



Biogeography and biofacies patterns of Middle Cambrian polymeroid trilobites from North Greenland: palaeogeographic and palaeo-oceanographic implications

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Fossils from Middle Cambrian rocks of Peary Land and Nyeboe Land, North Greenland, show that polymeroid trilobite biofacies were strongly segregated near the shelf margin of Laurentia. Some biofacies include trilobites of Laurentian aspect that lived in warm, relatively shallow water, and other biofacies have trilobites of Baltic aspect that lived in cool, deeper water. Polymeroids in the *Glossopleura* and *Ptychagnostus gibbus* zones are from open-shelf lithofacies and are mostly of Laurentian aspect. Polymeroids in the *Lejopyge laevigata* Zone are from deep, outermost shelf to upper slope lithofacies and are entirely of Baltic aspect. Polymeroids in the *Ptychagnostus atavus* Zone are from an intermediate, outer-shelf setting and are of mixed Laurentian and Baltic aspect. Mixing of polymeroids from different biofacies is inferred to have occurred through downslope movement by localised sediment gravity flows. The presence of segregated trilobite biofacies at the shelf margin of Laurentia is the first evidence for a thermocline in marine waters surrounding Laurentia during the Middle Cambrian, although evidence for a thermocline during the Early and Late Cambrian has been reported previously.

The presence of polymeroids of Baltic aspect in Laurentian rocks of North Greenland has important implications for the analysis of tectonostratigraphic terranes. The presence of cool-water trilobites is not sufficient evidence to conclude that the terrane originated in high palaeolatitudes. Identification of an autochthonous terrane of a continental margin is possible, however, on the basis of fossil assemblages containing mixed biofacies representatives. Provenance identification is possible because the assemblages are expected to include taxa characteristic of warm-water cratonic areas along which the terrane originated.

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Historically, Cambrian trilobite faunas from the circum-Atlantic region have been assigned to either an Atlantic or Pacific faunal province. These provinces have also been called Acado-Baltic and North American, respectively. Several biogeographical studies (e.g., Lochman-Balk & Wilson, 1958; Palmer, 1969, 1972, 1979; Cowie, 1971, 1974; Theokritoff, 1979, 1985; Shergold, 1988) have shown that the Pacific province is characterised by polymeroid trilobites that were mostly endemic to the shelf of Laurentia, whereas the Atlantic province is characterised by polymeroids that were first described from localities in Scandinavia, southern Great Britain, Maritime Canada, or New England.

Trilobites of the Atlantic province have been important in studies of early Palaeozoic biostratigraphy and palaeogeography. Zonations developed for Middle Cambrian trilobites worldwide are commonly compared to the zo-

nation of Sweden's trilobites (Westergård, 1946, 1953). Information about trilobite biogeography is also routinely used to supplement palaeomagnetic, stratigraphic, structural, or other geologic evidence about the configuration and history of continents and oceans during the early Palaeozoic.

The biogeography of Cambrian trilobites has been central to some arguments concerning the origin of tectonostratigraphic terranes in the Appalachian Orogen (see Keppie, 1989 and Horton *et al.*, 1989 for definitions of terranes). The presence of polymeroids having Atlantic affinities in rocks of Maritime Canada and New England (e.g., Howell, 1925; Hutchinson, 1952, 1962; Poulsen & Anderson, 1975; Bergström & Levi-Setti, 1978) has been used to infer the exotic origin of these terranes and subsequent accretion to North America during the middle or late Palaeozoic (see Williams & Hatcher, 1982; Secor

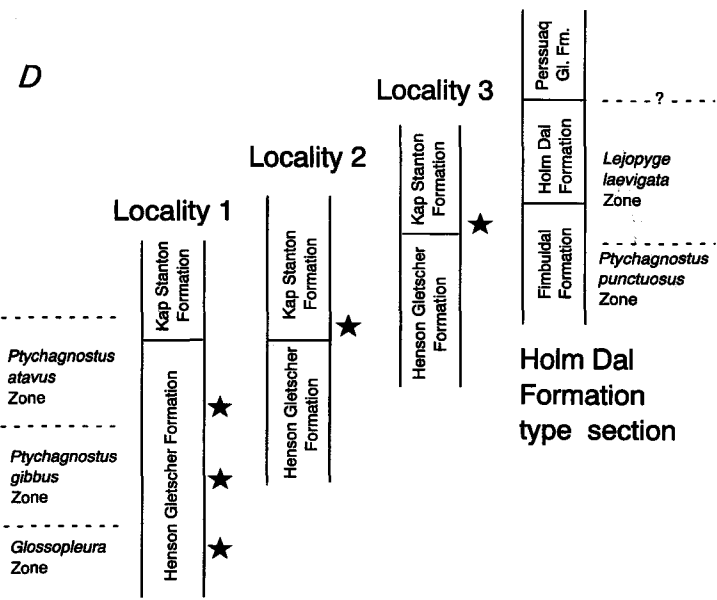
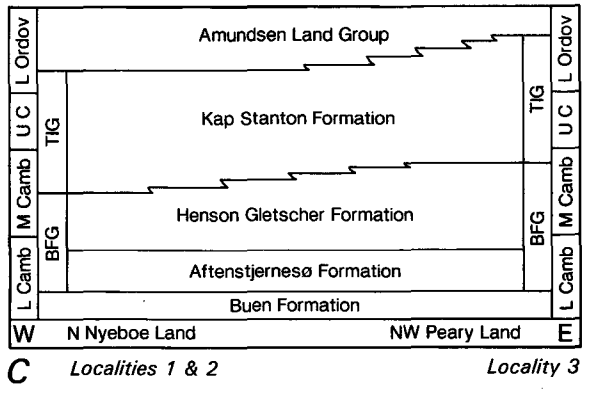
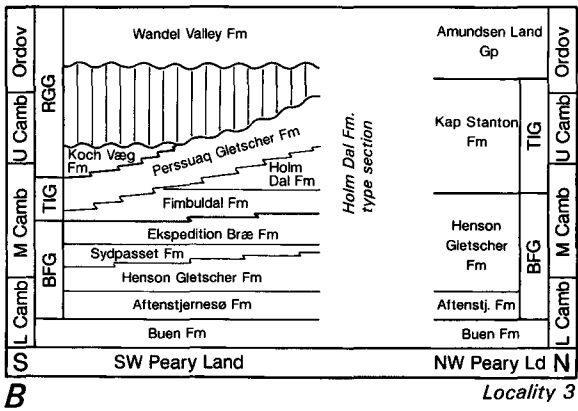
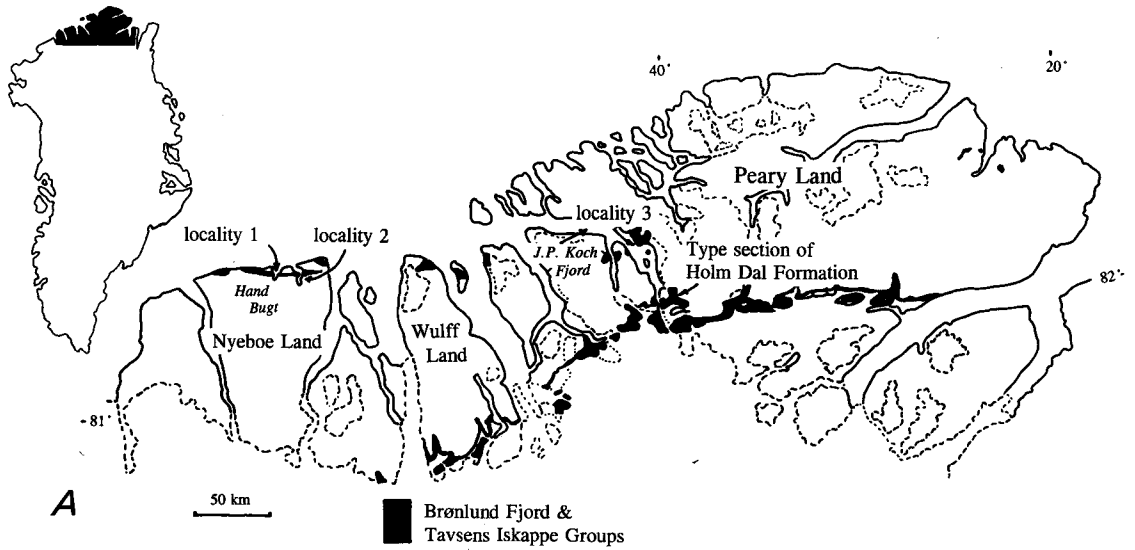


Fig. 1. Derivation of fossiliferous samples. A, map showing the distribution of the Brønlund Fjord and Tavsens Iskappe Groups in North Greenland and collection localities discussed in the text. B, C, geological cross-sections through Cambrian – Lower Ordovician strata in North Greenland. BFG, Brønlund Fjord Group; TIG, Tavsens Iskappe Group (from Ineson *et al.*, 1994). D, biostratigraphy of fossiliferous samples (stars) discussed in the text.

et al., 1983; Gromet, 1989; Keppie, 1989). Although not all examples of Atlantic trilobites in North America have been associated with accreted terranes, common practice has been to suspect an exotic origin for a terrane that contains such a fauna (see Secor *et al.*, 1983; Gromet, 1989; Horton *et al.*, 1989; Samson *et al.*, 1990), particularly if structural and stratigraphic evidence suggests that it was previously decoupled from North American shelf rocks.

