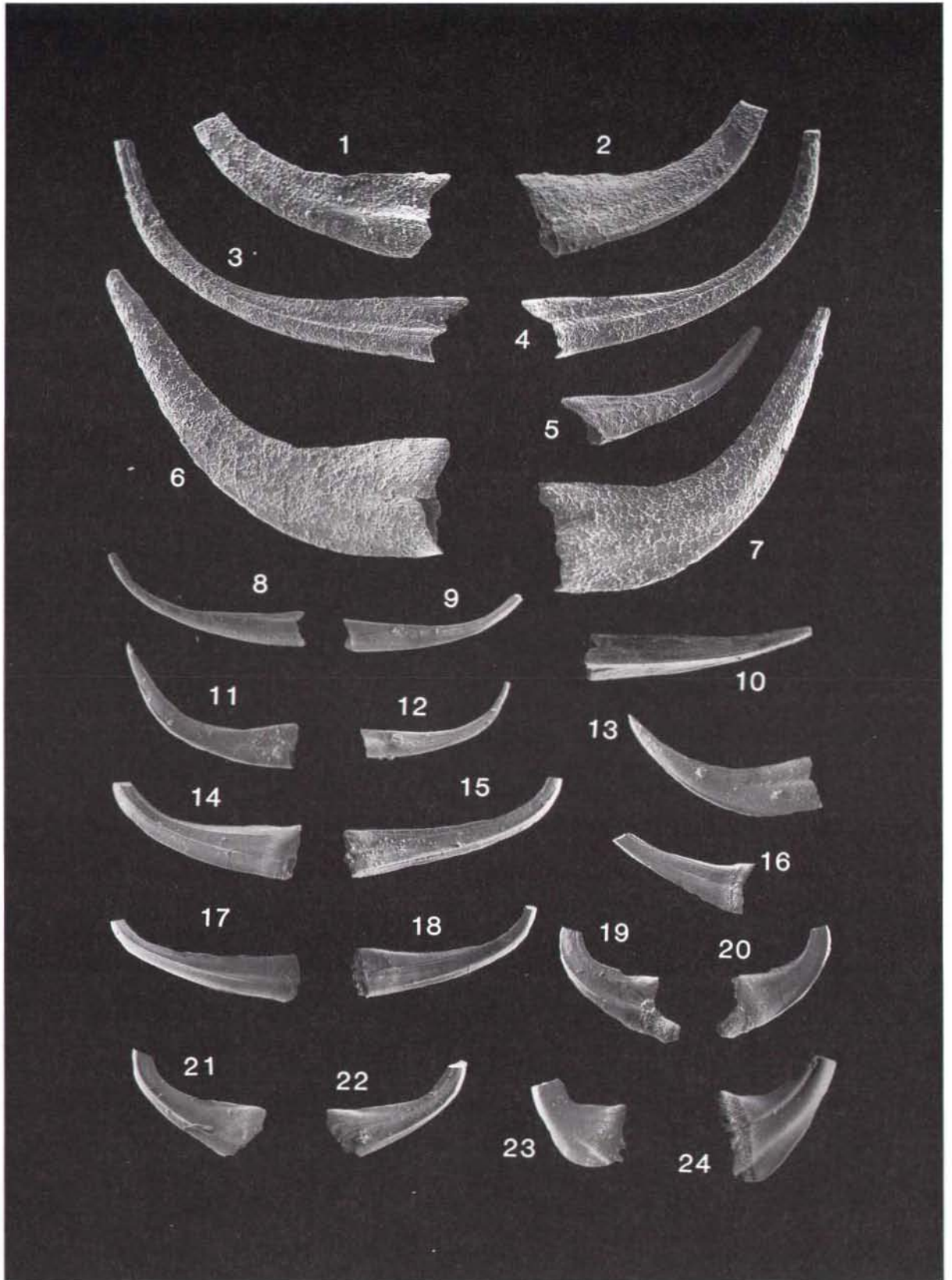
- 1, 2, outer and inner-lateral view of aq element; MGUH 14.074.
- 3, 4, inner and outer-lateral view of sym. p element; MGUH 14.073.
- 5, inner-lateral view of tp element; MGUH 17.904.
- 6, 7, outer and inner-lateral view of sq element; MGUH 14.072.

Figs 8–13. *Panderodus aff. P. unicastatus* (Branson & Mehl).
All specimens from GGU 216719, × 60.

- 8, outer-lateral view of sym. p element; MGUH 17.905.
- 9, inner-lateral view of sym. p element; MGUH 17.906.
- 10, upper view of sym. p element; MGUH 17.907.
- 11, outer-lateral view of aq element; MGUH 17.908.
- 12, inner-lateral view of aq element; MGUH 17.909.
- 13, lateral view of sq element; MGUH 17.910.

Figs 14–24. *Panderodus aff. P. spasovi* Drygant.
All specimens × 60.

- 14, outer-lateral view of sym. p element; MGUH 17.911 from GGU 82687.
- 15, inner-lateral view of sym. p element; MGUH 17.912 from GGU 216852.
- 16, inner-lateral view of ?tp element; MGUH 17.913 from GGU 82687.
- 17, outer-lateral view of aq element, slender morphotype; MGUH 17.914 from GGU 216773.
- 18, inner-lateral view of aq element, slender morphotype; MGUH 17.915 from GGU 216773.
- 19, inner-lateral view of r element; MGUH 17.916 from GGU 216773.
- 20, outer-lateral view of r element; MGUH 17.917 from GGU 216773.
- 21, outer-lateral view of aq element, broad morphotype element; MGUH 17.918 from GGU 216773.
- 22, inner-lateral view of aq element, broad morphotype element; MGUH 17.919 from GGU 216773.
- 23, outer-lateral view of sq element; MGUH 17.920 from GGU 216852.
- 24, inner-lateral view of sq element; MGUH 17.921 from GGU 82687.



less prominent and the sq element is more slender. McCracken & Barnes (1981) noted that the elements of *P. gracilis* were more variable; Lennart Jeppsson (Lund, personal communication) regards these species as synonymous. I have not studied relevant holotypes and all specimens are referred to *P. unicastatus*, the name more commonly used by Silurian workers.

Cooper (1975) distinguished *P. serratus* only by the presence of an additional upwardly serrate (aq) element in its apparatus. This element may be a minor reiterative variant within the *P. unicastatus* apparatus and consequently *P. serratus* is cited questionably in synonymy.

Occurrence. Found throughout North Greenland.

Panderodus aff. *P. unicastatus* (Branson & Mehl, 1933a)

Plate 17, figs 8–13

aff. 1933a *Paltodus unicastatus* Branson & Mehl, p. 42, pl. 3, fig. 3.

aff. 1933a *Paltodus simplex* Branson & Mehl, p. 42, pl. 3, fig. 4.

aff. 1976 *Panderodus unicastatus*; Cooper, p. 213, pl. 1, figs 1–7, 22.

Description. sym. p element. This thin walled element differs from that of *P. unicastatus* in having a triangular, midheight cross section and prominent lateral costae which extend from the basal margin to the apex. White matter is restricted to the tip of the cusp, and a low zone of weak basal wrinkles occurs around each element. This zone is barely visible without the use of the scanning electron microscope.

aq element. Morphologically transitional from the sym. p element. The inner face is similar to that of the sym. p element, but the costa is less prominent and does not extend to the basal margin, there is no central groove. The shallowly concave outer face has a costa close to and subparallel with the lower margin extending from the basal margin to the apex. A shallow longitudinal depression may be located centrally at the base.

sq element. Biconvex, gently curving, laterally compressed, keeled element, the lateral faces are smooth, the inner bears a shallow, longitudinal furrow, which does not extend beyond the midheight of the base.

Remarks. This apparatus comprises slender, thin walled, laterally costate elements. In many respects it is similar to elements previously described as *Coelocerosodontus tetragonus* Ethington, but differs in the shape of its basal cavity and white matter distribution. The remaining elements are typically much thinner walled and

more slender than their counterparts in *P. unicastatus*. Nowlan & Barnes (1981, p. 16, pl. 6, figs 20, 23, 27) described similar elements as *P. gracilis*; however, the costae of their sym. p element do not extend to the basal margin. With the current geographically and stratigraphically restricted samples, it is difficult to assess whether this apparatus represents a new species or a localised ecological or geographical variant of *P. unicastatus*.

Occurrence. Found in middle Llandovery strata in Washington Land. Particularly common in GGU 216724.

Panderodus sp. A

Plate 16, figs 16–21

Remarks. These specimens are mainly fragments of sym. p, aq and sq elements, and it is uncertain whether they constitute a single multi-element species. The sym. p element differs from that of *Panderodus greenlandensis* in having a much narrower base and a complex inner furrow; the sq element is similar though more strongly compressed, the furrow on each of its lateral faces is narrower. The sq element of this apparatus suggests an affinity with *P. greenlandensis*.

Occurrence. Found in the Turesø Formation of Peary Land.

Panderodus sp. B

Plate 16, fig. 22

Remarks. This species is known only from its fragmented sym. p element and is found only in the Turesø Formation of central Peary Land. Its robust nature, deep lateral furrows, prominent costae and basally extended keel suggest an affinity with *P. greenlandensis*. Only two specimens are recorded.

Panderodus sp. C

Plate 16, figs 23, 24

Remarks. Rare specimens of this taxon are found in middle to upper Llandovery strata in Washington Land. The r element, with short base and a long proclined to erect cusp, possesses a narrow, groove-like, medial, inner furrow and prominent basal notches in the basal margins.

Panderodus sp. D

Plate 18, figs 1-2

Remarks. The straight lower margin of the sym. p element is similar to *P. spasovi* Drygant (1969b), but the element differs in the shape of the base, in lacking the double lateral costae and in having basal wrinkles which extend to the basal margin.

Occurrence. Fourteen specimens of this species occur in *Pterospathodus celloni* Biozone strata of East Peary Land.

Pseudobelodella n. gen.

Name derivation. From the superficial similarity to *Belodella* Ethington.

Type species. *Pseudobelodella silurica* n. gen. n. sp.

Diagnosis. Quadrimembrate; sym. p, ap, aq and sq elements. All strongly compressed and bearing upper edge dentides.

Remarks. The presence of an ap and the morphology of the sym.p element distinguish this genus from *Belodella* Ethington.

Pseudobelodella is apparently restricted to deeper water environments in the upper *Pterospathodus celloni* and *P. amorphognathoides* Biozones.

Pseudobelodella silurica n. gen. n. sp.

Plate 18, figs 3-9

1978 *Belodella* n. sp. A; Miller, p. 341, pl. 1, figs 19-231987 *Belodella* n. sp. A; Over & Chatterton, pl. 6, figs 4, 8-11.

Name derivation. From the apparent restriction of this species to Silurian strata.

Holotype. Specimen MGUH 17-947; pl. 18, fig. 4 a sym. p. element from GGU 216853 within the Lafayette Bugt Formation. *Pterospathodus amorphognathoides* Biozone, at Kap Schuchert, Washington Land, western North Greenland.

Diagnosis. As for the genus.

Description. sym. p element. Strongly compressed, erect element, with a slightly inwardly bowed cusp. The element has a broad base and tapers gradually towards the apex. Its upper margin bears numerous short, almost

completely fused, apically inclined, peg-like denticles. Basally, the upper margin is adenticulate and forms a short heel, of which the extreme basal corner is slightly extended. The lower margin is straight to gradually posteriorly curved, curvature increasing apically, particularly in forms with an inwardly twisted apex. The basal margin is straight beneath the lower lateral faces and inclined beneath the heel, a prominent basal notch is located centrally on both inner and outer-basal margins. The entire surface is deeply excavated. The faces are laterally identical, a broad flat lower face being separated from an apically tapering, upper face by a narrow groove-like furrow and step-like costa, both extending to the tip of the cusp from the basal notch. At the base of the cusp both costa and groove migrate towards the posterior edge of the cusp, continuing to the apex just beneath the denticle row. The cavity is tall and apically triangular, terminating close to the lower margin at approximately two-thirds the height of the element. White matter is concentrated into the apex, above the basal cavity tip and occasionally is apparent within the denticles.

ap element. Less strongly compressed than the slightly inwardly bowed sym. p. element. Distinguished from the aq in having a straight lower margin, more erect. The upper edge bears apically inclined, almost completely fused denticles. The basal margin is commonly straight, developing a shallow furrow on the outer face. A weakly developed step-like costa runs parallel to the lower margin from the base to the apex. The inner face bears a prominent costa close to and parallel with the lower margin, extending from the top of the basal wrinkles to the apex. Basal cavity outline and white matter distribution are as described for the sym. p. element.

aq element. Identical to the ap element in all features except greater recurvature.

sq element. Compressed, strongly recurved, biconvex element. The base is broad, the cusp steeply proclined to erect. The upper margin of the base is straight and bears four to six tall, peg-like, partially fused denticles. Basally the edge is adenticulate and forms a heel of similar morphology to that of the other elements in the apparatus. The upper edge of the cusp is sharp and more or less straight, the lower margin develops a low keel, extending from just apical of the lower-basal corner to the apex of the element. The lower face is subdivided as in the sym. p element by a step-like costa, the costa migrates upwards and just below the base of the cusp is extremely close to the upper margin. The outer face is smooth and broadly convex. A zone of fine basal wrinkles passes around the base, these are more conspicuous on the outer face. The entire basal surface is excavated and, though shorter, the basal cavity is as

described for the other elements. White matter is restricted to the cusp and has not been seen in the denticles.

Occurrence. *P. silurica* is restricted to the *P. celloni* and *P. amorphognatoides* Biozones of Peary Land, Kronprins Christian Land, Hall Land and Washington Land.

Remarks. Miller (1978, p. 341) described *Belodella* n. sp. A from the Hidden Valley Dolomite of California, noting that these specimens (aq elements) were distinct from previously reported species of Silurian or Devonian age. Over & Chatterton (1987, pl. 6, figs 4, 8–11) reconstructed *Belodella* n. sp. A, Miller as four 'forms', a (aq), b (?aq), c (sym. p.) and d (ap). An additional sq element occurs in the Greenland collection.

Genus *Pseudooneotodus* Drygant, 1974c

Type species. *Oneotodus* (?) *beckmanni* Bischoff & Sannemann 1958, p. 98.

Diagnosis. Refer to Barrick (1977, p. 57).

Remarks. Barrick (1977, p. 57) emended the generic diagnosis and reconstructed the apparatus of *P. bicornis* and *P. tricornis*, each comprising a slender conical element, a squat conical element and a diagnostic bi- or tri-denticulate squat conical element. Bischoff (1986) emended the diagnosis of *Pseudooneotodus* based upon

his conclusion that the apparatus was unimembrate. The Greenland collection confirms a trimembrate apparatus. Unidenticate elements appear to be vicarious. Homology of elements in the *Pseudooneotodus* apparatus with those in other coniform apparatus plans is problematical. *Pseudooneotodus* elements lack lateral costae for orientation and no obvious morphological transition occurs between the elements. The slender conical element is erect and may homologue with the p elements of other genera; the squat conical elements are the most abundant and show the greatest morphological variation, characters commonly found in the q elements in other coniform genera.

