Trilobite and lithofacies relationships in the Holm Dal Formation (late Middle Cambrian), central North Greenland

KENNETH C. HOOD and RICHARD A. ROBISON

Hood, K. C. & Robison, R. A. 1988. Trilobite and lithofacies relationships in the Holm Dal Formation (late Middle Cambrian), central North Greenland. Meddr Grønland, Geosci. 20: 105–112. Copenhagen 1988-12-31.

Multivariate techniques show a strong relationship between trilobite species and lithofacies of the Holm Dal Formation. Presence-absence data on 58 species of trilobites, including 43 polymeroids and 15 agnostoids, were analyzed. Q-mode cluster analysis produced three lithologically homogeneous groups of samples: lime grainstones from Peary Land, lime mudstones from Freuchen Land, and lime mudstones from Peary Land. Nonmetric multidimensional scaling supports the reliability of the Q-mode groups, and stepwise discriminant function analysis indicates that lithology can be discriminated using a four-variable model of *Catillicephala rotunda*, *Hemirhodon* sp., *Marjumia brevifrons*, and *Modocia planata*. R-mode cluster analysis produced four groups of species: grainstone species, Peary Land mudstone species, Freuchen Land mudstone species, and agnostoid species present in all lithofacies. The intersections of Q-mode and R-mode clusters define lithofacies-related faunal associations. These techniques also call attention to samples with unusual faunal compositions and species with unusual distributions.

The distribution of most agnostoids differs from that of most polymeroids, supporting the conclusion that agnostoids were adapted to a different mode of life from that of polymeroids. The distribution of agnostoids was probably controlled by physical and chemical factors that were not dependent on bottom sediment or conditions.

K. C. Hood and R. A. Robison, Department of Geology, University of Kansas, Lawrence, Kansas 66045, U. S. A.

Quantitative analysis of trilobite data from the Holm Dal Formation (late Middle Cambrian) of central North Greenland (Fig. 1) using multivariate techniques was used to explore patterns of faunal association and environmental control of faunal distribution. Results of these analyses revealed strong lithofacies relationships for some of the Holm Dal fauna and elucidated subtle differences and associations. Presence-absence data on 58 species of trilobites (Robison, this volume, figs 2–6), including 43 species of polymeroids and 15 species of agnostoids, were analyzed. These data are especially suited for evaluation of lithofacies relationships of fauna because many species range through much of the formation and because collections are all from a small geographical area. Differences in faunal associations, therefore, are likely to have resulted from local environmental factors rather than evolutionary changes or geographical isolation.

Trilobites were identified (Robison, this volume) from 34 carbonate samples collected by J. S. Peel of the Geological Survey of Greenland (GGU). Samples were assigned to lithological categories following Dunham (1962) and relate to lithofacies described by Ineson (this volume). The 34 samples include 11 grainstones, 2 packstones, 2 wackestones, and 19 mudstones. The relatively few packstones and wackestones, together with the necessarily arbitrary classification of borderline samples, make it preferable to discuss lithology in terms of the grainstone and mudstone end members. Differences in depositional conditions between grainstone and mudstone end members are more pronounced than if intermediate lithological categories are considered. Affinities of the packstones and wackestones will be discussed subsequently.

To reduce the size of the data matrix and to simplify interpretations, species that are limited to only 1 or 2 collections were eliminated from analyses. Such rare species may be important components of individual collections, but they provide little comparative information and tend to lower similarities. The smaller data matrix contains 41 species, including 30 polymeroids and 11 agnostoids, from 34 collections. Both the complete and the reduced matrices were analyzed with similar results. Therefore, only results based on the smaller matrix are discussed. Binary (presence-absence) data were chosen because samples were neither of uniform size nor of the same ecologic meaning (Kaesler 1966), and the numerical abundance of preserved taxa probably does not represent the original faunal composition (Staff et al. 1986).