This paper documents the biogeographic and biofacies distributions of polymeroid trilobites from Middle Cambrian rocks of the Henson Gletscher and Kap Stanton formations of Nyeboe Land and Peary Land, North Greenland (Fig. 1). Systematic descriptions are given in an accompanying paper (Babcock, 1994). An additional accompanying paper by Robison (1994) describes agnostoid trilobites from the same formations. The newly described faunas are preserved in open-shelf to deep outermost shelf or upper slope? lithofacies; the palaeogeographic setting is described in a third accompanying paper by Ineson *et al.* (1994). The Henson Gletscher and Kap Stanton formations are coeval in part with the Holm Dal Formation (Peel, 1988), and were in close palaeogeographic proximity (Fig. 1). The Holm Dal Formation contains polymeroid genera that are characteristic of open-shelf environments of Laurentia (Robison, 1988). Middle Cambrian strata in relevant parts of Nyeboe Land and Peary Land are relatively undisturbed structurally, and lithostratigraphic correlations in the region have been made with a high degree of confidence over scores of kilometres (J. S. Peel, personal communication, 1988; cf. Higgins *et al.*, 1991). Fossiliferous localities (Fig. 1) are in native terranes, as defined by Keppie (1989), of the Laurentian palaeocontinent.

The faunas from the Henson Gletscher, Kap Stanton, and Holm Dal formations provide an opportunity to compare open-shelf faunas with those of nearby, deeper marine environments along the Innuitian margin of Laurentia. Sharp biofacies differences between open-shelf lithofacies and deep outermost shelf lithofacies are interpreted to result from differences in either water temperature or environments that covary with temperature. Polymeroids of Laurentian aspect were present in warm shelf waters, whereas polymeroids of Baltic aspect were present in deeper, cool waters.

Biogeographic terminology

The terms Atlantic (or Acado-Baltic) and Pacific (or North American) previously have been used both for the geographic origins of Cambrian trilobite faunas and for faunal provinces. Boundaries of the faunal provinces do not always agree with the boundaries of tectonic plates as

presently understood. The terms Pacific and North American, for example, have been used for trilobites or faunas typical of shelf lithofacies of North America as well as Greenland and other regions. The terms Atlantic and Acado-Baltic have been used for trilobites or faunas first described from Scandinavia, Britain, or parts of eastern North America. Similar trilobites, however, also have been found in such other regions as Siberia, Australia, and Antarctica. Poulsen (1969) even applied the term 'Atlantic' to sparse agnostoid assemblages from North Greenland.

To reduce ambiguity, I use separate terms for the geographic origin of a fauna and its aspect. The geographic origin of a fauna is simply the geographic or palaeogeographic locality from which the fauna was collected. The aspect of a fauna refers to a recognised geographic or palaeogeographic region with which an assemblage of taxa is most characteristically associated. It is not necessarily equivalent to a faunal province as previously interpreted. Both types of terms are derived from recognised geographic or palaeogeographic names. The aspect of a fauna, although it bears the name of a geographic region, is recognised as an entity separate from any geographic region. As an example, a fauna collected from Laurentia is a Laurentian fauna, but it may contain taxa of Laurentian, Baltic, Gondwanan, or other aspect.

Palaeogeography and biogeography

Current palaeogeographic reconstructions (e.g., Scotese, 1987; Scotese & McKerrow, 1990) show the Cambrian world as comprising four principal cratonic areas, Laurentia, Baltica, Gondwana, and Siberia, as well as other smaller tectonic plates (Fig. 2). Terminology and definitions of tectonic plates used in this paper generally follow those of Scotese *et al.* (1979). Exceptions are England, Acadia, and Armorica, which are defined according to Young (1986).

Laurentia included cratonic North America, Greenland, western Newfoundland, northern Ireland and Scotland, Spitsbergen, western Norway, and the Chukotsk Peninsula of eastern Siberia. During the Cambrian, Laurentia was in tropical latitudes. At times, extensive carbonate platforms developed in surrounding warm, shallow seas. Development of the platforms led to marked differentiation of trilobite faunas in restricted-shelf and open-shelf habitats (e.g., Palmer, 1972, 1973; Robison, 1976).

Siberia, which consisted of the present-day Siberian platform, Mongolia, Manchuria, and Taymyr, was also in low latitudes during the Cambrian. It too was the site of carbonate-platform development during parts of the Cambrian.

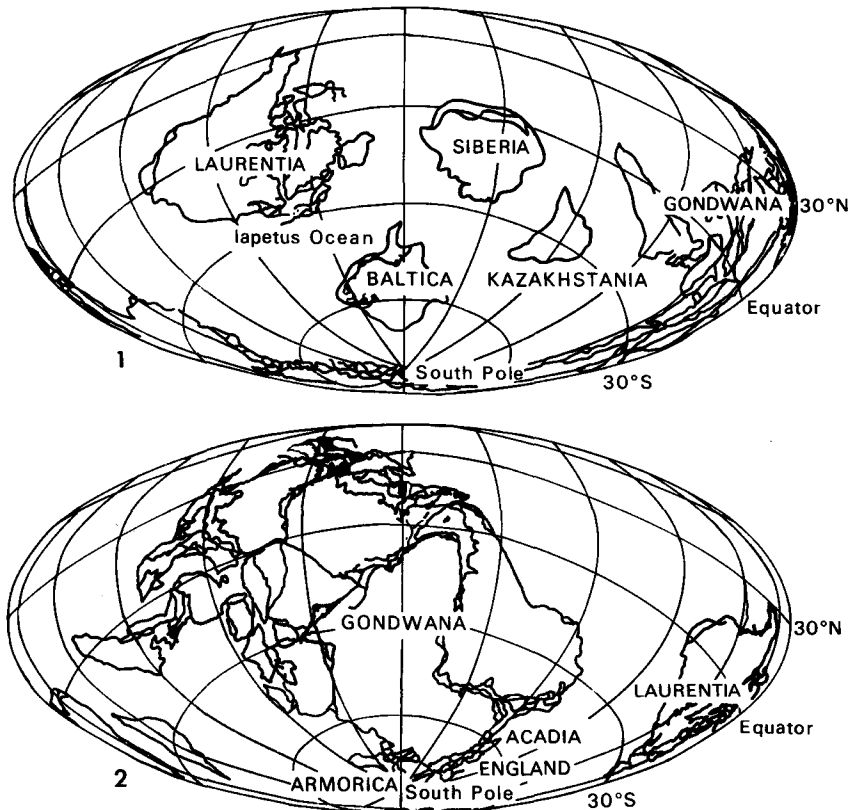


Fig. 2. Maps of reconstructed Middle Cambrian paleogeography (after Scotese & Denham, 1988). Outlines of present-day geographic areas are included for reference. The view is from 30 degrees south latitude. 1, View emphasising the relationships of Laurentia, Baltica, and Siberia. 2, View emphasising Gondwana and the peri-Gondwanan terranes.

Baltica, which consisted of north-western Europe exclusive of the British Isles and western Norway, was probably in moderately high to high southern latitudes during most of the Cambrian (Scotese *et al.*, 1979; Scotese, 1987; Scotese & McKerrow, 1990; Torsvik *et al.*, 1991; but see Smith *et al.*, 1981). Shelf sedimentation was dominated by fine-grained siliciclastics, including alum shales. Carbonate units comprise a minor part of the Cambrian section.

Major components of Gondwana were South America, Africa, Florida, Arabia, Turkey, Iran, Afghanistan, India, Madagascar, Australia, and parts of Antarctica. Gondwana extended from tropical to polar latitudes. England (Wales, southern Ireland, and southern England), Acadia (eastern New England and Maritime Canada except for eastern Nova Scotia and western Newfoundland), and Armorica (Bohemia, southern Germany, France, Iberian Peninsula, northern Morocco, and eastern Nova Scotia) were three important peri-Gondwanan terranes. All were located in polar or subpolar latitudes of the North African sector of Gondwana.

Other important terranes include those of Kazakhstania (including present-day Kazakhstan, Tien Shan, and the Aral Sea area) and present-day China. Recent evidence suggests that Kazakhstania is composed of several fused

microcontinental blocks, and includes an archipelago located in low palaeolatitudes (Cook & Taylor, 1989; Cook *et al.*, 1991). Considerable uncertainty remains concerning the palaeogeographic positions of tectonostratigraphic terranes of China.

A variety of geophysical, stratigraphic, structural, petrologic, and palaeontologic evidence has been used to assess plate-tectonic history. Faunal evidence is of particular importance in the lower Palaeozoic because other reliable geologic and geophysical evidence can be more difficult to obtain than for other intervals of the Phanerozoic. Distributions of fossils played a major role in Wilson's (1966) hypothesis of a proto-Atlantic Ocean, as well as in many subsequent studies of the history of the Iapetus Ocean. Distributional data continue to be important in current arguments about the definition and history of terranes in the circum-Atlantic region (e.g., Williams & Hatcher, 1982; Secor *et al.*, 1983; Samson *et al.*, 1990) and elsewhere.