Pseudooneotodus cf. *P. beckmanni* (Bischoff & Sannemann, 1958)

cf. 1958 *Oneotodus?* *beckmanni* p. 58, pl. 15, figs 22–25.
cf. 1977a *Pseudooneotodus beckmanni*; Cooper, p. 1068, pl. 2, figs 14, 17.

Description. Squat, unidenticate, broad based, conical elements. Specimens from Greenland are indistinguishable from the squat, conical, unidenticate element of *Pseudooneotodus bicornis* Drygant (pl. 20, figs 11, 12).

Remarks. The apparatus of *O. beckmanni* has previously not been fully described. Jentzsch (1962, p. 969, pl. 1, fig. 8) reported the slender conical element *Oneotodus variabilis* Lindström in association with a uni-

Plate 18

Figs 1, 2. *Panderodus* sp. D.

- 1, outer lateral view of sym. p element, × 60; MGUH 17.945.
- 2, microstriations on outer lateral face of sym. p element, × 240; MGUH 17.945.

Figs 3–9. *Pseudobelodella silurica* n. gen. n. sp.

All specimens from GGU 216853 unless otherwise stated, × 60.

- 3, lateral view of sym. p element; MGUH 17.946.
- 4, lateral view of sym. p element; MGUH 17.947 (holotype).
- 5, inner lateral view of slender aq element; MGUH 17.948.
- 6, outer lateral view of slender aq element; MGUH 17.949.
- 7, inner lateral view of broad aq element; MGUH 17.950.
- 8, inner lateral view of sq element; MGUH 17.951.
- 9, outer lateral view of sq element; MGUH 17.952 from GGU 229037.

Figs 10–15. *Pseudooneotodus bicornis* Drygant.

All specimens from GGU 228978 unless otherwise stated.

- 10, lateral view of slender conical element, × 60; MGUH 17.953 from GGU 228975.
- 11, upper view of squat unidenticate element, × 40; MGUH 17.954.

- 12, lateral view of squat unidenticate element, × 40; MGUH 17.955.

- 13, lateral view of squat bidenticulate element, × 40; MGUH 17.956.

- 14, upper view of squat bidenticulate element, × 40; MGUH 17.957.

- 15, upper view of squat bidenticulate element, × 40; MGUH 17.958.

Figs 16–18. *Pseudooneotodus tricornis* Drygant.

All specimens × 60.

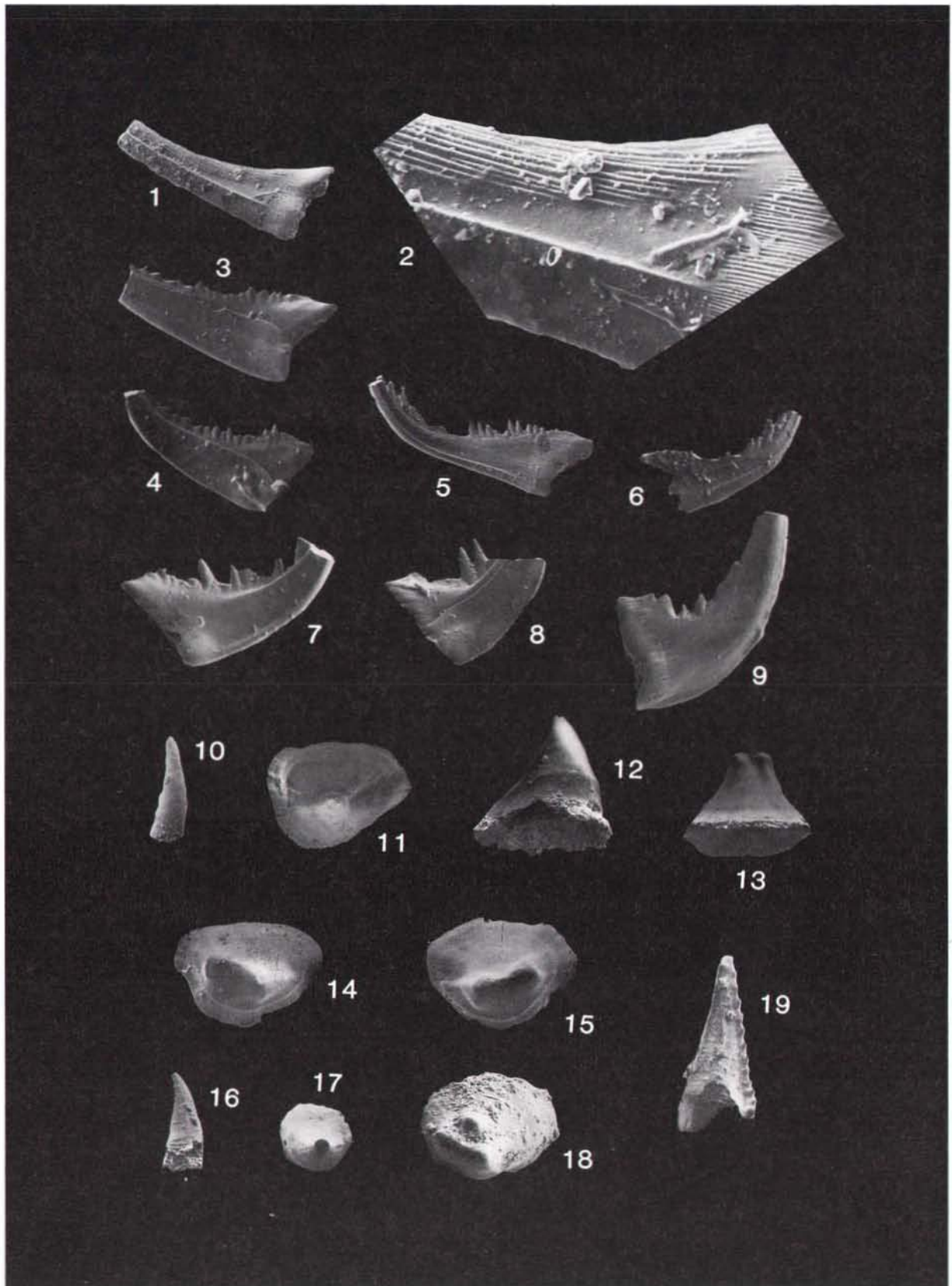
- 16, lateral view of slender conical element; MGUH 17.959 from GGU 228978.

- 17, upper view of squat unidenticate element; MGUH 17.960 from GGU 228975.

- 18, upper view of tridenticate element; MGUH 17.961 from GGU 228975.

Fig. 19. *Pseudooneotodus* n. sp.

- 19, lateral view of slender conical element, × 60; MGUH 17.962 from GGU 216852.



denticulate squat conical element from the Lower Devonian of Thuringia. Cooper (1977a), Nowlan & Barnes (1981, p. 23) and the Greenland collections suggest that late Ordovician to mid Llandovery *Pseudooneotodus* had a unimembrate apparatus.

Occurrence. Found infrequently in pre-*Pterospirifer celloni* Biozone samples from throughout North Greenland. Sample GGU 216835 (fig. 21) contains abundant elements.

Pseudooneotodus bicornis Drygant, 1974c

Plate 18, figs 10–15

- *1974c *Pseudooneotodus bicornis* Drygant, p. 67, pl. 2, figs 40–48.
- 1976 *Pseudooneotodus bicornis*; Barrick & Klapper, p. 81, pl. 1, fig. 15.
- 1977a *Pseudooneotodus bicornis*; Cooper, p. 1069, pl. 2, figs 8, 9, 11.
- 1977 *Pseudooneotodus bicornis*; Barrick, p. 57, pl. 2, figs 14, 17, 19, 20.
- 1980 *Pseudooneotodus bicornis*; Helfrich, pl. 1, fig. 21.
- 1981 *Pseudooneotodus bicornis*; Aldridge, Dornig & Siveter, pl. 2.1, figs 1, 2.
- 1983 *Pseudooneotodus bicornis*; Wang & Ziegler, fig. 3, nos 18, 19.
- 1986 *Pseudooneotodus bicornis*; Bischoff, p. 234, pl. 27, figs 18, 19, 21–27.
- 1987 *Pseudooneotodus bicornis*; Over & Chatterton, pl. 6, figs 23, 24.

Holotype. *Pseudooneotodus bicornis* Drygant, 1974c, p. 67, pl. 2, figs 40–48.

Diagnosis. Refer to Barrick (1977, p. 58).

Description. The Greenland specimens conform to the descriptions given by Barrick (1977, p. 58). In the moderately large collections from Greenland, both sinistral and dextral bidenticate elements are present (plate 18, figs 14, 15).

Remarks. *P. bicornis* differs from *P. tricornis* and *P. cf. P. beckmanni* in having a bidenticate squat conical element within its apparatus. The ranges of *P. tricornis* and *P. bicornis* overlap in the Børglum Elv and Kap Schuchert sections. Mabillard & Aldridge (1985) recorded *P. bicornis* in small numbers in nearshore to offshore environments, but not in deep offshore environments. GGU 228977 (fig. 6) from within graptolitic shale contains the most abundant specimens of *P. bicornis* in Greenland, though the size distribution of specimens and sample lithology suggest these specimens have undergone some sorting. Phylogenetically, *P. bicornis* appears to be descended from *P. cf. P. beckmanni*, though its relationship with *P. tricornis* is un-

certain. Barrick (1977, p. 58) considered *P. bicornis* to be derived from *P. tricornis*, stratigraphical occurrences in Børglum Elv are consistent with this suggestion.

Occurrence. Found in seven samples of *Pterospirifer celloni* Biozone age in Washington Land and Peary Land.

Pseudooneotodus tricornis Drygant, 1974c

Plate 18, figs 16–18

- 1966 *Oneotodus* sp. Spasov & Filipović, p. 43, pl. 2, fig. 6.
- *1974c *Pseudooneotodus tricornis* Drygant, p. 67, pl. 2, figs 49, 50.
- 1977a *Pseudooneotodus tricornis*; Cooper, p. 1069, pl. 2, figs 15, 16.
- 1977 *Pseudooneotodus tricornis*; Barrick, p. 58, pl. 2, fig. 18.
- 1983 *Pseudooneotodus tricornis*; Wang & Ziegler, fig. 3, no. 9.
- 1986 *Pseudooneotodus tricornis*; Bischoff, p. 238, figs 20, 28–37.
- 1987 *Pseudooneotodus tricornis*; Over & Chatterton, pl. 6, figs 21, 22.

Holotype. *Pseudooneotodus tricornis* Drygant, 1974c, p. 67.

Diagnosis. Refer to Barrick (1977, p. 58).

Description. Slender conical element. This element is identical to that of *P. bicornis*.

Squat conical element. Conical element with a circular basal outline, bearing a single apex which may be slightly curved. The entire element is excavated, and commonly has extremely thin walls.

Squat conical element, tridenticate. Refer to the description of this element in Barrick (1977, p. 58).

Remarks. Elements of *P. tricornis* are commonly much more fragile and have more circular basal outlines than those of the other species of *Pseudooneotodus*.

Occurrence. Found rarely in Peary Land, Kronprins Christian Land and Washington Land in strata of *Pterospirifer celloni* – *P. amorphognathoides* Biozone age.

Pseudooneotodus n. sp.

Plate 18, fig. 19

Description. Tall slender cone, completely excavated; height approximately twice the basal diameter. Slightly curved apically, compressed slightly in the plane of cur-

vature. A single serrate longitudinal costa bearing small nodose denticles distinguishes this species from others of *Pseudooneotodus*.

Remarks. A single specimen of late Silurian age described by Clark & Ethington (1966, p. 677, pl. 82, fig. 2) as *Coelocerdontus* sp., differs in having keeled anterior and posterior margins.

Genus *Pterospathodus* Walliser, 1964

1964 *Pterospathodus*, p. 66.

1972 *Llandoverygnathus* Walliser, p. 76.

Type species. *Pterospathodus amorphognathoides* Walliser, 1964, p. 67.

Diagnosis. Refer to Barrick & Klapper (1976, p. 82).

Pterospathodus amorphognathoides Walliser, 1964

Plate 19, figs 1-5

- 1962 n. gen. A n. sp. a Walliser, p. 283, fig. 1, no. 12.
 1962 fig. 1, no. 11 Walliser, p. 282.
 v*1964 *Pterospathodus amorphognathoides* Walliser, p. 67, pl. 6, fig. 7; pl. 15, figs 9-15; Text fig. 1f.
 v1964 *Ozarkodina gaertneri* Walliser, p. 57, pl. 6, fig. 6; pl. 27, figs 12-19; Text fig. 1g.
 v1964 *Neoprioniodus triangularis triangularis* Walliser, p. 52, pl. 6, fig. 13; pl. 28, figs 25-30; Text figs 6d-f.
 v1964 *Neoprioniodus costatus costatus* Walliser, p. 48, pl. 6, fig. 14; pl. 28, figs 36-41; Text figs 6l-n.
 1966 *Pterospathodus amorphognathoides*; Spasov, pl. 1, fig. 1.
 1966 *Neoprioniodus costatus costatus*; Spasov, pl. 1, fig. 5.
 1966 *Pterospathodus amorphognathoides*; Spasov & Filipović, p. 48, pl. 1, figs 4-5.
 ?1966 *Ozarkodina gaertneri*; Spasov & Filipović, p. 44, pl. 1, figs 1, 2.
 ?1966 *Neoprioniodus costatus costatus*; Spasov & Filipović, p. 42, pl. 1, figs 10, 11.
 1967 *Pterospathodus amorphognathoides*; Flajs, pl. 13, fig. 10.
 1967 *Ozarkodina gaertneri*; Flajs, pl. 3, fig. 9.
 1967 *Neoprioniodus triangularis triangularis*; Flajs, pl. 3, fig. 12.
 1967 *Neoprioniodus costatus costatus*; Flajs, pl. 3, fig. 11.
 1968 *Pterospathodus amorphognathoides*; Igo & Koike, p. 16, pl. 2, figs 12-13.
 p1968 *Ozarkodina gaertneri*; Igo & Koike, p. 14, pl. 1, figs 5, 6, 9.
 v1969 *Pterospathodus amorphognathoides*; Nicoll & Rexroad, p. 56, pl. 3, figs 1-7.
 v1969 *Ozarkodina gaertneri*; Nicoll & Rexroad, p. 49, pl. 2, figs 12-14.
 v1969 *Ozarkodina neogaertneri* Nicoll & Rexroad, p. 50, pl. 2, figs 15, 16.
 1969 *Pterospathodus amorphognathoides*; Schönlaub, pl. 1, fig. 8.
 1969 *Ozarkodina gaertneri*; Schönlaub, pl. 1, fig. 15.
 1969a *Pterospathodus amorphognathoides*; Drygant, p. 49, pl. 1, fig. 6.
 1970 *Pterospathodus amorphognathoides*; Manara & Vai, p. 494, pl. 62, fig. 15; pl. 63, fig. 4.
 1970 *Ozarkodina gaertneri*; Manara & Vai, p. 487, pl. 62, fig. 17.
 1971 *Pterospathodus amorphognathoides*; Rexroad & Nicoll, pl. 2, figs 20, 21.
 1971 *Ozarkodina gaertneri*; Rexroad & Nicoll, pl. 2, fig. 22.
 1971 *Ozarkodina neogaertneri*; Rexroad & Nicoll, pl. 2, fig. 23.
 1971 *Pterospathodus amorphognathoides*; Schönlaub, p. 45, pl. 2, figs 6-12.
 1972 *Pterospathodus amorphognathoides*; Rexroad & Nicoll, pl. 1, figs 4-7.
 1972 *Ozarkodina gaertneri*; Rexroad & Nicoll, pl. 1, figs 1-3.
 1972 *Ozarkodina neogaertneri*; Rexroad & Nicoll, pl. 2, fig. 34.
 1972 *Neoprioniodus triangularis*; Rexroad & Nicoll, p. 67, pl. 2, figs 12-13.
 1972 *Neoprioniodus costatus*; Rexroad & Nicoll, pl. 2, figs 8-11.
 vp1972 *Pterospathodus amorphognathoides*; Aldridge, p. 208, pl. 3, figs 17, 19.
 vp1972 *Ozarkodina gaertneri*; Aldridge, p. 200, pl. 5, fig. 5.
 v1972 *Distomodus triangularis triangularis*; Aldridge, p. 174, pl. 6, fig. 12.
 v1972 *Neoprioniodus costatus costatus*; Aldridge, p. 193, pl. 5, fig. 22.
 1972 *Pterospathodus amorphognathoides*; Walliser, p. 76.
 v1974 *Pterospathodus amorphognathoides*; Aldridge, figs 1E-F.
 1975 *Pterospathodus amorphognathoides*; Klapper & Murphy, p. 27, pl. 2, fig. 1.
 1975 *Pterospathodus amorphognathoides*; Saladzius, pl. 2, fig. 7.
 v1975 *Pterospathodus amorphognathoides*; Aldridge, pl. 1, figs 22, 23.
 1976 *Pterospathodus amorphognathoides*; Barrick & Klapper, p. 82, pl. 1, figs 4, 9-11, 16.
 ?1976 *Pterospathodus amorphognathoides*; Kuwano, pl. 2, fig. 2.
 1976 *Pterospathodus amorphognathoides*; Miller, fig. 8, no. 20.
 1976 *Ozarkodina gaertneri*; Miller, fig. 8, no. 20.
 1977 *Pterospathodus amorphognathoides*; Liebe & Rexroad, pl. 1, fig. 9.
 1977 *Ozarkodina gaertneri*; Liebe & Rexroad, pl. 1, fig. 10.
 1977 *Distomodus triangularis*; Liebe & Rexroad, pl. 2, fig. 29.
 1977 *Neoprioniodus costatus*; Liebe & Rexroad, pl. 2, figs 30, 31.
 1977a *Pterospathodus amorphognathoides*; Cooper, p. 1065, pl. 2, figs 3, 6.
 1978 Apparatus 'C'; Miller, pl. 4, figs 8-11.
 1978 *Distomodus triangularis triangularis*; Miller, pl. 3, fig. 9.
 1980 *Pterospathodus amorphognathoides*; Helfrich, pl. 2, fig. 17-19.
 1980 *Pterospathodus amorphognathoides*; Cooper, p. 219, fig. 10.
 1981 *Pterospathodus amorphognathoides*; Uyeno & Barnes, pl. 1, fig. 24.
 1981 *Pterospathodus amorphognathoides*; Nowlan, pl. 7, fig. 6.