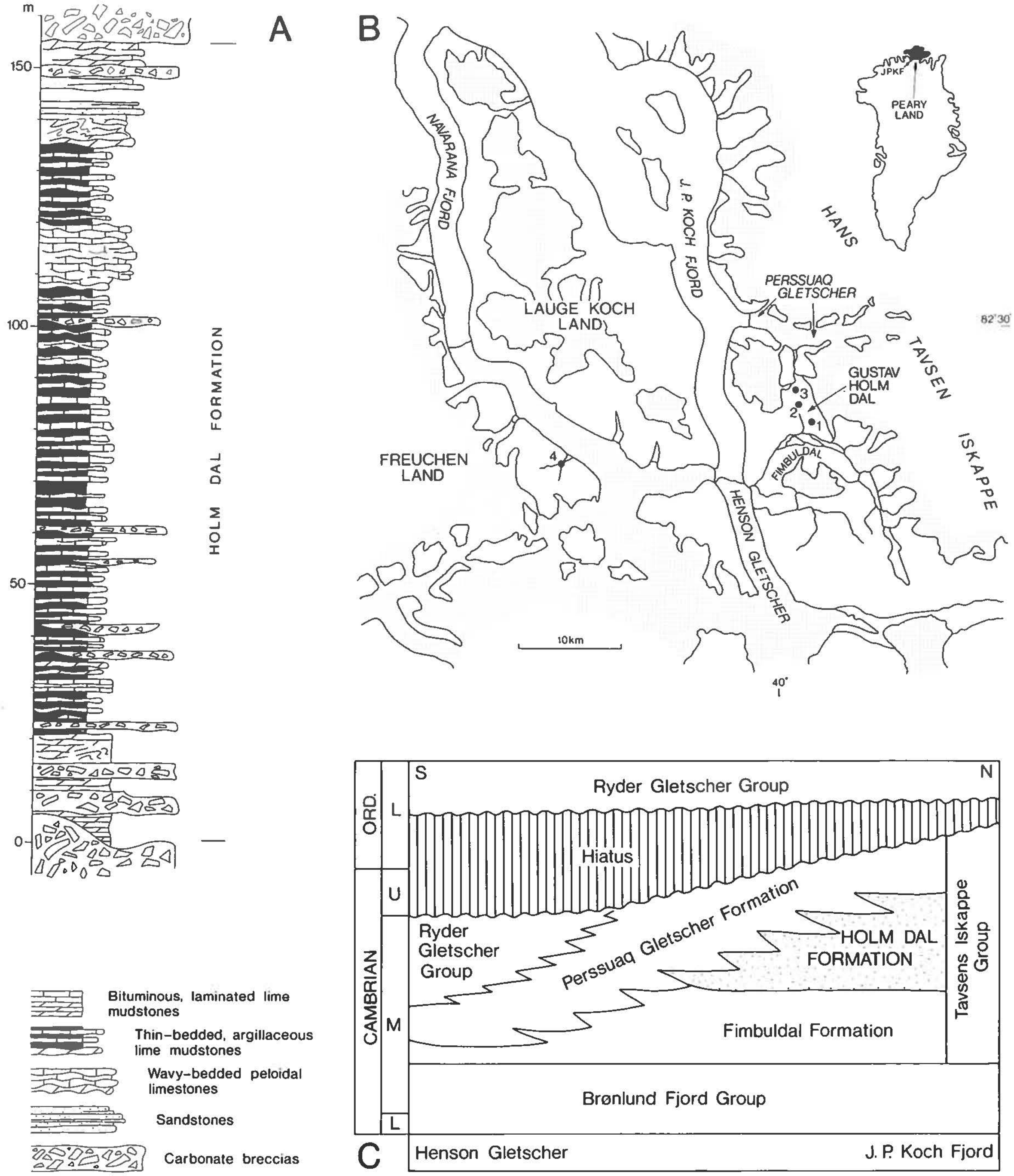

Fig. 1. Geographical and geological relationships of the Holm Dal Formation. A, stratigraphic section through the Holm Dal Formation at its type locality (locality 1 in Fig. 1B; from Ineson, this volume). B, map of the area around Gustav Holm Dal, westernmost Peary Land, central North Greenland showing collection localities within the Holm Dal Formation (1–4). 1, the type section and adjacent area, GGU samples in the sequence 225528–225567; 2, Gustav Holm Dal, GGU samples 225586, 271403, 271404, 271408, 271414, 271417; 3, Gustav Holm Dal, GGU samples 225592–225595; 4, south-east Freuchen Land, GGU samples 315007, 315009, 315011–315013. Inset map of Greenland shows location of Peary Land and J. P. Koch Fjord (JPKF). Full description of trilobites from the respective collections is given by Robison (this volume). C, stratigraphic relationship of the Holm Dal Formation (from Ineson, this volume).

Cluster analyses and nonmetric multidimensional scaling were done using the Numerical Taxonomy System of Multivariate Statistical Programs (NT-SYS; Rohlf et al. 1972), and discriminant function analysis was done using Biomedical Computer Programs (BMDP; Dixon 1983).