Studies of the distribution of Cambrian trilobites worldwide (e.g., Palmer, 1969, 1972, 1979; Jell, 1974; Burrett & Richardson, 1980; Shergold, 1988; Robison, 1991) have demonstrated that shelf seas of the major cratonic areas of Laurentia, Baltica, Siberia, and Gondwana tended to have relatively large numbers of endemic

trilobite genera and species. Endemism is strongest among polymeroids, most of which were probably benthic. Most genera and many species of the largely pelagic agnostoids had cosmopolitan distributions in world oceans (e.g., Robison, 1972, 1984, 1988; Öpik, 1979).

Patterns of distribution of early Palaeozoic trilobites in the circum-Atlantic region have traditionally been used to define Atlantic (or Acado-Baltic) and Pacific (or North American) faunal provinces (e.g., Palmer, 1969, 1972; Poulsen, 1969; Cowie, 1971, 1974). Biotic exchange between these regions has been generally thought to have been limited by several factors, including the time available for larval migration across geographic distances (McKerrow & Cocks, 1976; Burrett & Richardson, 1980; Fortey & Cocks, 1986). In this interpretation, Iapetus may have been wide during the Cambrian (Conway Morris & Rushton, 1988). A trend of increasing similarity between North American and western European faunas during the Ordovician and Silurian has been inferred to result from the progressive closure of Iapetus and the elimination of faunal barriers (McKerrow & Cocks, 1976).

Studies of distributional patterns in the circum-Atlantic region, like most that have used biogeographic data to help determine the configuration of plates during the early Palaeozoic, have incorporated three major assumptions (Taylor & Forester, 1979). First, faunal elements were assumed to have been largely restricted to shallow-shelf seas of single continental blocks. Second, the shallow-shelf seas were surrounded by deeper oceans, which inhibited dispersal. Third, the degree of faunal dissimilarity between areas is assumed to have been a function of their past geographic separation (also see Sneath & McKenzie, 1973). Mounting evidence from the distributions of trilobites (Palmer, 1973; Fortey, 1975; Taylor, 1976, 1977; Cook & Taylor, 1975; Taylor & Cook, 1976; Ludvigsen, 1978; Taylor & Forester, 1979; Babcock & Robison, 1989; Robison & Babcock, 1990) and other organisms (Skevington, 1974; Sweet and Bergström, 1974; Barnes & Fähræus, 1975; Bergström & Carnes, 1976; Bergström, 1977; Fortey & Cocks, 1986) indicates that these assumptions are not always valid. Factors of the marine environment other than distance have probably had an important influence on the degree of faunal resemblance between geographic regions. Such factors may include latitudinal climatic gradients (e.g., Ekman, 1953; Valentine, 1973) and differences between shelf seas and the deep sea (e.g., Hedgpeth, 1957; Bruun, 1957; Menzies *et al.*, 1973; Benson, 1975, 1988; Taylor, 1977). The effects of both of these factors on faunal distributions have been disregarded or accorded minor importance in many studies of early Palaeozoic faunas. Also, they have

often been disregarded when synthesising geological and geophysical data for palaeogeographic reconstructions.

Biogeographic affinities of North Greenland polymeroid trilobites

Middle Cambrian rocks of North Greenland contain polymeroid trilobite assemblages of both Laurentian and Baltic aspect. Most polymeroids described by Poulsen (1927), Poulsen (1964), Palmer & Peel (1981), and Robison (1988) have closest affinities with trilobites that are characteristic of open-shelf areas of Laurentia. Polymeroids identified by Poulsen (1969) from Nyeboe Land, including *Eodiscus punctatus* and a paradoxidid (possibly *Centropleura*) have closest affinities with taxa characteristic of cratonic areas of Baltica. The observed geographic distributions of polymeroid taxa identified from the Henson Gletscher and Kap Stanton formations are summarised in Tables 1 to 4.

All genera in new Geological Survey of Greenland (GGU) collections (Babcock, 1994, but see also a preliminary notice by Fletcher *et al.*, 1988) from the *Glossopleura* Zone (Table 1) are widely distributed in open-shelf lithofacies of Laurentia. One genus, *Kootenia*, is also known from shelf lithofacies of present-day Asia and Australia. Two species, *Ogygopsis klotzi* and *Glossopleura walcotti*, have been recognised elsewhere in Laurentia.

In addition to its occurrence in North Greenland, *O. klotzi* is known from the Stephen Formation of British Columbia (Rasetti, 1951), the Metalline Formation of Washington (McLaughlin & Enbysk, 1950), the Miller Mountain Formation of Nevada (Nelson, 1963), the Cow Head boulders of western Newfoundland (Young & Lud-

Table 1. Distributions of polymeroid genera in the *Glossopleura* Zone of the Henson Gletscher Formation

TAXA	AN	AM	GB	AL	CR	OL
<i>Glossopleura walcotti</i>	-	-	s	-	G	-
<i>Kootenia nodosa</i>	G	G	G	G	G	G
<i>Ogygopsis klotzi</i>	s	s	s	G	s	-
<i>Syspacephalus</i> sp. 3	G	G	G	-	G	-

Observed geographic distributions of polymeroid genera (G) or genera and species (s) identified in the *Glossopleura* Zone of the Henson Gletscher Formation (hyphen indicates absence of a genus). Abbreviations of geographic regions are AN, northern Appalachia (western Newfoundland and Quebec); AM, middle Appalachia (New York and Pennsylvania); GB, Great Basin (Utah, Nevada, and California); AL, east-central Alaska; CR, Canadian Rocky Mountains; and OL, tectonic blocks other than Laurentia.

Table 2. Distributions of polymeroid genera in the *Ptychagnostus gibbus* Zone of the Henson Gletscher Formation

TAXA	AN	AM	GB	AL	CR	OL
<i>Bathyriscus</i> sp.	G	G	G	G	G	-
<i>Bolaspidella</i> sp.	-	G	G	G	-	G
<i>Olenoides</i> sp.	G	G	G	-	G	G
<i>Syspacephalus</i> sp. 2	G	G	G	-	G	-
<i>Zacanthoides</i> sp.	G	G	G	G	G	-

Observed geographic distributions of polymeroid genera (G) identified in the *Ptychagnostus gibbus* Zone of the Henson Gletscher Formation (hyphen indicates absence of a genus). Abbreviations of geographic regions are AN, northern Appalachia (western Newfoundland and Quebec); AM, middle Appalachia (New York and Vermont); GB, Great Basin (Utah, Nevada, and California); AL, east-central Alaska; CR, Canadian Rocky Mountains; and OL, tectonic blocks other than Laurentia.

vigsen, 1989), and the Kinzers Formation of Pennsylvania (Campbell, 1971). Each occurrence represents an open-shelf setting near the ocean-facing side of a carbonate platform. Other occurrences of *Ogygopsis* (Nelson, 1963; Palmer & Halley, 1979) indicate that the genus is most commonly associated with platform-edge environments (Palmer & Halley, 1979).

G. walcotti was first described from the Cape Wood Formation of Inglefield Land, North-West Greenland. Later, abundant material was reported from the Carrara Formation of Nevada and California (Palmer & Halley, 1979). *Glossopleura* was previously identified primarily

from restricted-shelf lithofacies (e.g., Robison, 1976; Palmer & Halley, 1979), but examination of collections at the University of Kansas and the U.S. National Museum of Natural History indicates that some species were more eurytopic than previously thought. In the Henson Gletscher Formation, *G. walcotti* is associated with such characteristic open-shelf taxa as *Ogygopsis* and *Syspacephalus*. *Kootenia*, with which it is also associated, is eurytopic (Robison, 1976).

Genera of polymeroids in GGU collection 298970 from the *Ptychagnostus gibbus* Zone have strongest affinities with genera from open-shelf environments of Laurentia (Table 2). *Syspacephalus* and *Zacanthoides* are known only from Laurentia. *Bolaspidella* is known with certainty from Laurentia (Robison, 1988) and the Precordillera terrane of Mendoza, Argentina (Poulsen, 1960). The Precordillera terrane may have been derived from Laurentia (Ramos *et al.*, 1986; Robison, 1991). The reported occurrence of *Bolaspidella* from Kashmir (Shah & Sudan, 1982) is probably in error (Robison, 1988). Except for *Zacanthoides*, which is eurytopic, all the genera are most commonly associated with open-shelf lithofacies. *Olenoides* inhabited open-shelf sites in Laurentia but was also present in Siberia, Kazakhstan, and Gondwana. *Kootenia* is a eurytopic genus that is common in Laurentia, but like some other dorypygids, it was rather widely distributed in low palaeolatitudes. Finally, *Eodiscus* was widespread in open-shelf settings around much of the world. Functional analyses of morphology and wide geographic distributions indicate that most eodiscids were pelagic or perhaps planktonic (Jell, 1975).