- 1982 *Pterospathodus amorphognathoides*; Aldridge & Mohamed, pl. 2, figs 13–16.
 1983 *Pterospathodus amorphognathoides*; Uyeno & Barnes, pl. 24, pl. 8, fig. 24.
 1983 *Pterognathodus amorphognathoides*; Nowlan, fig. 4K.
 v1983 *Pterospathodus amorphognathoides*; Mabillard & Aldridge, pl. 2, figs 25–27.
 v1985 *Pterospathodus amorphognathoides*; Aldridge, p. 86, pl. 3.3, figs 7–10.
 1985 *Pterospathodus amorphognathoides*; Bischoff, p. 186, pl. 30, figs 19–22; pl. 31, figs 15–39.
 1987 *Pterospathodus amorphognathoides*; Over & Chatterton, pl. 4, figs 1–3.

Holotype. *Pterospathodus amorphognathoides* Walliser, 1964, p. 67. Pa element, specimen Wa 745/16 from sample 11D, Cellon Mountain, Carnic Alps, Austria.

Diagnosis. Refer to Barrick & Klapper (1976, p. 82).

Description. Pa element. The Greenland specimens conform to the description of *Pterospathodus amorphognathoides* Walliser in Aldridge (1972, p. 208). They differ only in possessing a sigmoidally curved posterior process.

Pb element. Greenland specimens are indistinguishable from those described as *Ozarkodina gaertneri* Walliser, by Aldridge (1972, p. 200).

M element. Greenland specimens conform to the description of *Distomodus triangularis triangularis* (Walliser) in Aldridge (1972, p. 174).

Sc element. Greenland specimens conform to the de-

scription of *Neoprioniodus costatus costatus* Walliser, in Aldridge (1972, p. 193).

Remarks. *P. amorphognathoides* elements are uncommon in the Greenland collection, occurring without other *Pterospathodus* species only in GGU 242833 (fig. 16). In other samples they occur with *P. pennatus rhodesi* Savage. Only the Pa, Pb, M and Sc elements of *P. amorphognathoides* are present in GGU 242833, the Pb, M and Sc elements are identical to their counterparts in *P. pennatus rhodesi*.

Specimens figured by Spasov & Filipović (1966) are cited questionably as they occur in a sample with both *P. amorphognathoides* and *P. pennatus rhodesi* Pa elements.

Pb elements referred by Link & Druce (1972, p. 64, pl. 6, figs 10, 13) to *Ozarkodina gaertneri*, from Ludlow strata in the Yass Basin, New South Wales are not closely similar to the Pb element in either *P. amorphognathoides* or *P. pennatus rhodesi*.

Walliser (1964, p. 16) considered *P. pennatus pennatus* to be the ancestor of *P. amorphognathoides*. On morphological and stratigraphical evidence *P. pennatus rhodesi* is an intermediate in this lineage. Complications arise with this hypothesis when considering *P. pennatus angulatus* Walliser (1964, pl. 14, fig. 21) which developed a bifurcating outer process in the lower *P. celloni* Biozone and ranged into the Wenlock (Aldridge, 1975, pl. 3, fig. 18). *P. pennatus angulatus* was thus coeval with *P. amorphognathoides* during the upper part of its range, but the nature of any relationship is uncertain.

Plate 19

Figs 1–5. *Pterospathodus amorphognathoides* Walliser. All specimens from GGU 242833, unless otherwise stated.

- 1, upper view of Pa element, $\times 20$; MGUH 17.842 from GGU 275048.
- 2, inner-lateral view of M element, $\times 60$; MGUH 17.843.
- 3, inner-lateral view of Pb element, $\times 60$; MGUH 17.844.
- 4, inner-lateral view of ?juvenile Sc element, $\times 60$; MGUH 17.845.
- 5, microstriations on the cusp of Pb element, $\times 200$; MGUH 17.844.

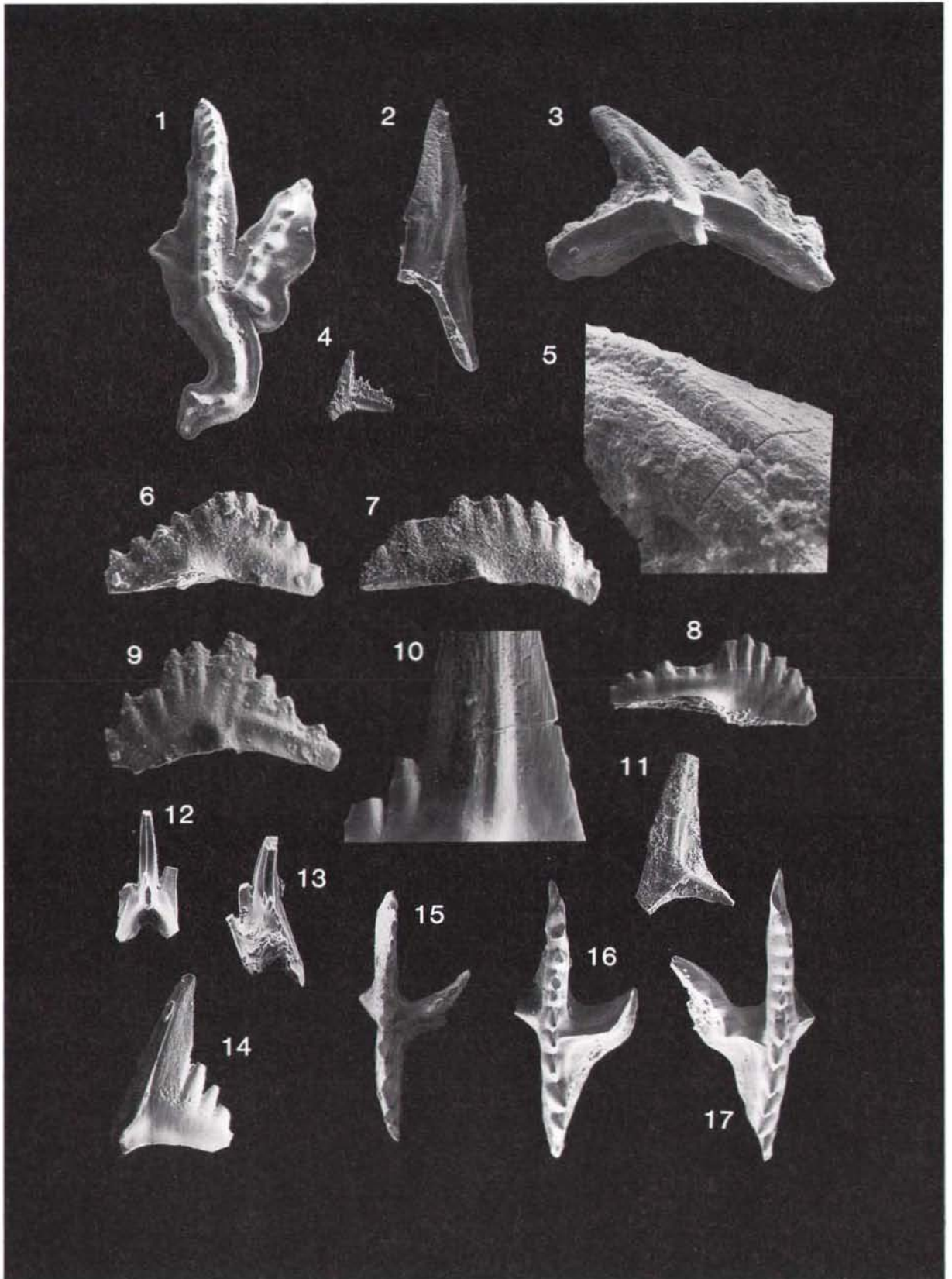
Figs 6–14. *Pterospathodus celloni* (Walliser). All specimens $\times 60$ unless otherwise stated.

- 6, inner-lateral view of Pa element; MGUH 17.846 from GGU 228975.
- 7, inner-lateral view of Pa element, MGUH 17.847 from GGU 184125.
- 8, inner-lateral view of Pa element; MGUH 17.848 from GGU 229037.
- 9, inner-lateral view of Pb element; MGUH 17.849 from GGU 228975.

- 10, microstriations on the inner-lateral face of the cusp of M element, $\times 200$; MGUH 17.850 from GGU 184125.
- 11, inner-lateral view of M element; MGUH 17.851 from GGU 184125.
- 12, posterior view of ?Sa element; MGUH 17.852 from GGU 229037.
- 13, posterior view of ?Sb element; MGUH 17.853 from GGU 229037.
- 14, inner-lateral view of Sc element; MGUH 17.854 from GGU 229037.

Figs 15–17. *Pterospathodus pennatus pennatus* (Walliser). All specimens $\times 60$.

- 15, upper view of Pa element; MGUH 17.855 from GGU 228970.
- 16, upper view of Pa element; MGUH 17.856 from GGU 216821.
- 17, upper view of Pa element; MGUH 17.857 from GGU 216821.



Pterospathodus celloni (Walliser, 1964)

Plate 19, figs 6-14

- 1962 *Spathognathodus* n. sp. b Walliser, p. 282, fig. 1, no. 9.
- 1962 *Ozarkodina* n. sp. a Walliser, p. 282, fig. 1, no. 7.
- v1964 *Spathognathodus celloni* Walliser, pp. 73-74, pl. 4, fig. 13; pl. 14, figs 3-16; Text figs 1b, 7b-f.
- v1964 *Ozarkodina adiutricis* Walliser, p. 54, pl. 4, fig. 14; pl. 27, figs 1-10; Text figs 1a, 7h-m.
- v1964 *Neoprioniodus triangularis tenuirameus* Walliser, p. 53, pl. 4, fig. 15; pl. 28, figs 21-24; Text figs 6a-c.
- ?v1964 *Roundya breviaulata* Walliser, p. 69, pl. 4, fig. 16; pl. 31, fig. 8-10.
- v1964 *Neoprioniodus costatus paucidentatus* Walliser, p. 48, pl. 4, fig. 23; pl. 28, figs 31-35; Text figs 6i-k.
- 1968 *Spathognathodus celloni*; Igo & Koike, pl. 18, pl. 2, figs 1-4.
- 1968 *Ozarkodina gaertneri*; Igo & Koike, p. 14, pl. 1, figs 5-9.
- 1968 *Neoprioniodus triangularis tenuirameus*; Igo & Koike, p. 13, pl. 3, figs 18-19.
- p1968 *Multioistodus* sp. Igo & Koike, p. 12, pl. 2, figs 16, 17, 19; non fig. 18.
- p1968 *Neoprioniodus costatus paucidentatus*; Igo & Koike, p. 12, pl. 3, fig. 16; non fig. 17.
- v1969 *Neospathognathodus celloni*; Nicoll & Rexroad, p. 45, pl. 2, figs 1-4.
- v1969 *Ozarkodina adiutricis*; Nicoll & Rexroad, p. 48, pl. 2, fig. 8.
- 1970 *Spathognathodus celloni*; Moskalenko, p. 18, pl. 2, fig. 3, 4.
- 1970 *Ozarkodina adiutricis*; Moskalenko, p. 14, pl. 2, fig. 1.
- 1971 *Spathognathodus celloni*; Schönlaub, p. 44, pl. 2, fig. 1-5.
- 1972 *Neospathognathodus celloni*; Rexroad & Nicoll, pl. 1, figs 2-4.
- 1972 *Ozarkodina adiutricis*; Rexroad & Nicoll, pl. 1, fig. 5.
- 1972 *Spathognathodus celloni*; Rexroad & Nicoll, p. 68, pl. 1, figs 17-19.
- 1972 *Ozarkodina adiutricis*; Rexroad & Nicoll, pl. 1, figs 15, 16.
- v1972 *Neospathognathodus celloni*; Aldridge, p. 197, pl. 3, figs 9-12.
- v1972 *Ozarkodina adiutricis*; Aldridge, p. 198, pl. 5, figs 2, 3.
- ?vp1972 *Exochognathus breviaulatus*; Aldridge, p. 177, pl. 7, fig. 8; non fig. 9.
- v1972 *Neoprioniodus costatus paucidentatus*; Aldridge, p. 193, pl. 5, figs 20-21.
- 1975 *Pterospathodus celloni*; Klapper & Murphy, p. 27, pl. 2, figs 2, 3.
- 1975b *Llandoverynathus celloni*; Schönlaub, p. 53, pl. 1, figs 18, 19.
- v1975 *Llandoverynathus celloni*; Aldridge, pl. 1, figs 20, 21.
- 1976 *Pterospathodus celloni*; Barrick & Klapper, p. 82, pl. 1, figs 3, 5.
- 1977 *Spathognathodus celloni*; Liebe & Rexroad, pl. 1, fig. 12.
- 1977 *Ozarkodina adiutricis*; Liebe & Rexroad, pl. 1, fig. 10.
- 1978 Apparatus 'B'; Miller, pl. 4, figs 1-4.
- 1978 *Exochognathus breviaulatus*; Miller, pl. 3, figs 7, 9.
- 1978 *Neoprioniodus costatus paucidentatus*; Miller, pl. 2, fig. 12.
- 1978 *Neospathognathodus celloni*; Pickett, pl. 1, fig. 26.
- 1978 *Ozarkodina adiutricis*; Pickett, pl. 1, fig. 17.
- v1979 *Llandoverynathus celloni*; Aldridge, pl. 1, figs 9, 10.
- ?v1979 *Llandoverynathus* sp. Aldridge, pl. 1, figs 12-15.
- 1980 *Pterospathodus celloni*; Helfrich, pl. 2, fig. 30.
- 1981 *Pterospathodus celloni*; Uyeno & Barnes, pl. 1, figs 20, 21.
- 1982 *Pterospathodus celloni*; Aldridge & Mohamed, pl. 2, fig. 7.
- 1983 *Pterospathodus celloni*; Uyeno & Barnes, p. 24, pl. 5, figs 17, 18, 20-24.
- v1985 *Pterospathodus celloni*; Aldridge, p. 80, pl. 3.1, figs 25, 26.
- 1986 *Pterospathodus celloni*; Bischoff, pl. 28, figs 34-39; pl. 29, figs 1-8.