Results of analysis

Cluster analysis is a convenient multivariate technique for distinguishing groupings within data (Sokal & Sneath 1963; Sneath & Sokal 1973). Both Q-mode and R-mode cluster analyses were performed. In Q-mode analyses, objects (samples) are related to each other on the basis of their attributes (species). In R-mode analyses, attributes are related to each other on the basis of the objects in which they are found (Hazel 1970). Clustering was performed on a similarity matrix of Jaccard's coefficients (Jaccard 1908) using unweighted pair group arithmetic means (UPGM). Similarity coefficients were used because they generally give more easily interpreted results than distance coefficients (Hazel 1970), and UPGM were used because they produce the smallest amount of distortion (Cheetham & Hazel 1969; Hazel 1970; Rowell et al. 1973). Most of the clusters form at relatively low levels, probably because Jaccard's coef-

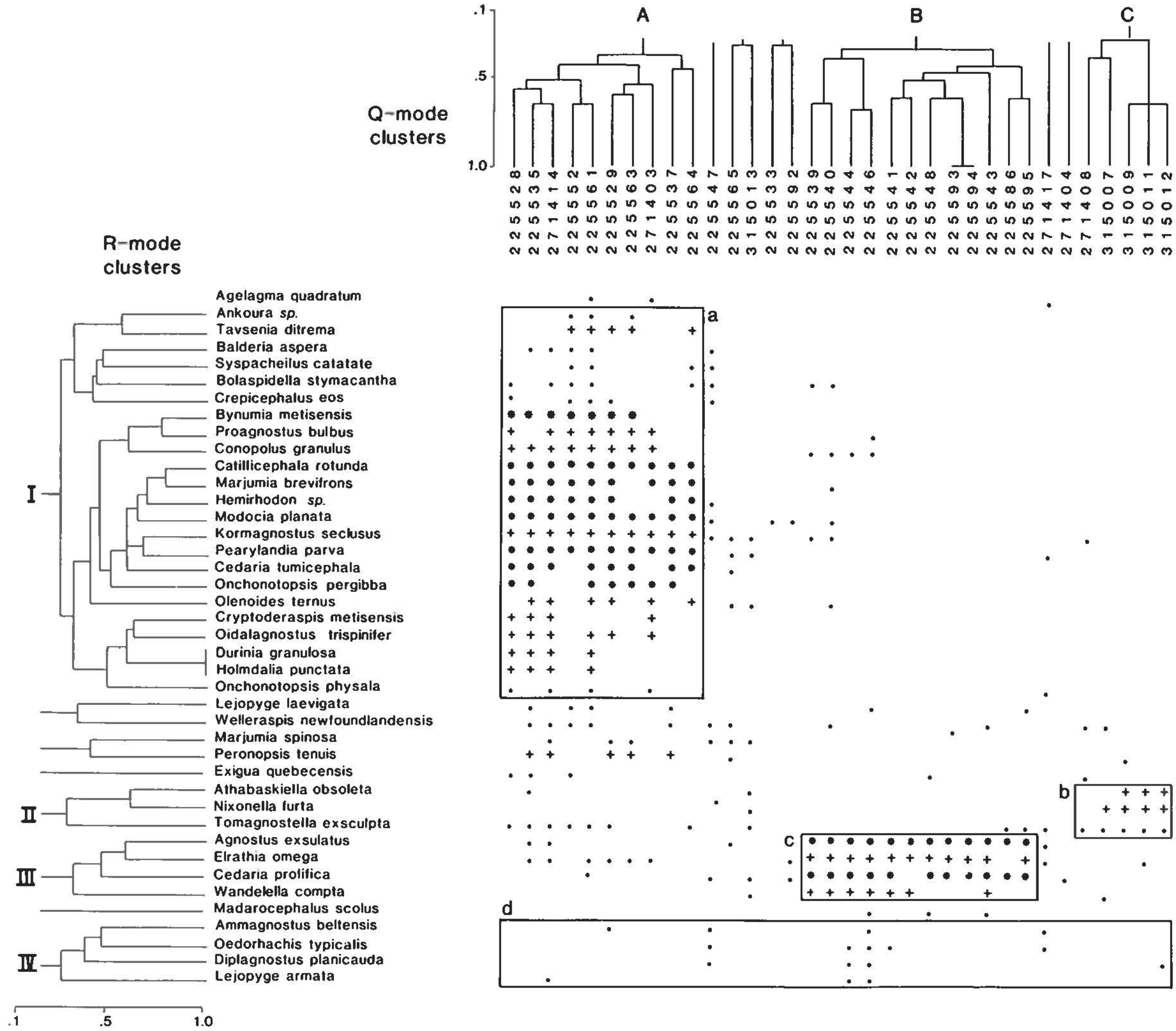

Fig. 2. Data matrix of Holm Dal trilobite species plotted in order formed by Q-mode clustering of collections and R-mode clustering of trilobite species. Meaningful clusters are labeled with roman numerals and capitol letters. The products of fidelity and constancy indices are plotted for each species in each cluster; periods (.) represent values less than or equal to 30, crosses (+) values greater than 30 and less than or equal to 60, and asterisks (*) values greater than 60. The intersection of Q-mode and R-mode clusters define four lithofacies-related faunal associations: grainstone association from Peary Land (a), mudstone association from Freuchen Land (b), mudstone association from Peary Land (c), and agnostoids having weak lithofacies relationships (d). Six-digit numbers are GGU sample numbers.

ficient emphasizes differences within the data (Cheetham & Hazel 1969), and because many species are present in only a small number of collections. Rare species, even with similar environmental adaptations, can have low similarity coefficients due to chance alone. Nevertheless, the clusters seem to represent the effects of real ecologic controls. Clustering was also performed on a similarity matrix of Dice coefficients, which emphasizes similarities (Cheetham & Hazel 1969). The resulting patterns of clustering were identical, differing only in the values of the coefficients.