Table 3. Distributions of polymeroid genera in the *Ptychagnostus atavus* Zone of the Henson Gletscher and Kap Stanton formations

TAXA	AN	AM	GB	CR	AL	CM	SW	EN	SP	AU
<i>Bathyriscus concavus</i>	G	G	G	G	G	-	-	-	-	-
<i>Corynexochus?</i> sp.	-	-	-	-	G	-	G	G	-	-
<i>Costadiscus minutus</i>	-	-	-	-	-	-	-	-	-	-
<i>Dasometopus groenlandicus</i>	-	-	-	-	-	-	G	-	G	-
<i>Eodiscus scanicus</i>	-	-	-	-	-	s	s	s	-	-
<i>Hartshillia inflata</i>	-	-	-	-	-	G	-	s	G	-
<i>Olenoides</i> cf. <i>O. convexus</i>	s	G	G	G	-	-	-	-	G	-
<i>Opsidiscus longispinus</i>	-	-	-	-	-	-	G	-	-	G
<i>Parasolenopleura aculeata</i>	-	-	-	-	-	-	s	G	-	-
<i>Solenopleurella transversa?</i>	-	s	-	-	-	G?	G	G?	-	-
<i>Syspacephalus</i> sp. 1	G	G	G	G	-	-	-	-	-	-

Observed geographic distributions of polymeroid genera (G) or genera and species (s) identified in the *Ptychagnostus atavus* Zone of the Henson Gletscher and Kap Stanton formations (hyphen indicates absence of a genus). Abbreviations of geographic regions are AN, northern Appalachia (western Newfoundland and Quebec); AM, middle Appalachia (New York and Pennsylvania); GB, Great Basin (Utah and Nevada); AL, east-central Alaska; CR, southern Canadian Rocky Mountains; CM, maritime Canada except for western Newfoundland; SW, Sweden; EN, England south of the Caledonian suture; SP, Siberian platform; and AU, Australia.

Table 4. Distributions of polymeroid genera in the *Lejopyge laevigata* Zone of the Kap Stanton Formation

TAXA	AM	GB	SW	NO	EN	CM	BO	BI	SP	AU
<i>Anomocarina excavata</i>	–	–	s	s	–	–	–	s	s	–
<i>Centroleura angelini</i>	G	G	s	–	G	G	G	G	G	G
<i>Centroleura loveni</i>	G	G	s	–	G	G	G	G	s	G
<i>Elyx trapezoidalis</i>	G	–	G	G	–	G	–	–	G	–
<i>Solenopleura bucculenta</i>	G?	–	s	G	G	–	–	–	G	–

Observed geographic distributions of polymeroid genera (G) or genera and species (s) identified in the *Lejopyge laevigata* Zone of the Kap Stanton Formation (hyphen indicates absence of a genus). Abbreviations of geographic regions are AM, middle Appalachia (New York and Vermont); GB, Great Basin (Nevada); SW, Sweden; NO, Norway; EN, England south of the Caledonian suture; CM, maritime Canada except for western Newfoundland; BO, Bohemia; BI, Bennett Island; SP, Siberian platform; and AU, Australia.

This, together with the numerous pelagic agnostoids in GGU 298970 (Robison, 1994), suggests that trilobites in this collection had unrestricted access to the open ocean.

Polymeroids in new collections (Babcock, 1994) representing the *Ptychagnostus atavus* Zone are of mixed Laurentian and Baltic aspect (Table 3), and those in the *Lejopyge laevigata* Zone are entirely of Baltic aspect (Table 4). Patterns in the palaeogeographic distributions of polymeroids occurring in these two zones in North Greenland were explored using multivariate methods. Results, summarised in the following section, reveal a strong distinction between major faunal associations (biofacies) and some subtle but important associations.

Multivariate analyses of trilobite collections

Multivariate methods were used to explore patterns of faunal association among polymeroid trilobites from selected localities in North Greenland, North America, Scandinavia, and Great Britain. Faunas analysed are from the *Ptychagnostus atavus* and *Lejopyge laevigata* zones.

Binary (presence-absence) data were analysed using cluster analysis (CA) and multidimensional scaling (MDS). Analyses were performed using version 3 of the SYSTAT statistical package (SYSTAT, Inc.) on an Apple Macintosh II computer. Cluster analysis was used to separate data sets into discrete groups (see Hazel, 1970, 1977). In Q-mode analyses, objects (collections) were related to each other on the basis of their attributes (genera). In R-mode analyses, attributes (genera) were related to each other on the basis of the objects (collections) in which they occur. Clustering was performed on Euclidean distance coefficients using average linkage and unweighted pair group arithmetic means. Euclidean distance has the advantage of producing a distribution that closely approximates to the binomial probability distribution with data that are not sparse (C. G. Maples, personal communication, 1990). Therefore, values of Euclidean

coefficients can be tested for statistical significance by using binomial probabilities (see Archer & Maples, 1987; Maples & Archer, 1988). Confidence intervals established for clusters on data from the *L. laevigata* and *P. atavus* zones are listed in Table 5.

To test further the reliability of clusters, MDS was used in a manner analogous to R mode. The rationale for using it is that CA can distort between-group relationships, although relationships within compact groups are likely to be accurate (Kruskal, 1964a, 1964b; Hazel, 1977). MDS distributes distortion evenly between large and small distances (Hazel, 1977). Lastly, fidelity and constancy indices (Hazel, 1970, 1977; Hood & Robison, 1988) were calculated for all genera in principal clusters as measures of how well they characterise a particular cluster. A fidelity index measures the extent to which a taxon is confined to samples of a cluster. Fidelity (F) is defined by

$$F_{ji} = N_i / \sum N_i \star 10$$

where N_i is the number of collections in each cluster in

Table 5. Confidence intervals for clusters of trilobite presence-absence data

ZONE	N	P<0.10	P<0.05	P<0.01
<i>Lejopyge laevigata</i>	27	0.75	0.81	0.89
<i>Ptychagnostus atavus</i>	21	0.77	0.83	0.90

Confidence intervals for clusters of trilobite presence-absence data produced in Q-mode and R-mode, derived from a comparison of Euclidean distance coefficients to a binomial distribution (data provided by C. G. Maples). Samples on which cluster analysis was performed are from the *Lejopyge laevigata* and *Ptychagnostus atavus* zones. Coefficients greater than the listed values are considered to be statistically dissimilar. N indicates the number of columns in the data matrices.

which the species is present, and $\sum N_i$ is the total number of collections in which the species is present. A constancy index measures the extent to which a taxon is present in samples of a cluster compared to all possible occurrences. Constancy (C) is defined by

$$C_{ji} = N_i / T_i \star 10$$

where T_i is the total number of samples in a cluster. Both indices are rounded to the nearest whole number. Genera having both high fidelity and high constancy indices best define a cluster (Hazel, 1970).

Data on genera from 9 localities in the *L. laevigata* Zone and 10 localities in the *P. atavus* Zone were analysed. Collections chosen for analysis are either new (GGU 298969, 301313, and 319790) or from the published literature. Data compiled from published sources are mostly based on well-described collections but some identifications by Kindle (1982) are considered to be preliminary. For some taxa, nomenclatural revisions have been made to bring names into conformity with current taxonomic concepts. Except for GGU collections, collections were agglomerative and commonly included taxa pooled from two or more geographically close localities. Binary data, rather than frequency data, were chosen because taphonomic factors, including effects of preservation, diagenesis, and collecting, can render comparisons between frequency data suspect (Archer & Maples, 1987). Samples used are not of uniform size, and are not necessarily from the same ecological context (see Kaesler, 1966). Furthermore, the numerical abundance of preserved and identified taxa probably does not faithfully represent the original faunal composition (see Staff *et al.*, 1986). Trilobite data from other parts of the world were not included in the analysis partly because of differences in some generic concepts as applied outside of North America and western Europe. Also, the tendency of many shelf-dwelling Cambrian polymeroid genera to be endemic to a region or continent would produce data sets containing few presences and a large number of absences. Such sparse data will tend to skew calculations to emphasise differences between localities. Furthermore, they will tend to truncate zones of statistical significance (Maples & Archer, 1988).

Complete and reduced data matrices were analysed. The complete data matrix for samples from the *L. laevigata* Zone consisted of 75 genera from nine localities (collections). For the *P. atavus* Zone it consisted of 37 genera from 10 localities. In the reduced data matrices, genera present in only one collection were eliminated from analyses. Such taxa may be important constituents of individual collections, but they yielded little comparative information and tended to increase distance coeffi-