Holotype. *Spathognathodus celloni* Walliser (1964), pl. 14, fig. 5. Specimen number Wa740/11 from sample 10J in the Cellon Mountains, Carnic Alps, Austria.

Diagnosis. Refer to Barrick & Klapper (1976, p. 83).

Description. *Pa element*. Refer to the description of *Neospathognathodus celloni* Walliser in Aldridge (1972, p. 197). Greenland specimens of the *Pa element* fall into the range of morphologies of *Spathognathodus celloni* illustrated by Walliser (1964).

Pb element. Refer to the description of *Ozarkodina adiutricis* Walliser in Aldridge (1972, p. 198).

M element. This element has been previously illustrated as *Neoprioniodus triangularis tenuirameus* and described fully by Aldridge (1972, p. 173).

Sa element. Small, modified alate element with denticulate antero-lateral processes and a short posterior process. The cusp is tall and posteriorly curved; its anterior face is broadly convex, its antero-lateral edges bear tall costae, and its posterior edge is sharp. The lateral processes are deep and form an angle of approximately 75° between lower edges; each process commonly bears a single, rarely two, tall, compressed denticles. The denticles are discrete when two are present. The posterior process is short and slightly inclined downwards, it bears up to three squat, partially fused, compressed denticles. The entire lower surface of the element is deeply excavated, the basal cavity extending as a tapering groove to the tips of the processes. Fine microstriations are situated on the postero-lateral faces of the cusp, the posterior faces of the antero-lateral processes, on the upper portion of the posterior process and lower half of the posterior denticles.

Sb element. Tertiopedate element, identical to the *Sa* except for the absence of the denticles on the inner-lateral process. The inner antero-lateral costa extends down the cusp to the tip of the inner-lateral process.

Sc element. Refer to the description on *Neoprioniodus costatus paucidentatus* Walliser by Aldridge (1972, p. 193). The angle of divergence of the outer lateral process of the Greenland specimens shows slight variation between 120° and 140° from the posterior process.

Remarks. Jeppsson (1979a, p. 236) and Mabillard & Aldridge (1983) suggested the inclusion of *Exochognathus brevialetus* (Walliser) as a possible Sa-Sb element. Similar specimens occur rarely in Greenland along with *P. celloni* and are questionably included in its apparatus as the Sa and Sb elements. The ancestry of *P. celloni* is currently obscure. Bischoff (1986, p. 195) emended the diagnosis of *P. celloni* based upon his reconstruction of *P. cadiaensis*. R. J. Aldridge (Nottingham, personal communication) is currently reviewing *Pterospathodus* and the old diagnosis for *P. celloni* is retained herein.

Occurrence. Found throughout North Greenland, elsewhere this species is the index species of the *P. celloni* Biozone, and is restricted to lower Telychian strata in Europe and North America.

Pterospathodus pennatus Walliser, 1964

Emended diagnosis. Five members of the apparatus are known: Pa, Pb, M, Sa and Sc. Species distinguished by the blade-like stelliscaphate or stelliplanate Pa element which develops a straight to markedly flexed, denticulate, anteriorly directed, outer-lateral process and a short offset adenticulate inner lobe.

Remarks. Walliser (1964) proposed three subspecies based on differences in the morphology of the outer process of the Pa element. These characters appear to vary within a single population (Walliser, 1964; Nicoll & Rexroad, 1969). Jeppsson (1979b) concluded that a full taxonomic revision of *Pterospathodus* was required.

Pterospathodus pennatus pennatus Walliser, 1964

Plate 19, figs 15–17; plate 20, figs 1–5

- v1964 *Spathognathodus pennatus pennatus* Walliser, p. 79, pl. 14, figs 23–26; pl. 15, fig. 1, text fig. 1d.
- pv1964 *Spathognathodus pennatus angulatus* Walliser, p. 79, pl. 14, figs 19, 22; non fig. 21.
- v*1964 *Spathognathodus pennatus pennatus* Walliser, p. 79, pl. 14, figs 23–26; pl. 15, fig. 1; text fig. 1d.
- v1969 *Neospathognathodus pennatus*; Nicoll & Rexroad, p. 47, pl. 2, fig. 5.
- v1972 *Neospathognathodus pennatus*; Aldridge, p. 197, pl. 3, figs 13, ?16.

- v1975 *Llandoverynathus pennatus*; Aldridge, pl. 1, figs 24, 25.
- 1975 *Pterospathodus pennatus angulatus*; Klapper & Murphy, p. 28, pl. 2, figs 5, 6.
- 1978 *Pterospathodus pennatus*; Miller, pl. 4, figs 12, 13.
- 1978 *Neospathognathus pennatus*; Pickett, pl. 1, fig. 24.
- v1979 *Llandoverynathus pennatus*; Aldridge, pl. 1, fig. 11.
- ?1981 *Pterospathodus pennatus*; Nowlan, pl. 7, fig. 1.
- ?1983 *Pterospathodus pennatus*; Nowlan, fig. 4S.

Holotype. *Spathognathodus pennatus pennatus* Walliser 1964, p. 79, pl. 14, fig. 26; specimen number Wa 740/22, from sample 10J, in the *P. celloni* Biozone of Cellon Mountain, Carnic Alps, Austria.

Emended diagnosis. Subspecies of *P. pennatus* with Pa element that develops a narrow single-branched, straight to slightly flared inner process.

Description. Refer to the description of *Neospathognathodus pennatus* by Aldridge (1972, p. 197).

Pb, M, Sa, and Sc elements. Samples containing only *P. pennatus pennatus* are not present in Greenland. Samples containing *P. pennatus pennatus* and *P. pennatus rhodesi*, however, allow the separation of the constituent elements. The latter has elements indistinguishable from those of *P. amorphognathoides*. The former has elements virtually indistinguishable from those in *P. celloni*. The Pb element of the *P. pennatus pennatus* has a slightly shorter anterior process than its counterpart in *P. celloni*, in other respects it is indistinguishable. The M element may be slightly more inwardly curved.

Sa element. The posterior edge of the cusp is flattened and passes downwards into a short adenticulate posterior process. Each lateral process bears only a short, single denticle or as in the figured example (plate 20, fig. 3) is adenticulate, the upper edge being broadly rounded.

Sc element. Dolabrate and laterally compressed, the cusp is tall, its inner face flat to shallowly concave, its outer face is broadly concave and towards its base has a short low costa projection, a weak trace of this may pass up the cusp. The outer face of the cusp bears vertical microstriations. The cusp is extended downwards into a short antiscusp which is occasionally slightly posteriorly recurved. A slightly inwardly bowed posterior process bears two or three tall, compressed denticles which are fused almost to their tips, these decrease in height gradually towards the posterior; the two proximal denticles are only slightly shorter than the cusp. The basal cavity is narrow and deeply excavated beneath the cusp, extending as a groove to the tip of the antiscusp; the cavity terminates before the tip of the posterior process.

Remarks. The holotypes of *S. pennatus angulatus* Walliser (1964, p. 79, pl. 14, fig. 22) and *S. pennatus pennatus* Walliser (1964, p. 79, pl. 14, fig. 26) differ only in the degree of basal cavity flare beneath the posterior of the inner process. This feature is seen to intergrade in specimens from Greenland, Gullet 4 (Aldridge, 1972) and Cellon (compare Walliser, 1964, pl. 14, fig. 26 and pl. 15, fig. 1). Walliser (1964, p. 79, pl. 14, fig. 24) illustrated a specimen of *S. pennatus angulatus* with a rudimentary denticle posteriorly offset at the flexure of the outer process. This specimen occurs in sample C.10B within the lower *Pterospathodus celloni* Biozone and cannot therefore be a juvenile of *P. amorphognathoides*. Specimens with a pronounced flexure of the outer process referred to *P. pennatus angulatus* (e.g. Aldridge & Mohamed, 1982, pl. 2, figs 8–11) should be assigned to a new subspecies.

The holotype of *P. pennatus procerus* Walliser (1964, p. 80, pl. 15, fig. 5) is also similar to that of *P. pennatus pennatus*. It has, however, a straighter outer process and narrow basal cavity beneath the posterior process, characters seen to be consistent in the paratypes (Walliser, 1964, pl. 15, figs 7, 8). Jeppsson (1979b, p. 235, pl. 71, figs 1–8) reconstructed the apparatus of this subspecies and included ramiform elements with morphology close to that in *Carniodus carnulus*. The apparatus structures of the other *P. pennatus* subspecies would not be consistent with this interpretation which is based on very low numbers of specimens. The *P. pennatus pennatus* 'plexus' appears to have evolved from *P. celloni* by the modification of the outer process (Walliser, 1964, p. 16, fig. 1).

Occurrence. *P. pennatus pennatus* occurs abundantly in the *Pterospathodus celloni* Biozone and rarely in *P. amorphognathoides* Biozone samples.

Pterospathodus pennatus rhodesi (Savage, 1985)
Plate 20, figs 6–16

- 1966 *Spathognathodus pennatus procerus*; Spasov & Filipović, p. 50, pl. 1, fig. 6.
1985 *Pterospathodus* n. sp. A; Stouge & Stouge, p. 109–110, pl. 1, figs 1–6.
1987 *Pterospathodus pennatus rhodesi*; Over & Chatterton, p. 20–21, pl. 4, figs 5, 6.

Holotype. Specimen USNM 371651 p. 714, figs 3A, B from bed 18, Heceta Limestone, Cap Island, south-eastern Alaska.

Diagnosis. Refer to Savage (1985, p. 714).

Description. *Pa element.* Stelliplanate, straight to posteriorly bowed and downturned carina; with two offset lateral processes situated close to the midlength. The carina bears up to twenty fused, nodose denticles, those to the anterior of the lateral processes are tall and more laterally compressed than those to the posterior. The entire element is surrounded by a narrow ledge-like platform. The outer process is long and anteriorly directed, diverging at an angle of 10°–45° from the carina; bears a central row of eight to ten nodose fused denticles which decrease in size distally; it is up to half the length of the carina. An inner process is anteriorly offset and marked by an anteriorly directed expansion

Plate 20

Figs 1–5. *Pterospathodus pennatus pennatus* (Walliser). All specimens from GGU 228970, × 60.

- 1, inner-lateral view of Pa element; MGUH 17.858.
- 2, inner-lateral view of Pb element; MGUH 17.859.
- 3, posterior view of Sa element; MGUH 17.860.
- 4, inner-lateral view of M element; MGUH 17.861.
- 5, inner-lateral view of Sc element; MGUH 17.862.

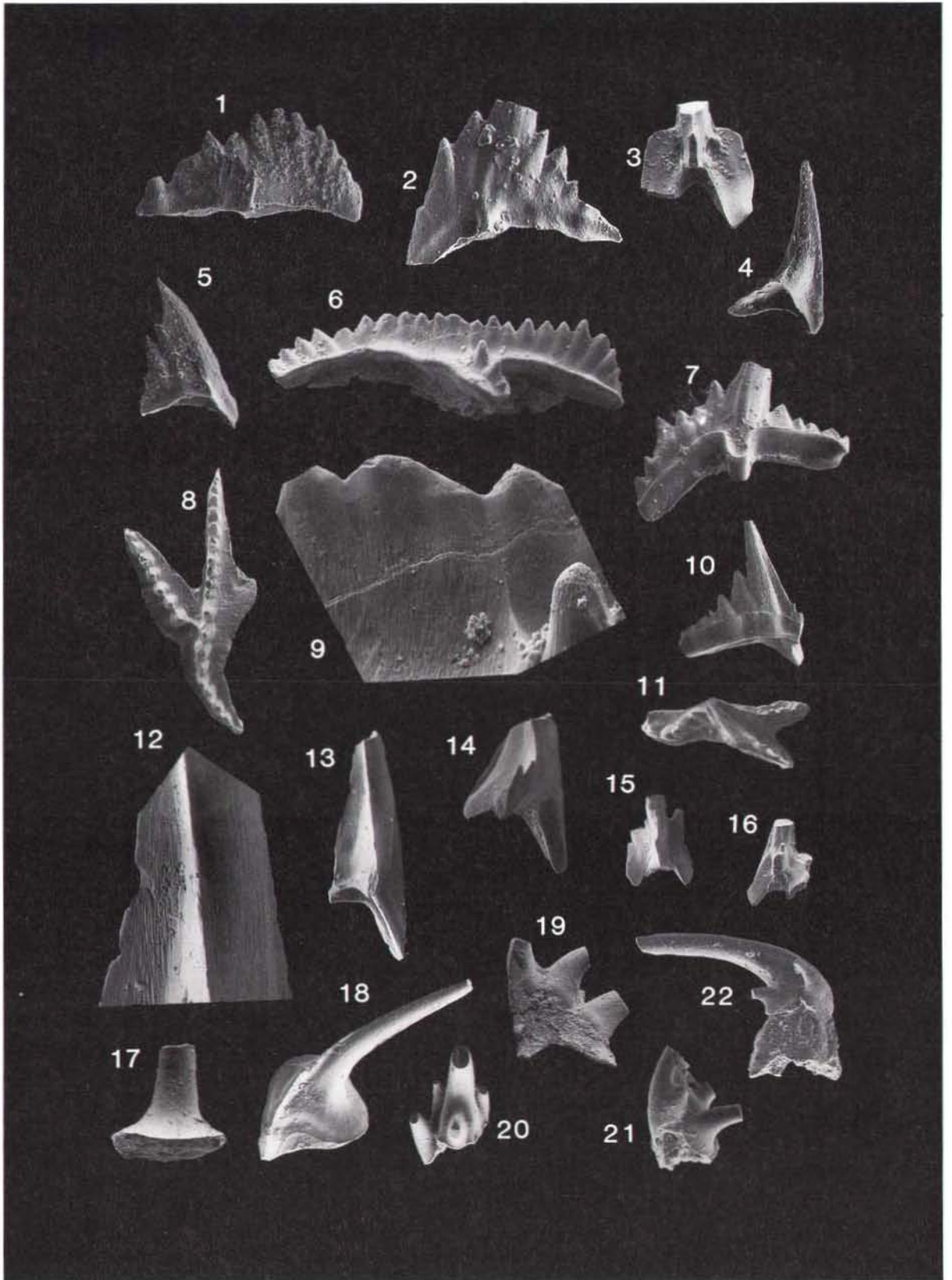
Figs 6–16. *Pterospathodus pennatus rhodesi* (Savage). All specimens from GGU 82637 unless otherwise stated.