Q-mode cluster analysis

Q-mode cluster analysis produced three clusters of samples containing similar species (Fig. 2, A-C). Most samples in each cluster are lithologically homogeneous. Cluster A includes 9 grainstones and 1 wackestone from Peary Land. Cluster B includes 11 mudstones and 1 wackestone from Peary Land. Cluster C includes 4 mudstones from Freuchen Land and 1 other mudstone. The species that characterize samples in Q-mode clusters will be discussed under R-mode cluster analysis.

Seven samples, including 3 mudstones, 2 packstones, and 2 grainstones, do not join clusters at meaningful levels and are atypical. For example, Freuchen Land mudstone 315013 contains all three species that characterize other Freuchen Land mudstones, but also contains species that characterize samples in clusters A and B. Consequently, it does not join with any cluster. Grainstone sample 225533 contains only a single specimen of one species, *Modocia planata,* and therefore does not join with the grainstone cluster. Finally, mudstone sample 271404 contains only a single species, *Cedaria prolifica,* and therefore does not join the mudstone cluster.

The reliability of the Q-mode clusters was tested using nonmetric multidimensional scaling (NMDS; Kruskal 1964a, b) because cluster analysis can impose artificial groupings on data. Results of the NMDS (Fig. 3) agree well with the results of the cluster analysis, and samples that form clusters also form reasonably tight groups in two-dimensional NMDS. The first axis represents a contrast between grainstones and mudstones, and the second axis represents a contrast between samples from Freuchen Land and Peary Land.

R-mode cluster analysis

R-mode cluster analysis produced four clusters of species that have similar relationships to lithology (Fig. 2, I-IV). Seven species did not join clusters at levels high enough to be meaningful. In general, cluster I includes species present mostly in grainstones, clusters II and III