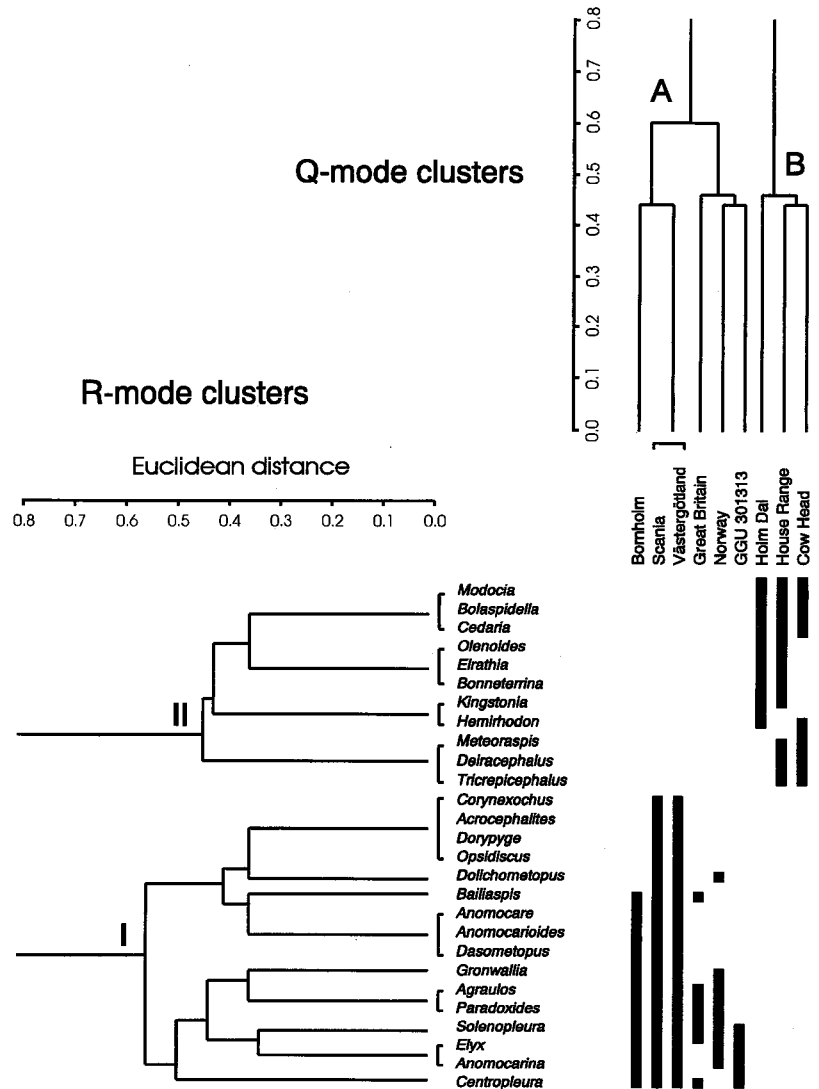
cients between collections. The smaller matrices contained 27 genera from the *L. laevigata* Zone and 21 genera from the *P. atavus* Zone. Both the complete and reduced matrices produced similar patterns of clusters. Different values of coefficients evidently resulted from collections that contained large numbers of genera not present in other collections. To illustrate better the similarities among collections, only results based on the smaller data matrices are discussed.

Analysed collections from the *L. laevigata* Zone include two from North Greenland (GGU 301313, herein; and Holm Dal Formation, Robison, 1988), four from Scandinavia (Scania and Västergötland in Sweden, Bornholm in Denmark, and Norway; Westergård, 1946, 1953), one from southern Great Britain (Thomas *et al.*, 1984), one from eastern Canada (Cow Head Group of Quebec, Kindle, 1982), and one from western North America (House Range, Utah; Robison, 1964, personal communication, 1989; Beebe, 1989).

Q-mode CA produced two principal clusters containing similar genera (Fig. 3, A, B). The average distance coefficient between clusters A and B is 0.82. The null hypothesis that there is no difference between these clusters is rejected at the 0.05 level (see Table 5). Cluster A includes GGU 301313 and collections from localities in Scandinavia and Great Britain south of the Caledonian suture. Cluster B includes collections from the Holm Dal Formation of North Greenland, the House Range of Utah, and the Cow Head boulders of western Newfoundland. The principal clusters correspond to localities that have polymeroid genera entirely of Baltic and Laurentian aspect, respectively. The lack of taxonomic overlap between collections may be partially a function of the collections chosen for study, but in large measure it seems to be indicative of a fundamental difference between trilobite biofacies. Examination of available literature shows that less than five percent of all polymeroids recorded from shelf lithofacies in the *L. laevigata* Zone of Laurentia are also present in coeval rocks of Baltica and the peri-Gondwanan terranes.

R-mode cluster analysis produced two primary clusters (Fig. 3, I, II) that show which groups of genera are responsible for the Q-mode clusters. The average distance coefficient between clusters I and II is 0.82. The null hypothesis that there is no difference between clusters is rejected at the 0.05 level (see Table 5). Cluster I contains 16 genera that are either geographically widespread or restricted to sites in North Greenland, Scandinavia, or Great Britain. Genera that previously have been observed only in Baltica include *Acrocephalites*, *Dolichometopus*, and *Gronwallia*. *Agraulos*, *Bailiaspis*, and *Paradoxides* have wider distributions but are best known from regions that were in high palaeolatitudes, including

Fig. 3. Cluster analysis of data on polymeroid collections from the *Lejopyge laevigata* Zone of North Greenland and selected localities in North America, Scandinavia, and Great Britain. Data are plotted in order formed by Q-mode clustering of collections and R-mode clustering of genera. Primary clusters are labelled with Roman numerals and uppercase letters. Cluster A contains genera of Baltic aspect, and cluster B contains genera of Laurentian aspect.



Baltica, Gondwana, and peri-Gondwanan terranes. *Anomocarina*, *Anomocarioides*, and *Dasometopus* are known from sites in Baltica and Siberia. *Dasometopus* and *Anomocarina* are reported by Babcock (1994) from North Greenland. *Elyx* has now been observed in Baltica, Siberia, Acadia, and North Greenland. From published records, *Centropheura*, *Corynexochus*, *Opsidiscus*, and *Solenopleura* all have relatively wide distributions, although not necessarily during the *L. laevigata* Biochron.

Cluster II contains eleven genera which are restricted to Laurentia except *Olenoides* and *Modocia*. *Olenoides* is diverse in Laurentia but was also present in shelf seas of Siberia, Kazakhstan, China, and the Precordillera terrane of Argentina. It, like some other genera assigned to the Dorypygidae (Poulsen in Harrington *et al.*, 1959: O217–O219), seems to have been widely distributed in

low palaeolatitudes. *Modocia* is a common and diverse genus in Laurentia, and the only verified occurrence other than Laurentia is a single specimen from England (Rush-ton, 1978).

Results using MDS (Fig. 4) are in close agreement with results of the CA. Genera that formed clusters in R-mode analysis form discrete, rather compact groups in two-dimensional MDS. The first dimension represents a contrast between the 16 genera of Baltic aspect and the 11 genera of Laurentian aspect. The second dimension primarily represents a contrast between more widespread genera and less widespread ones.

Fidelity and constancy indices for clusters (Fig. 3) are listed in Table 6. Cluster I contains 16 genera that define cluster A and have been collected from localities in Scandinavia, Great Britain, or Peary Land, North Greenland

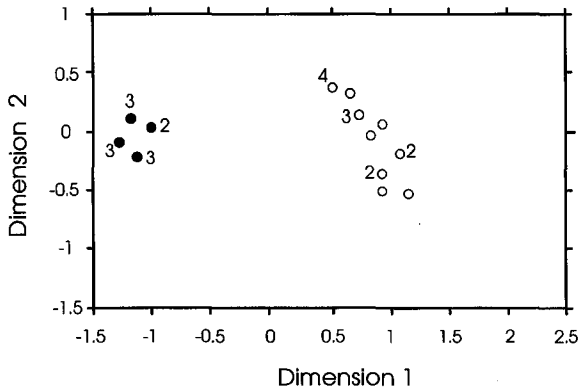


Fig. 4. Scattergram of coordinates of genera analysed by multi-dimensional scaling. Taxa analysed are from the *Lejopyge laevigata* Zone. Open circles correspond to polymeroid genera of Baltic aspect as defined in Q-mode cluster analysis, and closed circles correspond to genera of Laurentian aspect. A numeral next to a circle indicates the number of genera that are stacked vertically at that point.

(GGU 301313). All have high fidelity indices. Genera that also have high constancy indices are *Agraulos*, *Anomocarina*, *Bailiaspis*, *Centropleura*, *Elyx*, *Gronwallia*, *Paradoxides*, and *Solenopleura*. Some genera appear to have been largely restricted to Baltica and England but, as indicated above, this is an artifact of the localities that were chosen for analysis. Cluster II includes genera that define cluster B and that are most common in open-shelf lithofacies of North America. All have high fidelity and constancy indices. Except for *Olenoides* and *Modocia*, all are restricted to Laurentia. Extra-Laurentian samples containing these genera, however, were not included in the analysis.

Trilobite samples from the *L. laevigata* Zone of the Kap Stanton Formation are interpreted to represent autochthonous associations of trilobites in deep, outermost shelf or possibly upper slope lithofacies. Specimens are commonly articulated and fragile fossils preserved parallel to bedding in dark, organic-rich lime mudstone. Disarticulated sclerites are also common, but are generally unbroken. Some specimens represent undisturbed moulted exoskeletons. Specimens range from small mesaspides to large holaspides. Little post-mortem or post-moulted transportation of sclerites is indicated. Furthermore, the presence of undisturbed laminae indicates little or no faunal mixing by bioturbation. All four genera and four of five species present in these collections (Table 4) are also present in coeval rocks of Scandinavia. Some genera or species are found in open-shelf lithofacies of southern Great Britain, Siberia, Kazakhstan, Australia, or China. None of the genera is present in coeval rocks of the Holm Dal Formation (see Robison, 1988). This is

remarkable in view of the fact that section 3, where trilobites of Baltic aspect were found, is only about 40 km from the type section of the Holm Dal Formation in Peary Land (Fig. 1). The Holm Dal Formation contains trilobites primarily of Laurentian aspect (see Robison, 1988). Major tectonic dislocation has not been observed in this region (Fletcher *et al.*, 1988; Higgins *et al.*, 1991). Rocks of the Holm Dal Formation represent an inferred low energy, open-shelf environment (Ineson, 1988); water depths were probably significantly less than those in which the sediments of the lower Kap Stanton Formation, as seen along J. P. Koch Fjord, were deposited.