- 6, lateral view of Pa element, × 20; MGUH 17.863 from GGU 275048.
- 7, inner-lateral view of Pb element, × 40; MGUH 17.864 from GGU 275048.
- 8, upper view of Pa element, × 20; MGUH 17.865 (holotype) from GGU 275049.
- 9, microstriations on the carina of Pa element, × 170; MGUH 17.863 from GGU 275048.
- 10, inner-lateral view of Sc element, × 60; MGUH 17.867.
- 11, upper view of Sc element, × 60; MGUH 17.868.

- 12, microstriations on the cusp of M element, × 120; MGUH 17.869.
- 13, inner-lateral view of M element, × 60; MGUH 17.869.
- 14, posterior view of M element, × 60; MGUH 17.870.
- 15, posterior view of ?Sa element, × 60; MGUH 17.871.
- 16, posterior view of ?Sb element, × 60; MGUH 17.872.

Figs 17–22. *Dentacodina* aff. *D. dubia* (Rhodes).

- 17, inner-lateral view of Pa element, × 100; MGUH 17.873 from GGU 216873.
- 18, oblique upper view of Pb element, × 60; MGUH 17.874 from GGU 216853.
- 19, inner-lateral view of M element, × 60; MGUH 17.875 from GGU 216873.
- 20, posterior view of Sa element, × 60; MGUH 17.876 from GGU 216853.
- 21, inner-lateral view of Sb element, × 60; MGUH 17.877 from GGU 216853.
- 22, inner-lateral view of Sc element, × 60; MGUH 17.878 from GGU 216873.



of the platform ledge and a shallow depression which crosses the platform obliquely towards the carina. In lateral view the platform runs at approximately the mid-height of the carina, beneath it the element narrows. The basal cavity is shallow, slightly expanded beneath the junction of the processes, extending to the tips of the carina and processes as a narrow tapering groove.

Pb, M and Sc elements. These elements are inseparable from their counterparts in the apparatus of *P. amorphognathoides*.

?Sa element. Alate with tall, costate cusp, the costae run laterally and posteriorly, downwards into the processes. The lateral processes are compressed, deep and usually bear a single or rarely two denticles. These are shorter than the equivalent denticles in the *P. celloni* Sa element. The posterior process rarely has short, peg-like denticles preserved. The basal cavity is deeply excavated beneath the cusp, extending almost to the tips of the processes.

?Sb element. Lacks the denticulate outer lateral process of the Sa element; but in all other respects is identical.

Remarks. Sample GGU 275048 from Valdemar Glückstadt Land (fig. 4) contains 27 *P. amorphognathoides* Pa elements and 323 *P. pennatus rhodesi* Pa elements; the twenty Pb, one ?Sa, one ?Sb and one Sc element are more likely derived from an apparatus of the latter.

Occurrence. Found in samples of uppermost *Pterospathodus celloni* – *P. amorphognathoides* Biozone age from Hall Land, Valdemar Glückstadt Land and Kronprins Christian Land.

Genus *Walliserodus* Serpagli, 1967

Type Species. *Acodus curvatus* Branson & Branson, 1947, by subsequent designation of Cooper (1975, p. 995).

Diagnosis. Refer to Cooper (1975, p. 995).

Remarks. Midheight cross sections for homologous *Walliserodus* elements are illustrated in fig. 34.

Walliserodus bicostatus (Branson & Mehl, 1933a) Plate 21, figs 1–5

- *1933a *Acodus bicostatus* Branson & Mehl, p. 42, pl. 3, fig. 1.
- 1971 *Acodus biostatus*; Rexroad & Craig, p. 686, pl. 82, fig. 17.
- 1971 *Acodus curvatus*; Rexroad & Craig, p. 686, pl. 82, fig. 17.

Holotype. *Acodus biostatus* Branson & Mehl, 1933a, p. 42, pl. 3, fig. 1.

Diagnosis. Apparatus quinquemembrate containing tall, laterally costate sym. p and ap elements and recurved, laterally acostate aq, sq and r elements. This species is distinguished by the sym. p and aq elements which possess double lower-lateral costae.

Description. *sym. p element.* Laterally compressed, bilaterally symmetrical, broad based cone; base and cusp are subequal in length, the cusp is shallowly proclined. The upper margin is sharp, lacking a prominent keel

Plate 21

Figs 1–5. *Walliserodus bicostatus* (Branson & Mehl). All specimens from GGU 216845, × 60.

- 1, lateral view of sym. p element; MGUH 17.963.
- 2, lateral view of ap element; MGUH 17.964.
- 3, lateral view of sq element; MGUH 17.965.
- 4, inner lateral view of aq element; MGUH 17.966.
- 5, inner lateral view of r element; MGUH 17.967.

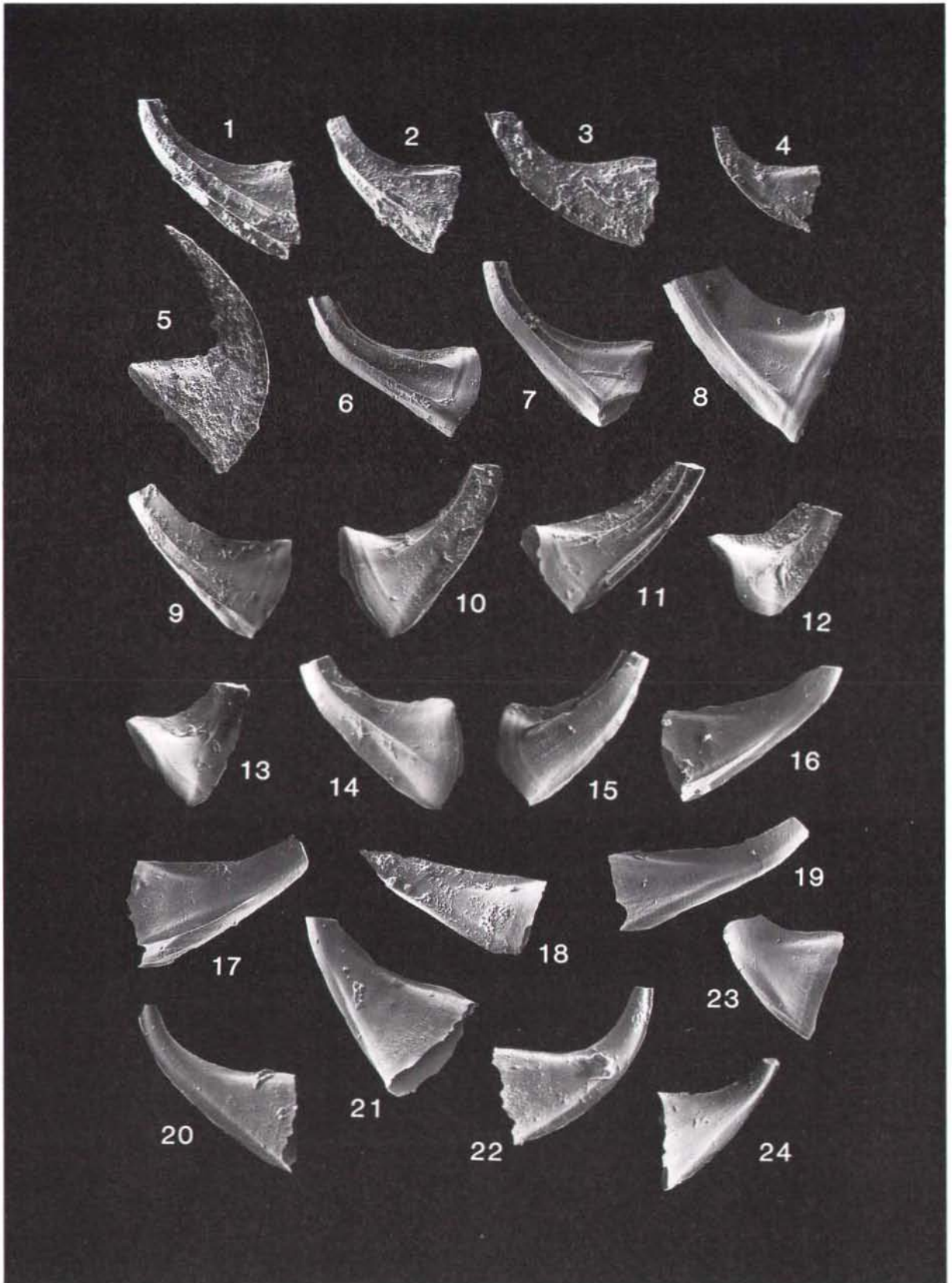
Figs 6–15. *Walliserodus curvatus* (Branson & Branson). All specimens from GGU 216842, × 60.

- 6, inner lateral view of sym. p element; MGUH 17.968.
- 7, outer lateral view of sym. p element; MGUH 17.969.
- 8, inner lateral view of ap element; MGUH 17.970.
- 9, outer lateral view of aq element; MGUH 17.971.
- 10, inner lateral view of unicostate aq element; MGUH 17.972.
- 11, inner lateral view of multicostate aq element; MGUH 17.973.

- 12, inner lateral view of costate r element; MGUH 17.974.
- 13, inner lateral view of costate r element; MGUH 17.975.
- 14, inner lateral view of sq element; MGUH 17.976.
- 15, outer lateral view of sq element; MGUH 17.977.

Figs 16–24. *Walliserodus* cf. *W. sancticlairei* Cooper. All specimens from GGU 216852, × 60.

- 16, lateral view of sym. p element; MGUH 17.978.
- 17, lateral view of sym. p element; MGUH 17.979.
- 18, outer lateral view of ap element; MGUH 17.980.
- 19, inner lateral view of ap element; MGUH 17.981.
- 20, inner lateral view of aq element; MGUH 17.982.
- 21, outer lateral view of aq element; MGUH 17.983.
- 22, lateral view of sq element; MGUH 17.984.
- 23, outer lateral view of r element; MGUH 17.985.
- 24, inner lateral view of r element; MGUH 17.986.



and is more strongly curved than the lower margin. The lower margin is concave laterally and extended on either side by symmetrically disposed double costae; these converge upwards, but remain distinct to the tip of the cusp; a narrow, v-shaped groove separates them. Above the costae the lateral faces are shallowly concave to the upper margin. The basal margin is more or less straight, the basal surface completely excavated. The basal cavity is tall terminating at the base of the cusp close to the lower margin, white matter in all elements in this apparatus is concentrated above the basal cavity, the lateral costae are all filled with white matter.

ap element. Morphologically transitional from the sym. p element, almost identical in lateral outline. The inner face has double, lower costae situated closer to the midline which originate at a point just above the basal margin. When viewed from the inner side the upper margin appears weakly keeled with an additional short costa extending to midheight from the upper basal corner. Outwardly the face posterior of the costae is shallowly concave to the upper margin.

aq element. Slightly more recurved than the p elements. Upper and lower margins are sharp and bear low keels. The lower keel is directed slightly laterally. The cusp may be twisted in the same direction as this costa. Basally the element is laterally inflated; larger specimens may develop shallow longitudinal lateral faces; the cusp is compressed. This element lacks costae on the lateral faces, which allows its distinction from its counterpart in the *W. curvatus* apparatus.

sq element. Similar curvature to the aq element, laterally compressed and bilaterally symmetrical. Both upper and lower margins are sharp and bear keels, but these are not as prominent as those in other species of *Walliserodus*. The lateral faces are shallowly convex and lack lateral costae. The basal margin is straight, the entire basal surface excavated.

r element. Strongly recurved, shorter version of the aq element. Its base is shorter than the cusp and triangular cross section, the upper edge is straight, the lower edge gently, apically curved. The strongly, laterally compressed cusp is strongly recurved from its base and twisted inwardly. The lower margin bears a keel which is directed in the same plane as the cusp. The basal surface is entirely excavated.

Remarks. The q and r elements of *W. bicostatus* are similar to those of *W. cf. W. sancticlairei*, but can be distinguished by their broader bases and cusps and lower keels which are less prominent; the r element is much more strongly recurved.

Rexroad & Craig (1971) noted the rare occurrence of the sym. p element in the samples of Branson & Mehl

(1933a). The specimens of *P. multicostatus* (Rexroad & Craig, 1971, pl. 82, figs 20a, 20b) are fragmented, but show affinity to this group of elements. No multicostate aq element is recorded from Greenland, and until this specimen can be studied it is not included in the synonymy.

Occurrence. Found only in GGU 216845 and 242911 (figs 16, 21).

Walliserodus curvatus (Branson & Branson, 1947)

Plate 21, figs 6–15

- v1947 *Acodus unicostatus* Branson & Branson, p. 554, pl. 82, figs 9, 10, 41, 43.
- vp1947 *Paltodus acostatus* Branson & Branson, p. 554, pl. 82, figs 23, 24; non figs 1–5.
- v1947 *Acodus curvatus* Branson & Branson, p. 554, pl. 81, fig. 20.
- vp1947 *Paltodus unicostatus*; Branson & Branson, p. 554, pl. 82, figs 11–16; non figs 6–10, 17–22.
- ?1964 *Acodus cf. mutatus*; Serpagali & Greco, p. 196, pl. 34, figs 2a,b.
- v1967 *Acodus unicostatus*; Rexroad, p. 26, pl. 4, figs 13–16.
- v1967 *Acodus curvatus*; Rexroad, p. 25, pl. 4, figs 9–12.
- v1967 *Paltodus debolti* Rexroad, p. 41, pl. 4, figs 22–25.
- v1967 *Paltodus dyscritus* Rexroad, p. 42, pl. 4, figs 30–34.
- v1967 *Paltodus migratus* Rexroad, p. 44, pl. 4, figs 17–21.
- v1969 *Acodus unicostatus*; Nicoll & Rexroad, p. 23, pl. 7, figs 34–36.
- v1969 *Acodus curvatus*; Nicoll & Rexroad, p. 23, pl. 7, figs 19, 20.
- v1969 *Paltodus debolti*; Nicoll & Rexroad, p. 52, pl. 7, fig. 26.
- v1969 *Paltodus dyscritus*; Nicoll & Rexroad, p. 52, pl. 7, fig. 26.
- v1969 *Paltodus migratus*; Nicoll & Rexroad, p. 52, pl. 7, fig. 27.
- 1970 *Acodus unicostatus*; Pollock, Rexroad & Nicoll, p. 749, pl. 114, figs 36–37.
- 1970 *Acodus curvatus*; Pollock, Rexroad & Nicoll, p. 749, pl. 114, fig. 35.
- 1970 *Paltodus debolti*; Pollock, Rexroad & Nicoll, p. 758, pl. 114, figs 32, 33.
- 1970 *Paltodus dyscritus*; Pollock, Rexroad & Nicoll, p. 758, pl. 114, fig. 31.
- v1972 *Acodus unicostatus*; Aldridge, p. 162, pl. 9, figs 2, 3.
- v1972 *Acodus curvatus*; Aldridge, p. 162, pl. 9, fig. 1.
- v1972 *Paltodus debolti*; Aldridge, p. 202, pl. 9, fig. 18.
- v1972 *Paltodus dyscritus*; Aldridge, p. 203, pl. 9, fig. 19.
- v1972 *Paltodus migratus*; Aldridge, p. 203, pl. 9, fig. 20.
- 1972 *Acodus unicostatus*; Rexroad & Nicoll, pl. 1, figs 48, 49.
- 1972 *Paltodus dyscritus*; Rexroad & Nicoll, pl. 2, fig. 35.
- 1972 *Acodus? curvatus*; Miller, p. 558, pl. 1, figs 1, 2.
- 1972 *Paltodus trigonus*; Miller, p. 562, pl. 1, figs 18–20.