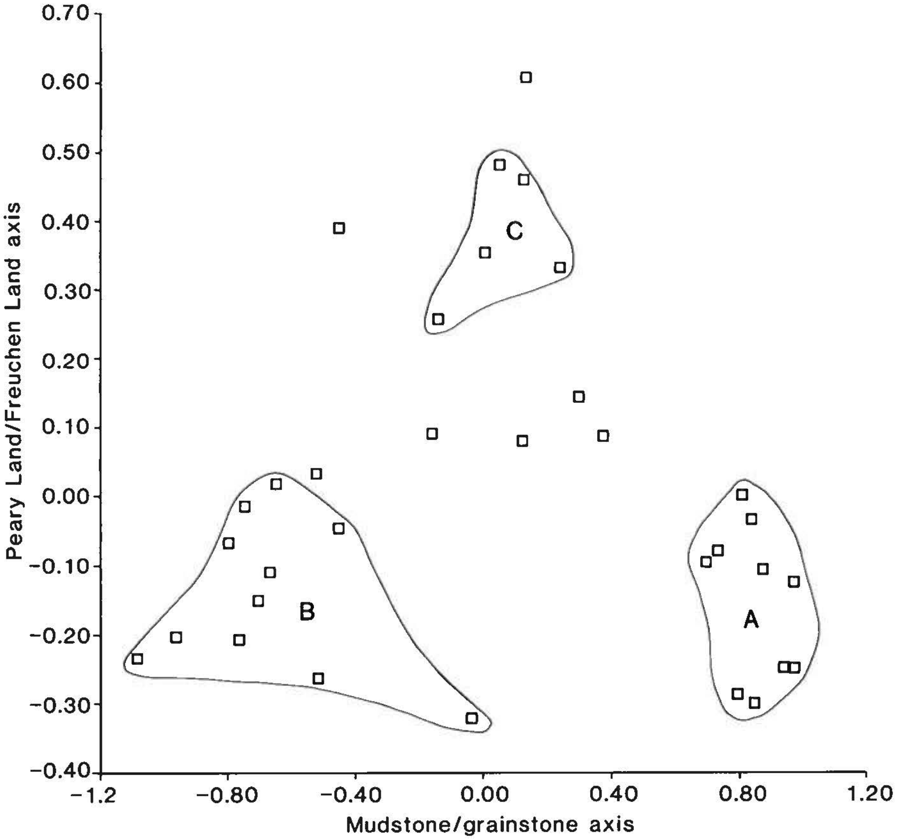

Fig. 3. Nonmetric multidimensional scaling showing the location of samples in two dimensions. The three groups (A-C) correspond to clusters from Q-mode cluster analysis. Group A contains grainstones from Peary Land, group B mudstones from Peary Land, and group C mudstones from Freuchen Land. Samples lying outside groups are the same as those that did not join clusters at meaningful levels.

Table 1. Fidelity (F) and constancy (C) indices for Holm Dal trilobite species in three Q-mode clusters. The number of collections containing a species is listed under N. A hyphen (-) indicates the absence of a species from a cluster.

	Cluster A			Cluster B			Cluster C		
	F	C	N	F	C	N	F	C	N
Agelagma quadratum	7	2	2	–	–	0	–	–	0
Ankoura *sp.*	10	3	3	–	–	0	–	–	0
Tavsenia ditrema	10	5	5	–	–	0	–	–	0
Balderia aspera	8	4	4	–	–	0	–	–	0
Syspacheilus catatate	8	3	3	–	–	0	–	–	0
Bolaspidella stymacantha	6	5	5	3	2	2	–	–	0
Crepicephalus eos	8	4	4	–	–	0	–	–	0
Bynumia metisensis	10	7	7	–	–	0	–	–	0
Proagnostus bulbus	9	7	7	1	1	1	–	–	0
Conopolus granulus	7	8	8	3	3	4	–	–	0
Catillicephala rotunda	10	10	10	–	–	0	–	–	0
Marjumia brevifrons	9	9	9	1	1	1	–	–	0
Hemirhodon *sp.*	9	8	8	–	–	0	–	–	0
Modocia planata	7	10	10	1	1	1	–	–	0
Kormagnostus seclusus	6	10	10	1	2	2	1	2	1
Pearylandia parva	8	10	10	–	–	0	–	–	0
Cedaria tumicephala	9	8	8	–	–	0	–	–	0
Onchonotopsis pergibba	10	7	7	–	–	0	–	–	0
Olenoides ternus	7	6	6	1	1	1	–	–	0
Cryptoderaspis metisensis	10	4	4	–	–	0	–	–	0
Oidalagnostus trispinier	10	6	6	–	–	0	–	–	0
Durinia granulosa	10	4	4	–	–	0	–	–	0
Holmdalia punctata	10	4	4	–	–	0	–	–	0
Onchonotopsis physala	8	3	3	–	–	0	–	–	0
Lejopyge laevigata	6	4	4	4	3	3	–	–	0
Welleraspis newfoundlandensis	5	5	5	2	2	2	2	4	2
Marjumia spinosa	5	3	3	–	–	0	–	–	0
Peronopsis tenuis	7	5	5	–	–	0	1	2	1
Exigua quebecensis	6	3	3	2	1	1	2	2	1
Athabaskiella obsoleta	2	1	1	–	–	0	6	6	3
Nixonella furta	–	–	0	–	–	0	8	8	4
Tomagnostella exsculpta	4	7	7	1	2	2	3	10	5
Agnostus exsulatus	1	2	2	8	10	12	–	–	0
Elrathia omega	3	6	6	6	9	11	1	2	1
Cedaria prolifica	–	–	0	7	9	11	–	–	0
Wandella compta	–	–	0	8	6	7	1	2	1
Madarocephalus scolus	–	–	0	10	3	3	–	–	0
Ammagnostus beltensis	3	1	1	3	1	1	–	–	0
Oedorhachis typicalis	–	–	0	6	3	3	–	–	0
Diplagnostus planicauda	–	–	0	5	2	2	3	2	1
Lejopyge armata	3	1	1	7	2	2	–	–	0