Collections analysed from the *P. atavus* Zone include two from North Greenland (GGU 298969 and 319790; Babcock, 1994), one from western North America (House Range, Utah; Robison, 1964 and unpublished data), two from eastern Canada (Cow Head Group, Quebec, Kindle, 1982; and south-eastern Newfoundland,

Table 6. Fidelity and constancy indices for polymeroids from the *Lejopyge laevigata* Zone

	CLUSTER A			CLUSTER B		
	F	C	N	F	C	N
<i>Modocia</i>	-	-	-	10	10	3
<i>Bolaspidella</i>	-	-	-	10	10	3
<i>Cedaria</i>	-	-	-	10	10	3
<i>Olenoides</i>	-	-	-	10	7	2
<i>Elrathia</i>	-	-	-	10	7	2
<i>Bonneterina</i>	-	-	-	10	7	2
<i>Kingstonia</i>	-	-	-	10	7	2
<i>Hemirhodon</i>	-	-	-	10	7	2
<i>Meteoraspis</i>	-	-	-	10	7	2
<i>Deiracephalus</i>	-	-	-	10	7	2
<i>Tricrepecephalus</i>	-	-	-	10	7	2
<i>Corynexochus</i>	10	3	2	-	-	-
<i>Acrocephalites</i>	10	3	2	-	-	-
<i>Dorypyge</i>	10	3	2	-	-	-
<i>Opsidiscus</i>	10	3	2	-	-	-
<i>Dolichometopus</i>	10	5	3	-	-	-
<i>Bailiaspis</i>	10	7	4	-	-	-
<i>Anomocare</i>	10	5	3	-	-	-
<i>Anomocarioides</i>	10	5	3	-	-	-
<i>Dasometopus</i>	10	5	3	-	-	-
<i>Gronwallia</i>	10	7	4	-	-	-
<i>Agraulos</i>	10	8	5	-	-	-
<i>Paradoxides</i>	10	8	5	-	-	-
<i>Solenopleura</i>	10	10	6	-	-	-
<i>Elyx</i>	10	8	5	-	-	-
<i>Anomocarina</i>	10	8	5	-	-	-
<i>Centropleura</i>	10	8	5	-	-	-

Fidelity (F) and constancy (C) indices for polymeroids in two Q-mode clusters shown in Fig. 3 from the *Lejopyge laevigata* Zone. The number of collections containing a genus is listed under N. A hyphen indicates the absence of a genus from a cluster.

Hutchinson, 1962), three from Scandinavia (Norway, Västergötland, and Bornholm; Westergård, 1946, 1953), and one from southern Great Britain (Thomas *et al.*, 1984). The GGU collections include specimens in both mudstone and packstone. Genera preserved in both lithologies were grouped together in this analysis because all that are present in mudstone are also present in packstone.

CA in Q mode produced two primary clusters (Fig. 5, A, B) that show major faunal differences between collections containing polymeroids of Laurentian and Baltic aspect. The Euclidean distance coefficient between clusters A and B is 0.76, which is considered to be of borderline statistical significance at the 0.1 level (see Table 5). Cluster A contains collections from Great Britain, south-eastern Newfoundland, Scandinavia (Västergötland, Bornholm, Scania, and Norway), and North Greenland (GGU 298969 and 319790). Cluster B con-

tains collections from the House Range, Utah, and the Cow Head Group, western Newfoundland.

GGU collections 298969 and 319790 from North Greenland and collections from boulders of the Cow Head Group of Newfoundland all consist of mixed assemblages of polymeroids having Laurentian and Baltic aspect. All polymeroids in the GGU collections preserved in mudstone are of Baltic aspect and probably represent trilobites indigenous to the deep, outermost shelf lithofacies. Most polymeroids preserved in packstone are also of Baltic aspect. One of 5 genera (20 percent) in GGU 298969 and 2 of 6 genera (33 percent) in GGU 319790, however, are of Laurentian aspect. Most polymeroids from the Cow Head collections are of Laurentian aspect but 4 of 10 genera (40 percent) are of Baltic aspect. A few trilobites of Laurentian or Baltic aspect may have coexisted in some places, but the differences between taxa preserved in mudstone and packstone in North Greenland

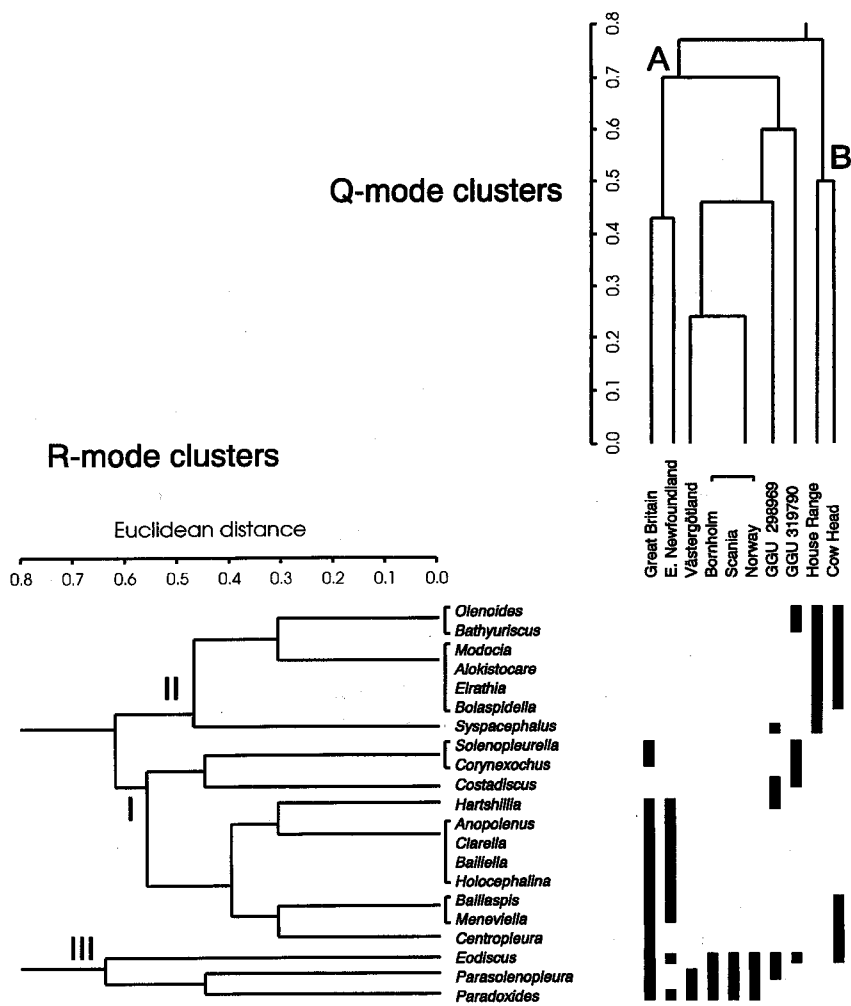


Fig. 5. Cluster analysis of data on polymeroid collections from the *Ptychagnostus atavus* Zone of North Greenland and selected localities in North America, Scandinavia, and Great Britain. Data are plotted in order formed by Q-mode clustering of collections and R-mode clustering of genera. Primary clusters are labelled with Roman numerals and uppercase letters. Cluster A contains genera of Baltic aspect (except *Olenoides*, *Bathyriscus*, and *Syspacephalus*), and cluster B contains genera of Laurentian aspect.

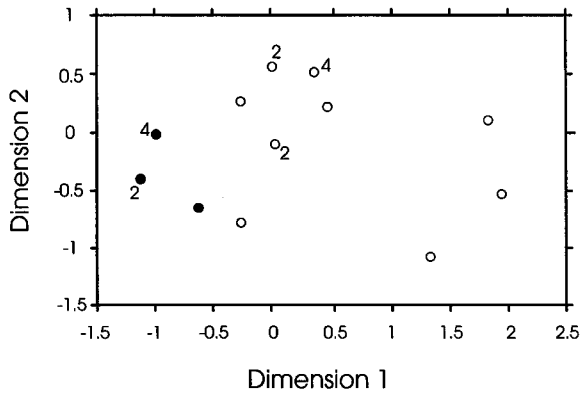


Fig. 6. Scattergram of coordinates of genera analysed by multi-dimensional scaling. Taxa analysed are from the *Ptychagnostus atavus* Zone. Open circles correspond to polymeroid genera of Baltic aspect as defined in Q-mode cluster analysis, and closed circles correspond to genera of Laurentian aspect. A numeral next to a circle indicates the number of genera that are stacked vertically at that point.

suggest that biofacies of polymeroids were strongly differentiated.