- 1972 *Paltodus debolti*; Miller, p. 562, pl. 1, figs 15–17.
 1974c *Paltodus debolti*; Drygant, pl. 2, fig. 1.
 1974c *Acodus unicosatus*; Drygant, pl. 2, fig. 2.
 1974c *Paltodus dyscritus*; Drygant, pl. 1, fig. 34.
 1975 *Walliserodus curvatus*; Cooper, p. 995, pl. 1, figs 10, 11, 16–21.
 1975 *Paltodus dyscritus*; Thompson & Satterfield, fig. 5D.
 1977 *Acodus unicosatus*; Liebe & Rexroad, pl. 2, figs 20, 21.
 1977 *Acodus curvatus*; Liebe & Rexroad, pl. 2, figs 14, 15.
 1977 *Paltodus dyscritus*; Liebe & Rexroad, pl. 2, fig. 1.
 1977 *Paltodus debolti*; Liebe & Rexroad, pl. 2, figs 2, 3.
 1977 *Paltodus multicosatus*; Liebe & Rexroad, pl. 2, fig. 4.
 ?1977 *Paltodus fragilis*; Liebe & Rexroad, pl. 2, figs 5, 6.
 ?1977 *Paltodus* sp. A Liebe & Rexroad, pl. 2, fig. 7.
 ?1977 *Paltodus* sp. B Liebe & Rexroad, pl. 2, figs 5, 8, 9.
 1978 *Walliserodus curvatus*; Rexroad, Noland & Pollock, pl. 12, pl. 1, figs 1–5.
 1978 *Walliserodus curvatus*; Miller, p. 341, pl. 1, figs 10–17.
 1981 *Walliserodus curvatus*; McCracken & Barnes, pl. 2, figs 2, 4.

Holotype. *Acodus curvatus* Branson & Branson, 1947, p. 554; from loc. 1923, the lower Silurian Brassfield Formation of Kentucky.

Emended diagnosis. Five elements known with short cusps and long broad bases. The sym. p and ap elements bear single laterally directed keel-like lower costae, the aq, sq and r elements are more markedly recurved and have keeled lower margins. The aq element bears between one and three longitudinal costae on the inner face.

Description. *sym. p element*. Refer to the description of *Paltodus dyscritus* Rexroad in Aldridge (1972, p. 203). Basal cavity outline is illustrated in fig. 34; white matter is concentrated above the basal cavity apex, extending basally along the lateral costae in large specimens.

ap element. Refer to the description of *Acodus unicosatus* Branson & Branson in Aldridge (1972, p. 162). Maybe morphologically transitional from the sym. p element, intermediates occur only infrequently in large collections.

Unicostate – aq element. Refer to the description of *Paltodus debolti sensu* Rexroad in Aldridge (1972, p. 202). The more common of the two aq elements differs from the p elements in being more steeply and gradually apically curved and lacks costae on the outer side.

A rare multicostate morphotype occurs in which three additional costae are developed on the inner face. The most prominent of these is situated close to the

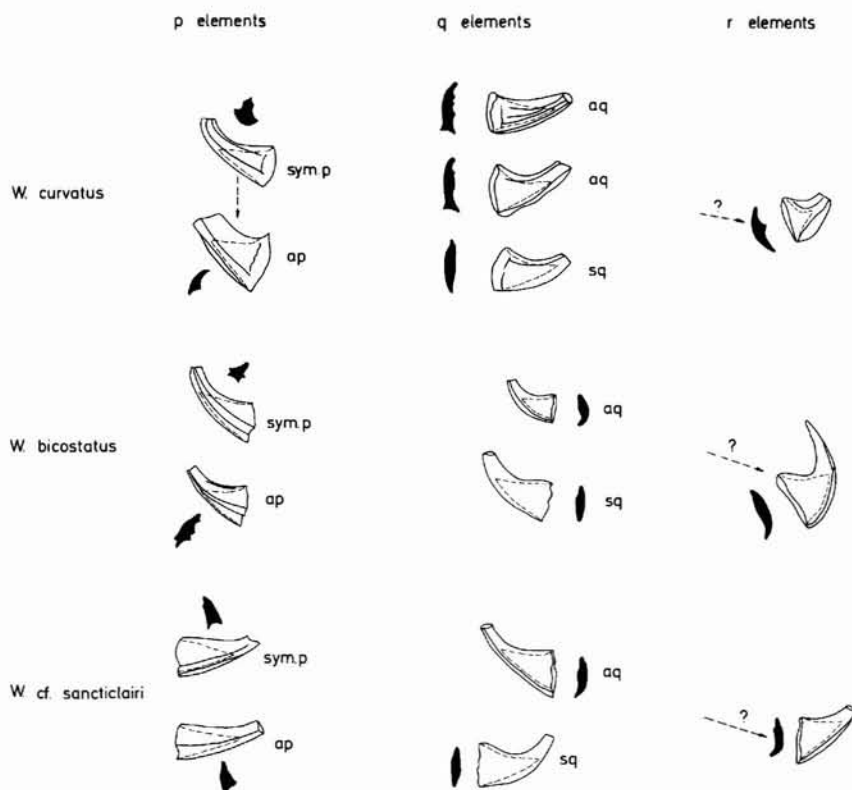


Fig. 34. Species of *Walliserodus* illustrating the distribution of costae, outline of basal cavity and cross-section at midheight. Camera lucida drawings. MGUH numbers, p elements (from top to bottom) 17.968, 17.970, 17.963, 17.964, 17.978, 17.981; q elements (top to bottom) 17.973, 17.972, 17.975, 17.966, 17.965, 17.982, 17.984; r elements (top to bottom) 17.977, 17.967, 17.986.

upper margin extending from the basal ridge to the apex. Below this lie less prominent shorter costae.

sq element. Refer to the description of *Acodus curvatus sensu* Branson & Branson in Aldridge (1972, p. 162). The outer face is similar to that of the *aq* element in that it bears a single prominent costa close to its lower edge. In the *sq* element this costa is closer to the midline; the face is shallowly convex below and above this costa.

r element. Morphologically transitional from the *aq* element, it is much shorter, apically bowed and more strongly recurved. The base and cusp are subequal in length; the former is inflated and upwardly tapering, the latter is broad and laterally compressed. The lower and upper margins are extended by broad keels, the lower is directed slightly inwardly and is broader at its base than the upper keel. Above the base the inner face of the cusp may be raised centrally and rarely possesses a low, inconspicuous costa (plate 21, fig. 12). The outer face is shallowly convex, slightly raised towards the lower margin. As in the other elements the base is entirely excavated.

Remarks. Cooper (1975, p. 996) reconstructed the apparatus of *W. curvatus*, and like Barrick (1977) suggested a continuous symmetry between the elements in the *Walliserodus* apparatus, applying the M and S element terminology of Sweet & Schönlaub (1975). In the collections from Greenland, several separate transitions appear to be present: firstly, the *sym. p-ap* transition though this is not as well developed in this apparatus as in the apparatuses of *W. biostatus* and *W. cf. W. sancticlairei*; secondly the *sym. p-aq-r* transition, displayed through recurvature, increased apical bowing and twisting of the cusp and reduction of the inner, lower-lateral costa. In this respect the *q* elements retain both lower-lateral costae, whereas the *ap* element loses one. The *sq* element is not involved in these transitions, though it does show similar curvature to the *aq* elements. The multicostate *aq* specimens may be of a separate element, or an extreme development of the *aq* element.

Walliserodus debolti Serpagli (1967) contains elements similar to those of *W. curvatus*. These were noted by Cooper (1975, p. 996) to be extremely diverse and not exactly like those of *W. curvatus*. It is likely that *W. debolti* is the ancestor of *W. curvatus*.

Occurrence. Particularly common in the pre-*Pterospodus celloni* Biozone strata of Washington Land. Outside Greenland Cooper (1975, p. 996) documents its range through the lower Silurian of Europe and North America.

Walliserodus cf. W. sancticlairei Cooper, 1976
Plate 21, figs 16-24

cf. 1976 *Walliserodus sancticlairei* Cooper, p. 215, pl. 1, figs 8-11, 16-21.

Description. sym. p element. Slender, suberect element with a long, laterally inflated base or shorter, shallowly proclined cusp. The upper margin of the base is more or less straight with a low keel along its length; the edge of the cusp is sharp. The lower margin is rounded and terminates laterally as two symmetrically disposed, lower-lateral costae. These are directed downwards and are keel-like, both extending from the basal corners and terminating at the base of the cusp. They diverge apically. The anterior edge of the cusp is sharp. Above the costae, the base is inflated slightly, with the lateral faces inclined towards the lower edge. The cusp is lenticular in cross section and may be slightly bowed. A narrow zone of faint basal wrinkles is visible on the scanning electron microscope, extending from the basal margin to approximately a quarter the height of the base. The basal margin is straight and basal surface entirely excavated. Basal cavity outline is illustrated in fig. 34. White matter in all elements is restricted to the cusp tip, lateral costae and lower margin keels.

ap element. Morphologically transitional from the *sym. p* element; slender, erect with a narrow, tall base. Basal outline and cusp morphology are similar in both elements, though the cusp tends to be more strongly bowed in the *aq*. The upper and lower margins of the base are sharp and bear prominent keels, the edges of the cusp are also sharp. The inner face bears a single, inconspicuous costa which extends from the basal margin, runs obliquely to the midline and terminates at the posterior edge close to the base of the cusp. Below the costa the lateral face is shallowly convex and steeply inclined towards the lower margin; above the costa the face is less steeply inclined. The outer face is broadly convex. Basally the lateral faces bear a narrow zone of faint basal wrinkles, the basal margin is more or less straight and the basal surface is entirely excavated.

aq element. With a much broader base and stronger recurvature than the *p* element. The base is laterally inflated and tapers apically to a slender, biconvex, proclined cusp, this may be twisted inwardly. The upper and lower margins of the base are more or less straight and keeled; the lower is much broader and is directed inwardly. Basally the lower keel is much taller and decreases in height along the cusp. The lateral faces of the base are broadly convex and lack costae, each has a narrow zone of basal wrinkles which may be extended

apically as faint microstriations. The basal margin is straight and the basal surface entirely excavated.

sq element. Laterally compressed, bilaterally symmetrical cone, more strongly recurved than the *aq element*. Upper and lower margins of the base are sharp, and the lower bears a prominent keel. The cusp is lenticular in cross section with shallowly biconvex lateral faces. These bear a narrow zone of basal wrinkles which may be extended centrally as faint microstriations. The basal margin is straight and entirely excavated.

r element. Short, highly recurved version of the *aq element* with a broad, short base which tapers rapidly, apically to a slender, biconvex cusp which may be twisted inwards. The upper margin of the base is sharp, the lower margin bears a prominent keel, directed slightly inwards. Apically the keel decreases in height along the edge of the cusp. The inner face is convex and smooth. The outer has a central inflated area, which tapers apically, terminating at the base of the cusp. A low inconspicuous costa, terminating at the base of the cusp, extends obliquely from close to the lower-basal corner, migrates to the lower margin and terminates level with the base of the cusp. A narrow zone of basal wrinkles passes around the base and, as in the other elements, extends centrally as an area of faint microstriations. The basal margin is straight, and the basal surface is entirely excavated.

Remarks. The apparatus of this species contains typically thin walled cones with weakly costate *p* elements and laterally acostate *q* elements. The sym. *p* element is distinguished from its counterpart in other *Walliserodus* species in having lower costae that are directed downwards and no upper lateral costae. The *q* and *r* elements are characterised by their basal outline and biconvex slender cusp.

W. sancticlairei (Cooper, 1976) consists of slender coniform elements with similar basal outline and cusp cross-section to elements in *W. cf. W. sancticlairei*. Differences in the costae of the sym. *p* element and the laterally acostate *q* elements allow the separation of these species. Cooper (1976) did not describe an *r* element. Barrick (1977, pl. 1, fig. 11) reconstructed the apparatus of *W. sancticlairei* as containing a compressed element with a prominent lateral costa and tall lower-margin keel along with slender elements. The former is not included by Cooper (1976) or in this work. The prominent costa is more typical of elements of *W. curvatus*, and it would appear that Barrick's reconstruction contains elements from more than one species.

Occurrence. Particularly abundant in the *Pterospathodus celloni* and *P. amorphognathoides* Biozone strata of

Washington Land; with additional specimens of similar age from the rest of North Greenland.

Ordovician conodont systematic palaeontology

Genus *Aphelognathus* Branson, Mehl & Branson, 1951

- 1951 *Aphelognathus* Branson, Mehl & Branson, p. 9.
1951 *Zygognathus* Branson, Mehl & Branson, p. 11.

Type series. *Aphelognathus grandis* Branson, Mehl & Branson, 1951.

Diagnosis. Refer to Sweet (1979, p. 55).

Remarks. The apparatus was reconstructed by Sweet (1979) and confirmed by Barnes *et al.* (1979); it is characterised by the *Pa* element which has a prominent gap just anterior of the cusp. The remaining elements are similar to their counterparts in *Oulodus* and in the darkened specimens of the Greenland collection are difficult to separate.

Aphelognathus pyramidalis (Branson, Mehl & Branson, 1951)

Plate 22, figs 1-5

- *1951 *Zygognathus pyramidalis* Branson, Mehl & Branson, p. 12, pl. 3, figs 10-16, 21.
p1951 *Trichonodella undulata?* Branson, Mehl & Branson, p. 14, pl. 3, figs 24-26; pl. 4, fig. 14.
?1951 *Microcoelodus panderi* Branson, Mehl & Branson, p. 16, pl. 4, fig. 12.
p1951 *Aphelognathus grandis* Branson, Mehl & Branson, p. 9, pl. 2, figs 11, 13, 14 only.
1951 *Zygognathus plebia* Branson, Mehl & Branson, p. 12, pl. 3, figs 22, 23; pl. 4, figs 1-9.
1951 *Aphelognathus acutidentata* Branson, Mehl & Branson, p. 9, pl. 2, figs 15, 16.
1981a *Aphelognathus pyramidalis*; Sweet, p. 47, *Aphelognathus* pl. 3, figs 1-6.