include species present mostly in lime mudstones, and cluster IV includes four agnostoid species having similar distributions. Distributions of the remaining species are not like one another or like those of species forming clusters. More than 70 percent of the collections containing species that join the grainstone and mudstone clusters are grainstones and mudstones respectively. Combining packstones with grainstones and wackestones with mudstones increases the percentage to nearly 80.

Fidelity and constancy indices (cf. Hazel 1970) were computed for each species as measures of how well it characterizes a particular cluster (Table 1). Fidelity is defined by

$$F_{ji} = \frac{N_i}{\Sigma N_i} * 10$$

where N_i is the number of collections in each cluster in which the species is present. It measures the extent to which a species is confined to a cluster. Constancy is defined by

$$C_{ji} = \frac{N_i}{T_i} * 10$$

where T_i is total number of samples in the cluster. It is a measure of the ubiquity of a species in a cluster. Species having both high fidelity and high constancy indices best delimit a cluster.

Cluster I includes 23 species that are more widely distributed in collections from lime grainstones. Species having high fidelity and high constancy indices are *Bynumia metisensis, Catillicephala rotunda, Cedaria tumicephala, Hemirhodon* sp., *Kormagnostus seclusus,* *Marjumia brevifrons, Modocia planata, Onchonotopsis pergibba,* and *Pearylandia parva.* Although some species in the cluster are not restricted to a single lithology, they are more prevalent in grainstones. Cluster I includes several subclusters that appear to be differentiated on the number of collections in which the species occur and not the presence or absence of a species from particular collections.

Clusters II and III include species that are more widely distributed in collections from lime mudstones. Cluster II contains three species, *Athabaskiella obsoleta, Nixonella furta,* and *Tomagnostella exsculpta,* that characterize mudstones from the Freuchen Land section. *T. exsculpta* is present in all lithologies, but groups with species from Freuchen Land because it is in all five of the collections. Cluster III contains four species, *Agnostus exsulatus, Cedaria prolifica, Elrathia omega,* and *Wandelella compta,* that characterize mudstones from Peary Land sections. *E. omega* is present in all lithologies and was probably eurytopic, but is relatively more widespread in mudstones. Only *N. furta* is restricted to collections from Freuchen Land. Several other species are present in mudstone collections from both Freuchen Land and Peary Land. This suggests that faunal composition varies because of subtle environmental differences at the time of deposition rather than geographic isolation. The mudstone species seem to indicate a stronger relationship to environment than to lithology, because the mudstone samples from Peary Land and Freuchen Land are not noticeably different.

Cluster IV contains four agnostoid species whose distribution is independent of lithology. As a group, these species are present in grainstones, packstones, wackestones, and mudstones, although each occurs in only a small number of collections. They group together because they are present in several of the same collections.

Some information can also be gleaned about species that do not join clusters. Five species, *Exigua quebecensis, Lejopyge laevigata, Marjumia spinosa, Peronopsis tenuis,* and *Welleraspis newfoundlandensis,* are somewhat more widespread in grainstones but do not join the grainstone cluster at meaningful levels. These species may have been relatively eurytopic, and their distributions in collections are neither similar to one another nor to the distributions of grainstone species. Two of the five species are agnostoids.

The distribution of *Agelagma quadratum* is unlike that of any other species and it joins no cluster at a meaningful level, perhaps owing to its presence in only a few collections. *A. quadratum,* however, is the only polymeroid species in the Holm Dal fauna having intercontinental distribution. Its morphology, small size, and geographic distribution collectively are in accord with an inferred pelagic mode of life (Robison, this volume).