Stratigraphic and sedimentologic evidence suggest that trilobites in GGU collections 298969 and 319790 and collections from the Cow Head Group have been mixed by sedimentary processes. All of these collections contain disarticulated and fragmented trilobite sclerites and occur in deeper-water successions that accumulated basinward of steep-rimmed, shallow-water carbonate platforms. The specimens from North Greenland that are preserved in packstone are crudely size-sorted, and are interpreted to have been redeposited by sediment gravity flows (see Ineson, 1980 and discussion in Ineson *et al.*, 1994). The Cow Head material was collected from limestone breccia that was inferred to have been deposited by gravity flow (Hubert *et al.*, 1977; Hiscott & James, 1985; James & Stevens, 1986). Boulders in the Cow Head Group represent several depositional lithofacies (Kindle, 1982; James & Stevens, 1986).

R-mode CA produced three primary clusters (Fig. 5, I–III). Cluster I contains all of the genera of Baltic aspect except *Eodiscus*, *Parasolenopleura*, and *Paradoxides*, which form cluster III. Genera in clusters I and III are responsible for cluster A produced in Q mode. Cluster II contains seven genera characteristic of open-shelf sites in Laurentia. These taxa are responsible for cluster B produced in Q mode. The average Euclidean distance coefficient between clusters I and II is 0.63. The null hypothesis that there is no difference between clusters I and II cannot be rejected ($P > 0.1$; see Table 5). The rather low distance coefficient is probably due mostly to the presence of three mixed collections (GGU 298969, GGU

319790, and Cow Head Group) in the analysis. The distance coefficient between clusters I + II and III is 0.82, which is considered to be of borderline statistical significance at the 0.1 level (see Table 5). Cluster III contains three genera that were evidently widespread. The cluster has a high level of dissimilarity from the other clusters probably because the contained genera are widely distributed among localities that contain polymeroids of Baltic aspect.

Results of MDS (Fig. 6) illustrate the relatively lower distance coefficients between clusters containing polymeroids of mostly Baltic aspect (Fig. 5, A) and Laurentian aspect (Fig. 5, B), compared to samples analysed from the *L. laevigata* Zone. Genera that comprise clusters A and B form loose clusters. Most of the taxa in cluster B have coordinates near those in cluster A. *Eodiscus*, *Paradoxides*, and *Parasolenopleura* have coordinates that are most distant from taxa in cluster A. The first axis has been fitted primarily to the contrast between polymeroids of Laurentian and Baltic aspect. The second axis is fitted primarily to the contrast between more widespread and less widespread genera.

Fidelity and constancy indices for polymeroids from

Table 7. Fidelity and constancy indices for polymeroids from the *Ptychagnostus atavus* Zone

	CLUSTER A			CLUSTER B		
	F	C	N	F	C	N
<i>Olenoides</i>	–	–	–	7	10	3
<i>Bathyriscus</i>	–	–	–	7	10	3
<i>Modocia</i>	–	–	–	10	10	2
<i>Atokistocare</i>	–	–	–	10	10	2
<i>Elrathia</i>	–	–	–	10	10	2
<i>Bolaspidella</i>	–	–	–	10	10	2
<i>Syspacephalus</i>	–	–	–	5	5	2
<i>Solenopleurella</i>	10	3	2	–	–	–
<i>Corynexochus</i>	10	3	2	–	–	–
<i>Costadiscus</i>	10	3	2	–	–	–
<i>Hartshillia</i>	10	4	3	–	–	–
<i>Anopolenus</i>	10	3	2	–	–	–
<i>Clarella</i>	10	3	2	–	–	–
<i>Bailiella</i>	10	3	2	–	–	–
<i>Holocephalina</i>	10	3	2	–	–	–
<i>Bailiaspis</i>	7	3	3	–	–	–
<i>Meneviella</i>	7	3	3	–	–	–
<i>Centropleura</i>	5	1	2	–	–	–
<i>Eodiscus</i>	9	9	8	–	–	–
<i>Parasolenopleura</i>	10	8	6	–	–	–
<i>Paradoxides</i>	10	8	6	–	–	–

Fidelity (F) and constancy (C) indices for polymeroids in two Q-mode clusters shown in Fig. 5 from the *Ptychagnostus atavus* Zone. The number of collections containing a genus is listed under N. A hyphen indicates the absence of a genus from a cluster.

the *P. atavus* Zone are listed in Table 7. Except for *Centropleura*, all 14 genera that produced cluster A have high fidelity indices. Those that also have high constancy indices are *Eodiscus*, *Paradoxides*, and *Parasolenopleura*. All genera in cluster B except *Syspacephalus* have high fidelity and constancy values. *Syspacephalus* is restricted to Laurentia, but disarticulated sclerites have been found in one mixed assemblage, GGU 298969, in which most polymeroids are of Baltic aspect.

In summary, collections from packstone beds of the *P. atavus* Zone of North Greenland (e.g., GGU 298969 and 319790) contain polymeroids of both Laurentian and Baltic aspects. Most examined specimens are disarticulated and fragmented. Polymeroids in the intervening mudstones are entirely of Baltic aspect, and tend to be found articulated. Trilobites in mudstone are interpreted to have been indigenous to the deep outermost shelf. Those in packstone, however, have probably been mixed by sediment gravity-flow processes introducing skeletal material typical of outer-shelf environments into the deeper-water setting.

Environmental relationships of trilobites

Middle Cambrian strata of the *L. laevigata* and *P. atavus* zones of North Greenland include biofacies dominated by polymeroids having either Laurentian or Baltic aspect. Trilobites of Baltic aspect were evidently indigenous to the deep outermost shelf or upper basin slope, whereas those of Laurentian aspect inhabited open-shelf lithofacies. Resedimentation of trilobite sclerites has resulted in the mixing of trilobites of different aspects in some beds of the *P. atavus* Zone (Fig. 7).

In recent years, faunal differences in Cambrian rocks have been commonly attributed to environmental gradients in which temperature played a major role (Cook & Taylor, 1975, 1977; Taylor, 1976, 1977; Taylor & Cook 1976; Taylor & Forester, 1979; Theokritoff, 1979; Conway Morris & Rushton, 1988; Shergold, 1988; Babcock & Robison, 1989; Robison & Babcock, 1990). Stratigraphic and biogeographic evidence has been presented to show that some oceans were thermally stratified during the Early Cambrian (Theokritoff, 1979) and the Late Cambrian (e.g., Taylor & Forester, 1979), just as they are during the Holocene (e.g., Benson, 1975, 1988). The results presented in this paper suggest that ocean waters

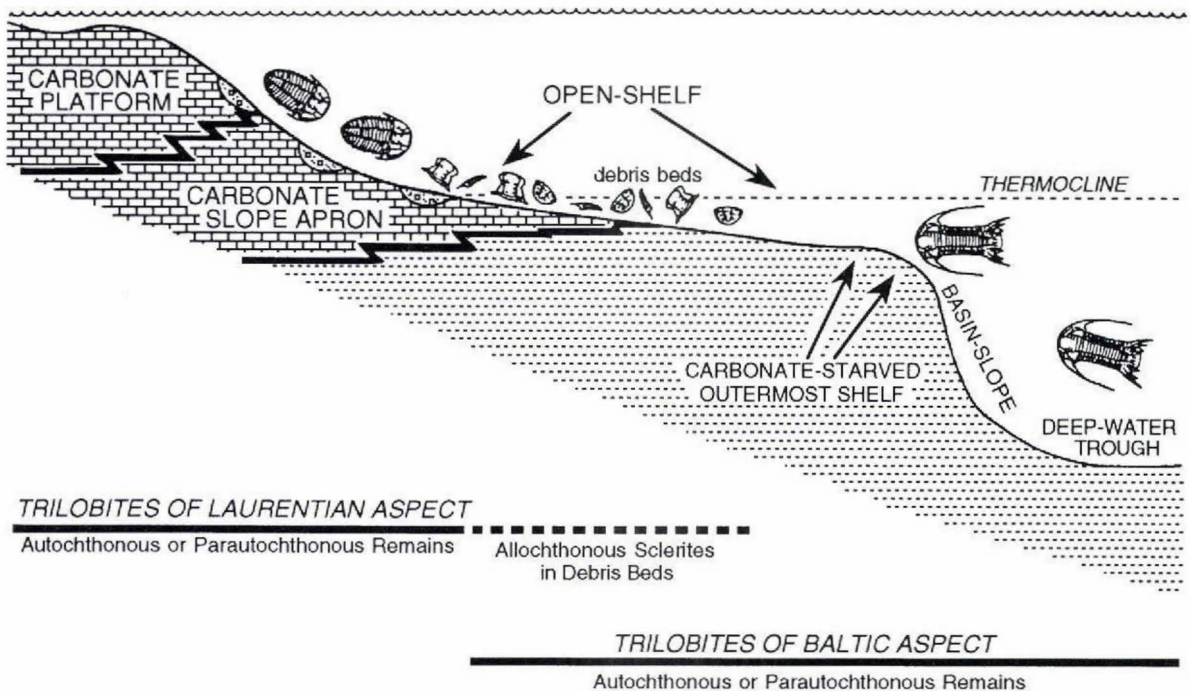


Fig. 7. Model of the Inuitian margin of Laurentia off present-day North Greenland during the Middle Cambrian illustrating the relationships of physiography, sedimentation patterns, and trilobite biofacies. Polymeroid trilobites of Baltic aspect (represented by *Centropleura*, right) are inferred to have lived below the permanent thermocline. Fossils of Baltic trilobites are preserved in lime mudstone and are commonly articulated. Polymeroids of Laurentian aspect (represented by *Bathyriscus*, left) are inferred to have lived in warm shallower water above the thermocline but their disarticulated remains (represented by isolated sclerites of *Bathyriscus*) were dispersed basinward by gravity displacement of sediment and redeposited in debris beds.

surrounding Laurentia were also thermally stratified during the Middle Cambrian (Fig. 7). Other postulated explanations for biogeographic barriers, including a deep-water basin (see Wilson, 1966; Cowie, 1971) and a land barrier (Ulrich & Schuchert, 1902), were reviewed by Theokritoff (1979). Theokritoff rejected the idea that a deep-water basin was alone sufficient to act as a biogeographic barrier on both uniformitarian arguments and evidence about the distribution of some Early Cambrian trilobites. The notion of a land barrier was rejected on the basis of biogeographic and stratigraphic evidence.