Holotype. *Zygognathus pyramidalis* Branson, Mehl & Branson, 1951, p. 12, pl. 3, fig. 21. Locality 1844 of Branson *et al.* (1951), Upper Ordovician (Richmondian stage) of Indiana.

Diagnosis. The original diagnosis was emended by Sweet (1981a, p. 47).

Remarks. *A. pyramidalis* is distinguished from other species of *Aphelognathus* in having a characteristic, angulate *Pa* element which possesses a broadly flaring

lower margin and short rudimentary denticles on its posterior process.

Occurrence. Elements were recovered from the Turesø Formation in Peary Land.

Aphelognathus sp.

Plate 22, fig. 6

Description. Pa element. Angulate, comprising a prominent posteriorly inclined cusp, a long, deep, anterior process and a shorter, downwardly inclined, posterior process. The upper edge of the anterior process is straight, bearing six short, triangular denticles; separated from the cusp by a narrow gap. The posterior process bears five similar denticles. The lower edge is arched upwards beneath the cusp at an angle of 160°. The basal cavity is a narrow groove along the entire length of the element.

Remarks. A single thermally mature specimen was recovered from GGU 274724 in the Turesø Formation (fig. 9). This is referred to *Aphelognathus* due to the narrow gap in the denticulation, just anterior to the cusp. This specimen is similar to *Spathognathodus elibatus* Pollock, Rexroad & Nicoll (1970), differing in the straight upper edge of the anterior process.

Genus *Belodina* Ethington, 1959

Type species. *Belodus compressus* Branson & Mehl, 1933b. Senior subjective synonym of *Belodus grandis* Stauffer.

Diagnosis. Refer to Sweet (1979, p. 58).

Belodina aff. *B. confluens* Sweet, 1979

Plate 22, figs 14–15

aff. 1979 *Belodina confluens* Sweet, p. 59, pl. 5, figs 10, 17; pl. 6, fig. 9.

Description. Compressiform rastrate element. Laterally compressed with a broad basal margin extending as a well developed heel. Cusp long and recurved, the upper edge bears three tall, almost completely fused denticles, the lower edge is narrow and rounded. The inner face bears a narrow groove extending from a central basal notch, running close to the base of the denticles and subparallel to the posterior edge of the cusp. Below the groove the lateral face is slightly inflated, the lower edge is compressed into a rudimentary keel. The outer face is smooth, lacking a furrow. The entire basal surface is excavated, the cavity terminating close to the lower edge, beneath the first or second proximal denticle. All specimens are thermally mature and white matter is not distinguishable.

Plate 22

Figs 1–5. *Aphelognathus pyramidalis* Branson, Mehl & Branson.

All specimens from GGU 256375, × 40.

- 1, inner lateral view of Pb element; MGUH 17.987.
- 2, inner lateral view of Pa element; MGUH 17.988.
- 3, posterior view of Sa element; MGUH 17.989.
- 4, posterior view of Sb element; MGUH 17.990.
- 5, inner lateral view of Sc element; MGUH 17.991.

Fig. 6. *Aphelognathus* sp.

6, inner lateral view of Pa element, × 40; MGUH 17.992.

Figs 7–10. *Drepanoistodus suberectus* (Branson & Mehl).

All specimens from GGU 256335, × 40.

- 7, lateral view of sym. p element; MGUH 17.993.
- 8, lateral view of sq element; MGUH 17.994.
- 9, inner lateral view of aq element; MGUH 17.995.
- 10, lateral view of r element; MGUH 17.996.

Figs 11–13. *Plegagnathus dartoni* (Stone & Furnish).

All specimens × 40.

11, lateral view of rastrate element; MGUH 17.997 from GGU 256337.

12, lateral view of rastrate element (?); MGUH 17.998 from GGU 254652.

13, lateral view of cordylodiform element (?); MGUH 17.999 from GGU 274726.

Figs 14–15. *Belodina* aff. *B. confluens* Sweet.

Specimens from GGU 245279, × 40.

14, lateral view of rastrate element; MGUH 18.000.

15, lateral view of oistodiform element; MGUH 18.001.

Figs 16–17. *Pseudobelodina dispansa* (Glenister).

Specimens from GGU 245271, × 80.

16, lateral view of rastrate element; MGUH 18.002.

17, lateral view of rastrate element; MGUH 18.003.

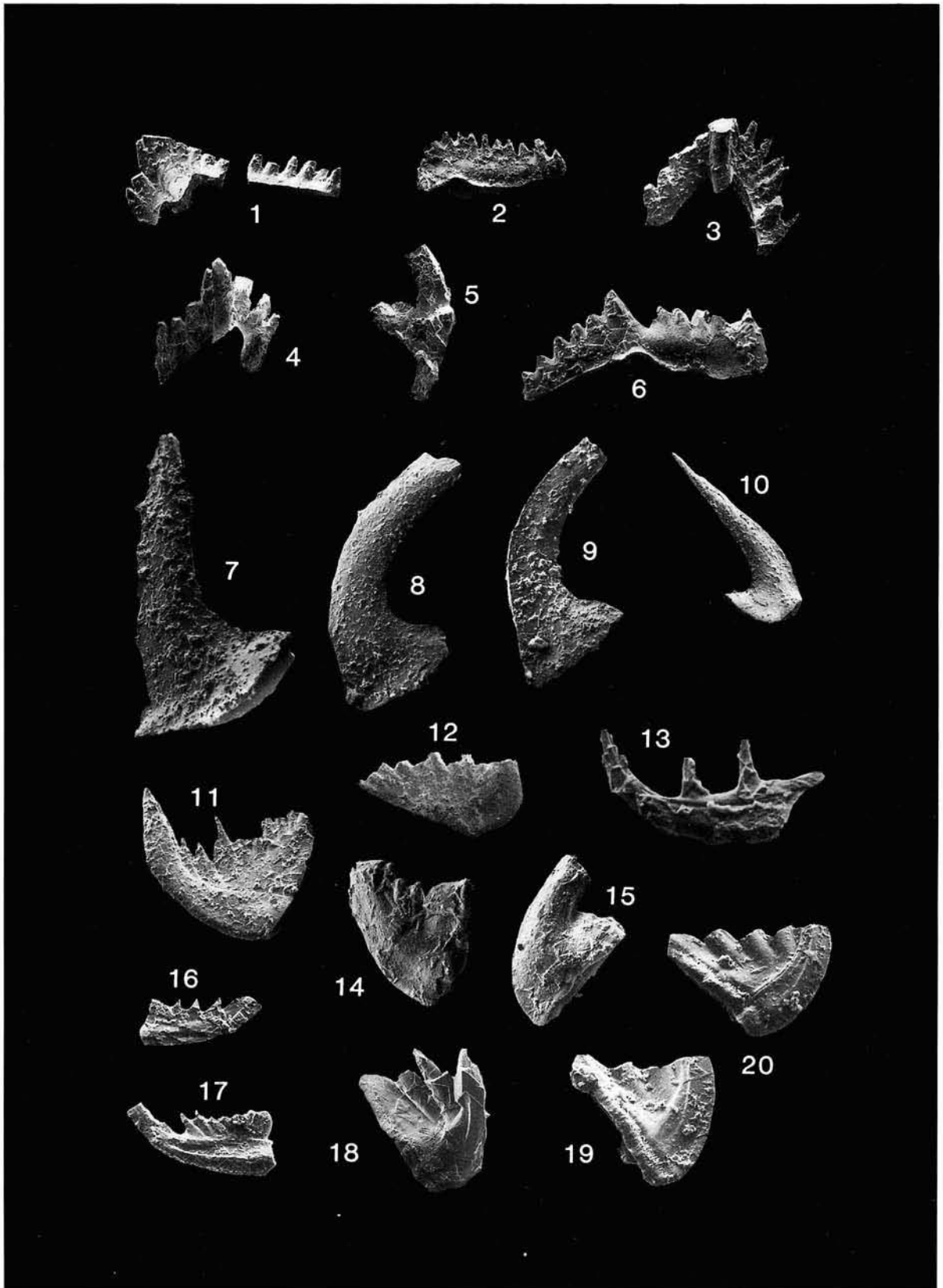
Figs 18–20. *Pseudobelodina vulgaris vulgaris* Sweet.

All specimens × 60.

18, lateral view of rastrate element; MGUH 18.004 from GGU 245273.

19, lateral view of rastrate element; MGUH 18.005 from GGU 274726.

20, lateral view of rastrate element; MGUH 18.006 from GGU 274726.



Eobelodiniform element. Bilaterally symmetrical, strongly recurved element. The cusp is slender, long and strongly recurved. The upper and lower edges are sharp, the lateral faces shallowly convex and smooth. On the inner face a narrow groove extends from just above the centre of the basal margin to the apex, lying close to the posterior edge. The entire base is excavated with a cavity outline identical to the rastrate element.

Remarks. The upper edge of the rastrate element of *B. confluens* bears six denticles rather than the three of *B. aff. B. confluens*.

Occurrence. Found only in GGU 245271, 245279 and 254869; one compressiform rastrate and four eobelodiniform elements (figs 11, 13).

Genus *Drepanoistodus* Lindström, 1971

Type species. *Oistodus forceps* Lindström 1955, p. 574.

Diagnosis. Refer to Lindström (1971, p. 42).

Drepanoistodus suberectus (Branson & Mehl, 1933b)

Plate 22, figs 7–10

- ?1930 *Distacodus arcuatus* Stauffer, p. 123, pl. 10, fig. 2.
- *1933b *Oistodus suberectus* Branson & Mehl, p. 111, pl. 9, fig. 7.
- 1933b *Oistodus curvatus* Branson & Mehl, p. 110, pl. 9, figs 4, 10, 12.
- 1933b *Oistodus inclinatus* Branson & Mehl, p. 110, pl. 9, fig. 8.
- 1955 *Drepanodus homocurvatus* Lindström, p. 563, pl. 2, figs 23, 24, 39.
- 1966 *Drepanodus suberectus*; Bergström & Sweet, p. 330, pl. 35, figs 22–27, (includes synonymy to 1966).
- 1974 *Drepanoistodus suberectus*; Uyeno, p. 14, pl. 1, figs 5–9.
- 1975 *Drepanoistodus suberectus*; Sweet, Thompson & Satterfield, pl. 1, figs 15–17.
- 1981 *Drepanoistodus suberectus*; McCracken & Barnes, p. 77, pl. 3, figs 1–6 (see for further synonymy).

Holotype. *Oistodus suberectus* Branson & Mehl, 1933b, p. 111. From the Middle Ordovician, Plattin Formation, Jefferson County, Missouri.

Emended diagnosis. Apparatus quadrimembrate containing strongly compressed sym. p, aq, sq and r elements with long curved cusps and short, laterally inflated bases.

Description. The sym. p, sq and r elements of this species have been described previously (see synonymy). An aq element, previously included in the taxa *Oistodus curvatus* Branson & Mehl (1933b) and *Drepanoistodus homocurvatus* Lindström (1955b) is separated.

aq element. Basally similar to the other elements in the apparatus, it is slightly longer, has reduced lateral flaring and reduced extension of the basal corners. The cusp is proclined and sharply recurved from approximately one-third its height. Upper edge is sharp, lateral faces shallowly biconvex and the lower edge bears an inwardly directed, low costa; extending from the basal corner to the apex, decreasing in height along the upper sixth of the cusp.

Remarks. *Drepanoistodus suberectus* has been described as a trimembrate apparatus (see McCracken & Barnes, 1981) consisting of drepanodontiform (= suberectiform and the p element herein), homocurviform (= q elements herein) and oistodontiform (= r element herein) elements. It is now possible to recognise aq and sq elements within the homocurviform element. Lindström (1971) noted the tendency for the elements of *D. suberectus* to become asymmetrical by bowing and twisting of the cusp. The aq element has an inwardly directed costa on the lower edge and a slightly different curvature from that of the sq element. The r element shows closer morphological affinities to the p element than to the q elements; this is different from many coniform genera (e.g. *Walliserodus*, *Panderodus* and *Dapsilodus*) in which the aq and r elements appear to be morphologically transitional.

Occurrence. Found in the uppermost Ordovician strata of Peary Land and Kronprins Christian Land.

Genus *Plegagnathus* Ethington & Furnish, 1959

Type species. *Belodina dartoni* Stone & Furnish, 1959, p. 220, pl. 31, fig. 15.

Diagnosis. Refer to Sweet (1979, p. 66).

Plegagnathus dartoni Stone & Furnish, 1959

Plate 22, figs 11–13

- *1959 *Belodina dartoni* Stone & Furnish, p. 220, pl. 31, fig. 15.
- 1959 *Plegagnathus dartoni*; Ethington & Furnish, p. 545, pl. 73, figs 6, 7.
- 1979 *Plegagnathus dartoni*; Sweet, p. 66, pl. 7, figs 28, 29.
- ?p1981 *Plegagnathus dartoni*; Nowlan & Barnes, p. 23, pl. 7, figs 13–15; non figs 10, 11.

Holotype. *Belodina dartoni* Stone & Furnish, 1959, p. 220, pl. 31, fig. 15. From the Bighorn Dolomite (late Ordovician, ?pre-Richmondian) of Johnson County, Wyoming.

Description. Refer to Sweet (1979, p. 66).

Remarks. This species is distinguished from *P. nelsoni* Ethington & Furnish (1959) in having a greater number of closely spaced needle-like denticles on the upper edge of the plegagnathiform element. The cusp is untwisted and laterally broader, maintaining a constant thickness to its apex. *P. nelsoni* has fewer, broader denticles and a slightly more recurved plegagnathiform element. In the terminology employed herein, this element is equivalent to an sq element.

Occurrence. Found only in GGU 256337 and 256370 (figs 6, 7). Outside Greenland, Sweet (1979, fig. 3) recorded a range for *P. dartoni* of middle to mid-upper Richmondian.

Genus *Pristognathus* Stone & Furnish, 1959

Type species. *Pristognathus bighornensis*, Stone & Furnish, 1959, p. 226.

Diagnosis. Refer to Sweet (1979, p. 67).

Remarks. Sweet (1979, p. 67) reconstructed the apparatus of the type species, as a seximembrate structure, similar to that of *Oulodus*. The Pb element of this apparatus is digyrate.

Pristognathus bighornensis Stone & Furnish, 1959

Plate 23, figs 2-3

- *1959 *Pristognathus bighornensis* Stone & Furnish, p. 226, pl. 32, figs 7, 8.
- 1979 *Pristognathus bighornensis*; Sweet, p. 67, pl. 9, figs 1, 4-6, 9, 10 (see for full synonymy).

Diagnosis. Refer to Sweet (1979, p. 67).

Description. *Pb element.* Refer to that of *Pristognathus bighornensis* Stone & Furnish (1959, p. 226) from which the Greenland specimens are indistinguishable.

Occurrence. Four specimens of the Pb element have been found in the Turesø Formation at Odin Fjord, samples GGU 254652 and 254656 (fig. 10).

Genus *Pseudobelodina* Sweet, 1979

Type species. *Belodina kirki* Stone & Furnish, 1959, p. 221.

Diagnosis. Refer to Sweet (1979, p. 68).