Madarocephalus scolus also does not join a cluster at a meaningful level. It is present in only three collections, all part of the Peary Land mudstone cluster. *M. scolus* is, on average, the smallest trilobite in the Holm Dal Formation, and could have been more readily transported than larger trilobites. It is possibly the only spe-

GGU sample	Incorrect classification
grainstones	
225528	
225529	
225533	mudstone
225537	
225547	
225552	
225561	
225563	
225564	
271403	
packstones	
225565	mudstone
271417	mudstone
wackestones	
225548	mudstone
271414	grainstone
mudstones	
225539	
225540	
225541	
225542	
225543	
225544	
225546	
225586	
225592	grainstone
225593	
225594	
225595	
271404	
271408	
315007	
315009	
315011	
315012	
315013	

Table 2. Classification of samples for discriminant function analysis. Samples are in lithological categories, and classifications are listed for samples that were misclassified. All samples were classified as either grainstones or mudstones. Six-digit numbers are GGU sample numbers.

cies found in the mudstone facies that was transported in from other environments.

Discriminant function analysis

Stepwise discriminant function analysis (Morrison 1976) was performed to determine independently how well samples could be separated into lithological categories and to determine which linear combination of species provides the best separation. Lithology was selected as the grouping variable because it is readily predetermined and because the cluster analyses suggested that species presence varied with lithology. Samples can be discriminated into grainstone and mudstone end members with a four-variable model of *Catillicephala rotunda, Hemirhodon* sp., *Marjumia brevifrons,* and *Modocia planata.* Jack-knife classification of grainstones and mudstones was 93 percent correct (Table 2). Jack-knife estimators are conservative and reliable when compared to standard estimators (Neff & Marcus 1980).

The classifications mostly agree with the results of the cluster analysis, suggesting that the results are reliable. The two grainstone and mudstone samples that were misclassified (225533, 225592) also did not join clusters at meaningful levels. With respect to the discriminant model, one wackestone (271414) was classified with grainstones and one (225548) with mudstones. Both packstones (271417, 225565) were classified with mudstones. A histogram of the canonical variable shows the separation of grainstones and mudstones (Fig. 4). Discriminant function analysis using four lithological categories produced less satisfactory results, probably because of the small number and high faunal variability of wackestones and packstones.

Discussion

Study of trilobite data from the Holm Dal Formation by multivariate techniques indicates a relationship between the presence of species and lithology. Q-techniques generally group samples into lithologically homogeneous categories on the basis of contained species, suggesting that the degree of lithofacies relationship for many species is high. These techniques also bring to attention samples that are unusual either because they contain a mixture of species that characterize different lithologies or because they lack several species that characterize a single lithology. Ineson (this volume) includes most of the Holm Dal mudstones in a single lithofacies (argillaceous lime mudstone). Grainstones, however, are included in two lithofacies (wavy-bedded peloidal limestone and grainstone laminae within argillaceous lime mudstone). Therefore, the lithological determinations used in this study do not correspond exactly with the lithofacies of Ineson, but the groups of samples produced by Q-techniques are similar. The Q-techniques allow further subdivision of mudstone samples into two groups.

R-techniques allow species to be grouped into those present mostly in grainstones, those mostly in Peary Land mudstones, those mostly in Freuchen Land mudstones, and those distributed through all three categories. In addition, the results allow comparison of the distributions of polymeroids and agnostoids. Of the species present in a large number of collections, only two, *Tomagnostella exsculpta* (agnostoid) and *Elrathia omega* (polymeroid), are evenly distributed among all lithologies. Nine of the less common species are relatively independent of lithology; of these, six are agnostoids. In

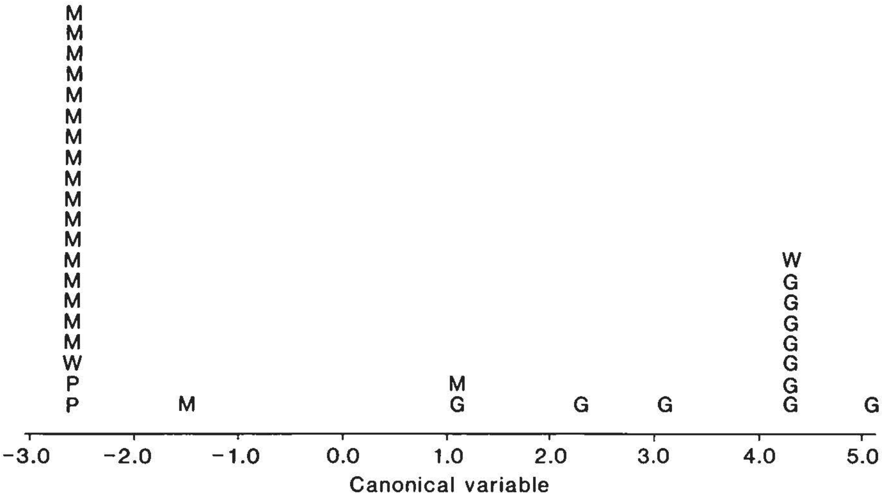

Fig. 4. Histogram showing the separation of grainstones (G) and mudstones (M) on the canonical variable and the affinities of packstones (P) and wackestones (W) with respect to the discriminant model. Mudstone and grainstone samples that plot together in the centre of the axis were misclassified by the model.