The terms thermosphere and psychrosphere (Bruun, 1957) describe the divisions of the world oceans that are respectively above and below the permanent thermocline. In low and intermediate latitudes, warmer, less dense waters of the thermosphere, which are characterised by temperatures higher than 10°C, float above cooler, more dense waters of the psychrosphere, which are characterised by temperatures lower than 10°C (Bruun, 1957; Benson, 1975). In present-day, high-latitude shelf areas, the thermosphere is not present.

Based on an analysis of modern isopod biofacies, Taylor & Forester (1979) found that faunas indigenous to warm shelves in low latitudes show strong similarities to other warm-water faunas and strong dissimilarities to faunas in cool marine waters. Those from cool waters show a high degree of similarity whether they are in high latitudes or in low latitudes below the permanent thermocline. It is likely that thermal stratification of water masses during parts of the early Palaeozoic similarly affected the biogeographic distributions of trilobites (see Taylor & Forester, 1979). The mostly endemic shelf faunas of Laurentia are inferred to have been adapted to warm water, whereas faunas described from shelf areas of Baltica and southern Gondwana or from peri-Gondwanan terranes located in south-polar regions are inferred to have been adapted to cool water.

Taylor & Forester (1979) listed three criteria that they considered to be necessary to demonstrate the presence of a two-layered thermally stratified Palaeozoic ocean. They are (1) evidence of deep-water environments, (2) strong biofacies differences between indigenous faunas of deep-water environments and those of adjacent warm shelves, and (3) widely distributed deep-water faunas that show greatest taxonomic resemblance to faunas in other deep-water environments and shallow-water environments of high latitudes.

Rocks and faunas of the *L. laevigata* and *P. atavus* zones of North Greenland meet Taylor & Forester's criteria. First, deep-water shelf environments, basinward of the carbonate platform are represented by the Henson Gletscher and Kap Stanton formations. Rocks from those units are interpreted (Ineson *et al.*, 1994) to represent

open-shelf to deep, outermost shelf (or possibly basin-slope) environments along the Inuitian margin of Laurentia.

Second, indigenous deeper-water polymeroid faunas of North Greenland show strong dissimilarities with coeval faunas from the adjacent warm-water Laurentian shelf. Polymeroid faunas of the *L. laevigata* Zone that were indigenous to putative deep, outermost shelf environments do not share any genera or species with a fauna reported from the coeval Holm Dal Formation (Robison, 1988), which was deposited in an inferred low energy, open-shelf setting (Ineson, 1988). Trilobites described from the type section of the Holm Dal Formation were collected approximately 40 km south of locality 3 (Fig. 1), indicating that faunal changes between the shelf and slope were abrupt.

Shallower water faunas from the *P. atavus* Zone of North Greenland were not available for comparison. Nevertheless, comparison of trilobites in mudstone and packstone from GGU collections 298969, 319789, and 319790 indicate a strong faunal dissimilarity between putative open-shelf-dwelling and deep, outermost shelf-dwelling polymeroids. Some polymeroids found as re-sedimented particles in GGU collections are interpreted to have been derived from open-shelf settings where polymeroids of Laurentian aspect predominated. Two species, *Olenoides* cf. *O. convexus* and *Solenopleurella transversa*, have been previously described from open-shelf sites elsewhere in Laurentia. Except for the eodiscid *Costadiscus*, which is known only from North Greenland, polymeroids in undisturbed mudstone are exclusively of Baltic aspect.

Finally, polymeroids indigenous to putative deep, outermost shelf or upper slope environments of the *L. laevigata* and *P. atavus* zones in North Greenland are taxonomically most similar to faunas from shallow-shelf environments of cool, high-latitude areas of Baltica, Acadia, Armorica, and England. Some taxa, including *Centropleura*, *Eodiscus*, and solenopleurids, are also known from deep-water Laurentian sites in north-western Vermont (Howell, 1937; Shaw, 1966), south-eastern New York (Rasetti, 1967) and central Nevada (Stewart & Palmer, 1967; Palmer & Stewart, 1968; Babcock, 1990). Indigenous deep-water polymeroids of the Henson Gletscher and Kap Stanton formations evidently did not also inhabit shallower water environments of the Laurentian shelf. Where trilobites of mixed Laurentian and Baltic aspect have been found in the same beds, evidence suggests that they were brought together by taphonomic processes.

Polymeroids of the *P. atavus* Zone in Nyeboe Land support stratigraphic and structural evidence (Fletcher *et al.*, 1988; Higgins *et al.*, 1991; Surlyk, 1991) that these

rocks are *in situ* and were not accreted by plate collision. Minimal fragmentation and lack of size sorting suggest that specimens preserved in mudstone probably are autochthonous or parautochthonous to environments at continental margins, including deep, outermost shelf and perhaps slope areas. Specimens in packstone, which are more fragmented and size sorted, are interpreted to have been redeposited. Many were probably carried basinward from proximal shelf sites by gravity flows. Analogous deposits containing resedimented trilobites that were near the Laurentian continental margin have been described from the Upper Cambrian of central Nevada (Cook & Taylor, 1975, 1977; Taylor, 1976; Taylor & Cook, 1976). There, redeposited warm-water trilobites of Laurentian aspect are interbedded with indigenous trilobites having an Asian aspect. Other possible continental slope deposits that contain resedimented trilobites of mixed provincial affinities (Taylor & Forester, 1979) include some in the Taconic sequence of New York (Bird & Theokritoff, 1968; Bird & Rasetti, 1968), the Cow Head Group of western Newfoundland (Babcock, 1991; see Kindle, 1982), and the Collier Shale of Arkansas (Hart *et al.*, 1987; Hohensee & Stitt, 1989).

Geological implications

During the Middle Cambrian, separate polymeroid biofacies developed in warm waters of the Laurentian open-shelf and in cool waters of deeper, outermost shelf to uppermost basin or slope? areas. Most genera and almost all species found in open-shelf lithofacies were endemic to Laurentia. Important exceptions are genera of the Dorypygidae (especially *Dorypyge*, *Kootenia* and *Olenoides*) which are widespread in shelf facies of some tectonic plates that were in low palaeolatitudes. Most genera and species of polymeroids from deeper-water habitats of North Greenland seem to be the same as those from cool, shallow-shelf sites of Baltica or peri-Gondwanan terranes.

The presence of polymeroids of Baltic aspect in Laurentian rocks of Nyeboe Land and Peary Land, North Greenland, has important implications for reconstructing the history of tectonic blocks during the early Palaeozoic. It is evident that the presence of trilobites of Baltic aspect in a suspect terrane attached to a tectonic plate that was in low palaeolatitudes is not sufficient evidence in itself to conclude that the terrane is exotic. An exotic terrane is one that has moved from a distant source and subsequently accreted to another tectonic plate. A native terrane, by comparison, can include deep-shelf, slope or basinal areas adjacent to or on the tectonic plate with which it is now associated. The presence of cool-water trilobites of Baltic aspect in a suspect terrane has been

commonly used as evidence of an origin in high latitudes. Some cool-water biofacies, however, are similar to each other regardless of latitude or depth and a suspect terrane containing such trilobites could in fact have an origin either in high latitudes or in deep water of low latitudes.

Cool waters evidently were avenues for the dispersal of some organisms (Taylor & Forester, 1979). On this account, the degree of taxonomic dissimilarity among cool-water faunas of different regions is not necessarily a function of the palaeogeographic distance between those areas. Thus, conclusions about the latitudinal separation of tectonic blocks during the geological past that are based on differences between warm-water and cool-water biofacies are suspect. Conclusions about palaeolatitude based on faunas and lithofacies from shelf successions are more reliable, but palaeomagnetic evidence remains the best indicator of the original latitudinal positions of terranes.

The presence of mixed assemblages of warm-water and cool-water biofacies in the *P. atavus* Zone of North Greenland illustrates a method by which autochthonous terranes of the outer continental shelf or slope can be identified (Babcock, 1991). Taphonomic, sedimentologic, and stratigraphic evidence needs to be examined before assemblages of mixed aspect can be determined to represent organisms that either lived together or were redeposited as bioclastic debris from ecologically separate biofacies. In addition to improving interpretations of the tectonic history of suspect terranes, study of mixed assemblages in continental shelf and slope environments may help to improve the resolution of biostratigraphic correlations between separate continents.

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