Pseudobelodina dispansa (Glenister, 1957)

Plate 22, figs 16-17

- 1957 *Belodus dispansus* Glenister, p. 729, pl. 88, figs 14, 15.
- 1959 *Belodina dispansa*; Stone & Furnish, p. 220, pl. 31, fig. 11.
- *1979 *Pseudobelodina dispansa*; Sweet, p. 68, pl. 5, figs 6, 18; pl. 6, figs 1, 6, 7, 8.

Hypotypes. Specimens OSU 34496-34501 inclusive from the Bighorn Group at OSU locality 75SD. Figured in Sweet (1979, pl. 5, figs 6, 18; pl. 6, figs 1, 6, 7, 8).

Diagnosis. Refer to Sweet (1979, p. 68).

Remarks. Two rastrate elements plus fragments are recorded from GGU 245271 (fig. 11) which have the characteristic furrow, upper margin denticulation and heel development of the ?p element proposed by Sweet (1979), these elements correspond to the sym. p elements proposed for Silurian genera.

Pseudobelodina vulgaris vulgaris Sweet, 1979

Plate 22, figs 18-20

- 1959 *Belodina profunda*; Stone & Furnish, p. 542, pl. 73, fig. 5.
- *1979 *Pseudobelodina vulgaris vulgaris* Sweet, p. 71, pl. 5, figs 2-4.
- 1981c *Pseudobelodina vulgaris vulgaris*; Sweet, p. 351, pl. 2, figs 2, 9, 10 (see for further synonymy)
- 1981 *Belodina profunda*; Nowlan & Barnes, p. 12, pl. 7, figs 1-9, 12.

Syntypes. *Pseudobelodina vulgaris vulgaris* Sweet, 1979, pl. 71, pl. 5, figs 2-4. From the Bighorn Group (late Ordovician) of Sheridan County, Wyoming.

Diagnosis. Refer to that of Sweet (1979, p. 71).

Description. Refer to Sweet (1979, p. 71). The Greenland specimens differ from those of Sweet in possessing more prominent lateral costae; individual elements are strongly recurved.

Remarks. Elements from Upper Ordovician of Kronprins Christian Land are characterised by long narrow

heels, moderate curvature and two or three denticles. *P. vulgaris ultima* Sweet (1979) has a much reduced heel and four denticles on the rastrate (p? of Sweet, 1979) element.

Occurrence. Found in GGU 274724–274726 (fig. 9). Specimens include a tridenticulate rastrate element (3) and bidenticulate rastrate (3). Outside Greenland this species is recorded from the uppermost Richmondian of the U.S.A. (Sweet, 1981c, p. 352).

Pseudobelodina sp.

Plate 23, fig. 1

Description. Laterally compressed, strongly recurved, rastrate, coniform element. The base is broad and short, extended postero-basally as a long, slender heel. The upper margin of the base is straight, bearing three broad, fused denticles, which are inclined slightly towards the upper-basal corner. The cusp curves strongly upwards at its base, to be almost erect; the denticles lie subparallel to the upper edge of the cusp. The lower margin of the element is narrow and rounded, gently recurved from the basal corner. The basal margin is inclined apically towards the upper corner and the basal surface is entirely excavated. On the inner face two short parallel costae are situated towards the lower corner, extending, subparallel with the lower margin, and terminating at the base of the cusp. The outer face is shallowly convex and acostate.

Remarks. A single element in GGU 254652 (fig. 10) is morphologically similar to the P? element of *Pseudobelodina torta* Sweet (1979, pl. 6, fig. 23), but lacks the prominent lower-lateral costa. Elements of *P. vulgaris vulgaris* are also present in the sample, and the element may represent a P? element in this apparatus, but Sweet (1979) and Nowlan & Barnes (1981) did not recognise a similar element in their large collections of *P. vulgaris vulgaris*.

Genus *Rhipidognathus* Branson, Mehl & Branson, 1951

Type species. *Rhipidognathus symmetricus* Branson, Mehl & Branson, 1951, p. 10.

Emended diagnosis. Apparatus seximembrate containing an angulate (Pa) element, angulate (Pb) element, a modified angulate (M) element and a symmetry transition series comprising palmate elements, alate (Sa), modified alate (Sb), and bipennate (Sc). All elements have a prominent cusp, tall triangular, partially fused denticles and a small laterally restricted basal cavity beneath the cusp.

Rhipidognathus symmetricus Branson, Mehl & Branson, 1951

Plate 23, figs 4–9

- *1951 *Rhipidognathus symmetrica* Branson, Mehl & Branson, p. 10, pl. 2, figs 29–37; pl. 3, fig. 31.
- 1951 *Rhipidognathus* sp. indeterminate Branson, Mehl & Branson, pl. 3, fig. 29.
- 1951 *Rhipidognathus paucidentata* Branson, Mehl & Branson, p. 10, pl. 3, fig. 30.

Plate 23

Fig. 1. *Pseudobelodina* sp.

1, lateral view of rastrate element, $\times 100$; MGUH 18.007 from GGU 254652.

Figs 2, 3. *Pristognathus bighornensis* Stone & Furnish. Specimens from GGU 254656, $\times 60$.

2, inner lateral view of Pb element; MGUH 18.008.
3, ?P element; MGUH 18.009.

Figs 4–9. *Rhipidognathus symmetricus* Branson, Mehl & Branson.
All specimens from GGU 274540, $\times 60$.

4, inner lateral view of Pa element; MGUH 18.010.
5, inner lateral view of Pb element; MGUH 18.011.
6, inner lateral view of M element; MGUH 18.012.
7, posterior view of Sa element; MGUH 18.013.
8, posterior view of Sb element; MGUH 18.014.
9, inner lateral view of Sc element; MGUH 18.015.

Fig. 10. Genus and sp. indet. A.

10, lateral view of element, $\times 40$; MGUH 18.016 from GGU 228959.

Fig. 11. Genus and sp. indet. B.

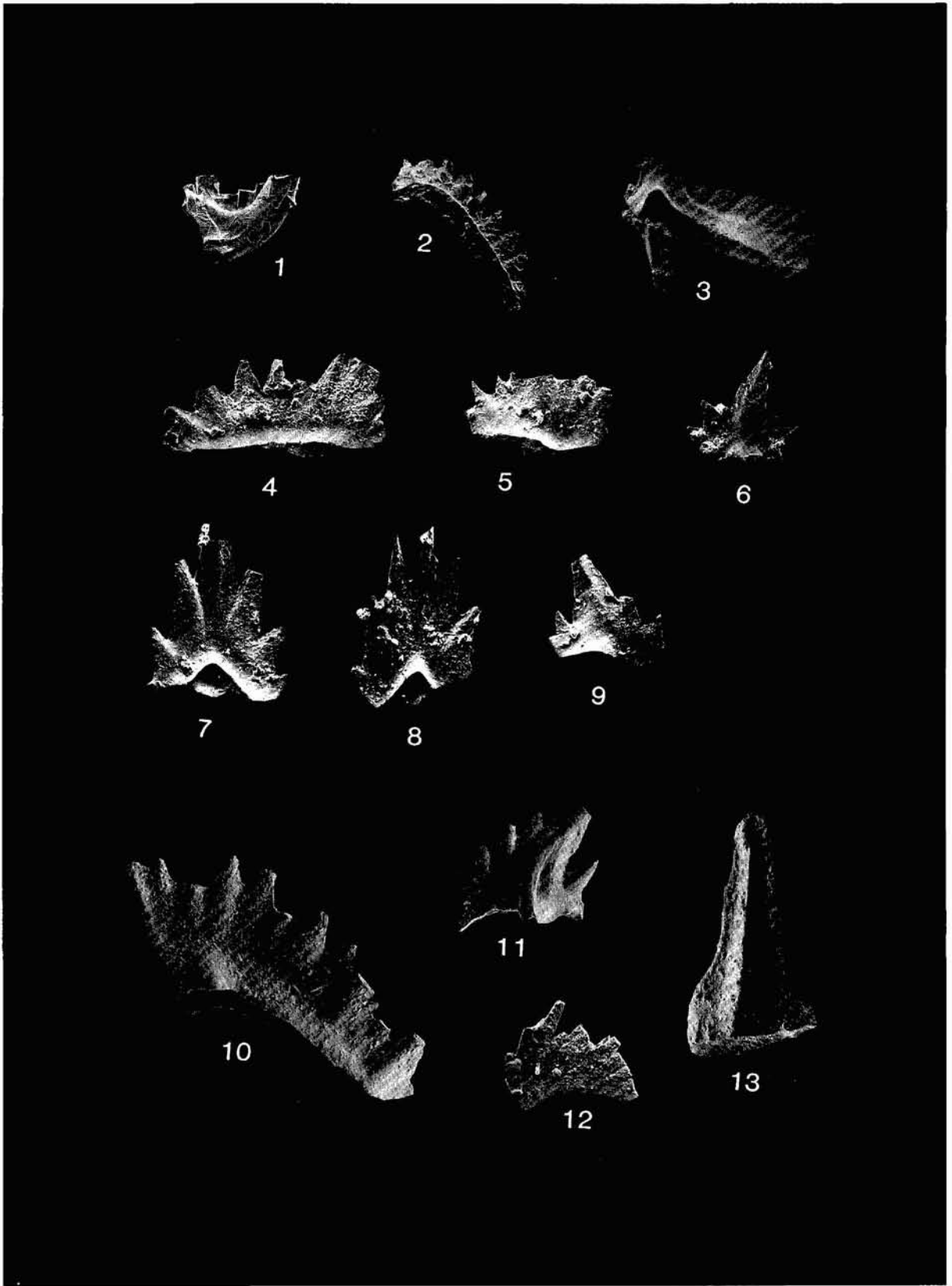
11, lateral view of Pb element, $\times 60$; MGUH 18.017 from GGU 274758.

Fig. 12. Genus and sp. indet. C.

12, lateral view of element, $\times 120$; MGUH 18.018 from GGU 254711.

Fig. 13. Genus and sp. indet. D.

13, upper view of Pa element, $\times 40$; MGUH 17.631 from GGU 254827.



- 1951 *Rhipidognathus curvata* Branson, Mehl & Branson, p. 10, pl. 3, figs 1-7.
 1966 *Rhipidognathus symmetrica*; Bergström & Sweet, p. 388.
 1966 *Rhipidognathus paucidentata*; Schopf, p. 72, pl. 2, fig. 31.
 1968 *Rhipidognathus symmetrica*; Kohut & Sweet, p. 1474, pl. 185, figs 21, 22, 25, 26, 29-31 (includes synonymy to 1968).
 1971 *Rhipidognathus symmetricus*; Sweet, Ethington & Barnes, pl. 1, fig. 42.
 1981 *Rhipidognathus symmetricus*; McCracken & Barnes, p. 89, pl. 4, figs 45, 46.

Holotype. *Rhipidognathus symmetrica* Branson, Mehl & Branson, 1951, p. 10, pl. 2, fig. 33. From the White-water Formation of Indiana, Richmondian in age.

Emended diagnosis. A species of *Rhipidognathus* with a Pa element with long anterior and short posterior processes and a broad inconspicuous cusp; M element with tall upwardly bowed cusp and short anterior processes of subequal length.

Description. *Pa element.* Angulate, straight to slightly bowed blade. An inconspicuous, posteriorly inclined cusp is situated close to the posterior tip of the blade, the anterior process is long and bears six to eight broad, partially fused, subequal denticles; the most proximal is almost completely fused to the cusp; the posterior process is much reduced and bears one to three smaller denticles. The lower edge is more or less straight, the inner margin of the cavity is straight, the outer is slightly inflated and projects downwards beneath the inner edge. The cavity is restricted to the area between the second proximal anterior denticle and the anterior edge of the cusp.

Pb element. Angulate and similar to the Pa it differs in having a central broad, prominent cusp. The anterior and posterior processes are subequal in length and each bears three or four small, partially fused denticles. Those on the anterior process are erect, those on the posterior tend to be slightly inclined towards the posterior. The basal cavity is narrow and groove-like with slightly flaring lateral lips beneath the cusp; (extending for a short distance to the anterior and posterior of the cusp).

M element. Modified, angulate element with a tall, broad, slightly inwardly bowed, posteriorly inclined cusp and short anterior and posterior processes of similar length. Each process bears two almost completely fused, laterally compressed denticles, which are inclined distally. The lower edge of the element is straight to slightly concave, with a narrow, slit-like, restricted basal cavity.

Sa element. Alate element; the cusp is tall and cen-

trally situated, the lateral processes subequal in length and each bearing two or three tall, partially fused denticles. These have broad bases, decrease in height and are inclined distally. The first proximal denticle on each process is almost completely fused to the cusp. The lower edge of the element is straight to slightly arched; the deep basal cavity is restricted beneath the cusp. Posteriorly the lower margin of the basal cavity is arched upwards.

Sb element. Modified tertio-pedate element, lacking a posterior process, is almost identical to the Sa element, except for the stronger, asymmetrical arching of the lower edge. The inner process bears only two denticles and is shorter than the outer process.

Sc element. Bipennate with a tall, broad, posteriorly inclined cusp. The anterior process is longer than the posterior bearing two broad, posteriorly inclined, partially fused denticles. The posterior process bears a single, small denticle, rarely two denticles. The lower edge of the element is straight to slightly arched; the basal cavity is restricted to and only slightly expanded beneath the cusp.

Remarks. Previous reconstructions of the *R. symmetricus* apparatus have been trimembrate, and the diagnosis has been emended to include the newly described elements.

Occurrence. Found sporadically throughout the Upper Ordovician sections of Peary Land to Wulff Land. Most abundant in GGU 274540 (fig. 4).

Acknowledgements

This work arises from a co-operative project on the Lower Palaeozoic micropalaeontology of North Greenland between the Geological Survey of Greenland and the Micropalaeontology Unit, Department of Geology, University of Nottingham.

Generalised section logs used in this work were measured and sampled by the following: H. A. Armstrong, J. M. Hurst, J. R. Ineson, J. F. Jepsen, P. D. Lane, J. E. Mabillard, J. S. Peel and A. T. Thomas. Full section details and field slips are held by the Geological Survey of Greenland in Copenhagen.

The author wishes to express his gratitude to R. J. Aldridge for his supervision of this work, for making available his personal reprint and research collections and for many suggestions for the improvement of the manuscript. Thanks are also expressed to the many officers of the Geological Survey of Greenland for their help in the field; J. R. Ineson, P. D. Lane, J. E. Mabillard and A. T. Thomas also supplied valuable assistance in collecting conodont samples. The author also wishes to express his gratitude to the many conodont workers and museum curators who willingly made available type specimens or provided reprints. In particular, Lennart Jeppsson

provided specimens from his Gotland collections. Hans Schönlaub is thanked for helpful referee's comments.

J. S. Peel and M. Sønderholm (GGU) are thanked for their thorough revision of the introductory sections and for the preparation of diagrams later drawn by Bente Thomas.

The use of processing and photographic facilities at the University of Nottingham and the University of Newcastle upon

Tyne are acknowledged. Technical and secretarial assistance was provided by L. Green, A. Swift, S. Hall, J. Wilkinson, D. Jones and E. Walton and the Geological Survey of Greenland.

Financial support from the N.E.R.C., from the Geological Survey of Greenland and the British Micropalaeontological Society is acknowledged.

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