all, 7 of 11 agnostoids (64 percent) are relatively independent of lithology, whereas only 4 of 29 polymeroids (14 percent) are. This difference is consistent with the conclusion that agnostoids were mostly pelagic and polymeroids were mostly benthic (Robison 1972). In contrast, *Agnostus exsulatus, Kormagnostus seclusus,* and *Oidalagnostus trispinifer* show strong lithofacies relationships. *A. exsulatus* is found mostly in mudstones, possibly because of adaptation to more oceanic environments. *K. seclusus* and *O. trispinifer,* however, are found mostly in grainstones, possibly because of adaptation to more neritic environments. A similar pattern of distribution of agnostoids was reported by Jago (1973). The distribution of agnostoids was probably controlled in part by changes in salinity, nutrients, or other physical and chemical factors that were not causally related to changes in lithology.

References

Cheetham, A. H. & Hazel, J. E. 1969. Binary (presence/absence) similarity coefficients. – J. Paleont. 43: 1130–1136.

Dixon, W. J. 1983. BMDP statistical software, 1983 printing with additions. – Univ. California Press, Berkeley: 726 pp.

Dunham, R. J. 1962. Classification of carbonate rocks according to depositional texture. In: Ham, W. E. (ed.) Classification of carbonate rocks. – Mem. Am. Assoc. Petrol. Geol. 1: 108–121.

Hazel, J. E. 1970. Binary coefficients and clustering in biostratigraphy. – Bull. geol. Soc. Am. 81: 3237–3252.

Ineson, J. R. this volume. Lithostratigraphy and depositional setting of the Holm Dal Formation (Middle Cambrian), central North Greenland. – Meddr Grønland, Geosci. 20.

Jaccard, P. 1908. Nouvelles recherches sur la distribution florale. – Bull. Soc. Vaud. Sci. Nat. 44: 223–270.

Jago, J. B. 1973. Cambrian agnostid communities in Tasmania. – Lethaia 6: 405–421.

Kaesler, R. L. 1966. Quantitative re-evaluation of ecology and distribution of recent Foraminifera and Ostracoda of Todos Santos Bay, Baja California, Mexico. – Paleont. Contr. Univ. Kansas Pap. 10: 1–50.

Kruskal, J. B. 1964a. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. – Psychometrika 29: 1–27.

Kruskal, J. B. 1964b. Nonmetric multidimensional scaling: a numerical method. – Psychometrika 29: 28–42.

Morrison, D. F. 1976. Multivariate statistical methods, 2nd edition. – McGraw-Hill, New York: 415 pp.

Neff, N. A. & Marcus, L. F. 1980. A survey of multivariate methods for systematics. – Numerical Methods in Systematic Mammalogy Workshop. – Am. Soc. Mammal. Annual Meeting: 243 pp.

Robison, R. A. 1972. Mode of life of agnostid trilobites. – Proc. 24 Internatl geol. Congr., Montreal 7: 33–40.

Robison, R. A. this volume. Trilobites of the Holm Dal Formation (late Middle Cambrian), central North Greenland. – Meddr Grønland, Geosci. 20.

Rohlf, F. J., Kishpaugh, J. & Kirk, D. 1972. Explanation manual for numerical taxonomy system of multivariate statistical programs available from Department of Ecology & Evolution, State University of New York, Stony Brook, New York 11790.

Rowell, A. J., McBride, D. J. & Palmer, A. R. 1973. Quantitative study of Trempealeauian (latest Cambrian) trilobite distributions in North America. – Bull. geol. Soc. Am. 84: 3429–3442.

Sneath, P. H. A. & Sokal, R. R. 1973. Numerical taxonomy. – W. H. Freeman, San Francisco: 573 pp.

Sokal, R. R. & Sneath, P. H. A. 1963. Principles of numerical taxonomy. – W. H. Freeman, San Francisco: 359 pp.

Staff, G. M., Stanton, R. J., Jr., Powell, E. N. & Cummins, H. 1986. Time-averaging, taphonomy, and their impact on paleocommunity reconstruction: death assemblages in Texas bays. – Bull. geol. Soc. Am. 97: 428–443.