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ORDOVICIAN GEOGRAPHY AND FAUNAL PROVINCES DEDUCED FROM TRILOBITE DISTRIBUTION

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CONTENTS

Lists of families and genera of trilobites from the stratigraphical series of the Ordovician have been compiled, using information considered adequate from various areas in the world. Dissimilarities between these faunas have been assessed at both generic and family level, using Simpson's index. These indices have been analysed by a non-metric multidimensional scaling technique, and the groupings revealed are interpreted as indicating faunal provinces. Four provinces are recognized in the Lower Ordovician, the faunal characteristics and geographical extent of three of them (the Bathyurid, Asaphid and Selenopeltis provinces) being as previously described. A fourth province, here named the Asaphopsis province, is proposed for South American and Australian faunas in the Arenig and Llanvirn; the affinities of faunas from southeast Asia are indeterminate. In the Caradoc, faunas from areas occupied earlier by Bathyurid, Asaphid and Asaphopsis faunas, together with trilobites from south-east Asia, constitute a single province, here named the Remopleuridid. The Selenopeltis province persists in southern Europe and North Africa. These two provinces are recognizable only by a generic analysis in the Ashgill, and the latest faunas of that series are world-wide.

It is assumed that a faunal province originally extended over parts of a single continental mass (cf. Wilson 1966), and that migration between provinces is inhibited by width of seas or temperature differences. An assemblage of continental masses consistent with these assumptions, and with palaeomagnetic data, is proposed to give four palaeogeographical maps for the Ordovician period. The position of the proto-Atlantic ocean proposed by Wilson (1966), and Gondwanaland of McElhinney & Luck (1970), are accepted; the remainder of Eurasia is divided into four blocks. The maps suggest relative movements between continental blocks that may have removed barriers to migration and resulted in progressive merging of the faunal provinces. They are models to be tested against distributions of other animal groups, new palaeomagnetic and palaeoclimatic evidence, and theories on lithosphere plates.

The geographical reconstructions imply that the faunas of South America, southern Europe and North Africa inhabited cool waters, those of North America, northern Europe, north-east Asia, south-east Asia and Australia, warm waters. Cooler water faunas appear to have been less diverse. Decreasing provinciality of faunas during the Ordovician appears to have been accompanied by a reduction in total diversity; supposed climatic deterioration does not seem to have resulted in increased diversity. The differences between contemporaneous faunas within the Bathyurid and Remopleuridid provinces are investigated, and are shown to reflect differences in environment and evolution and diversification of groups of trilobites which took place in these environments.

1. INTRODUCTION

In an examination of distribution and phylogeny of Ordovician trilobites (Whittington 1966), it was concluded that a number of faunal provinces existed in the world during the period. Each province was characterized by containing families peculiar to it, and endemic genera of more widespread families. During much of the Lower Ordovician evolution in each province appears to have been largely independent, implying a considerable degree of isolation between provinces. In the Upper Ordovician a progressive merging of the provinces occurred as isolation broke down. Subsequent studies (Dean 1967*a*; Spjeldnaes 1967; Williams 1969*a*, *b*) of trilobites and other fossils in particular areas have supported some of the conclusions.

Williams's studies are important in that the changing degree of relationship between faunas with time are analysed mathematically and graphically portrayed. Methods for such analyses have been developed considerably in recent years, and the first aim of this work has been to analyse dissimilarities between faunas by a method which we believe gives a readily comprehensible and accurate picture. These analyses have confirmed the main outlines of the previous study, while modifying many of the details. The faunal provinces appeared as widely disjunct parts when their distribution was plotted on today's geography (Whittington 1966, Figs. 2, 16), parts of different provinces being closely juxtaposed, and parts of a single province separated by an ocean. Such a distribution affords no clues as to why provinces were originally isolated, and later merged. A second aim of this contribution is to suggest explanations for these changes. Wilson (1966) used the assumption that a faunal province originally extended over parts of a single continental mass to propose a reconstruction of such masses on either side of the Atlantic. We accept this assumption, and combine faunal evidence with current views on palaeomagnetism and lithosphere plates to concoct four world maps, each portraying the geography of a part of Ordovician time. These palaeogeographical reconstructions are arranged so that each province is shown as occupying shallow waters around a single continental block; the oceans that separated these blocks in the early Ordovician were barriers to migration so that evolution was largely independent in each province. Progressive geographical changes that resulted from relative movements between blocks are portrayed. These movements closed certain oceans and so broke down barriers, thus facilitating migrations and causing the progressive merging of provinces through Ordovician time. We intentionally describe these maps as concocted, for within the limits of available palaeomagnetic evidence we have assembled and placed particular continental masses to explain the distribution of trilobites. These maps are intended to provoke critical comment from students of other groups of fossils, and from those interested in plate tectonics, so that a more adequate synthesis may be made.

Each map represents a long period of time, and each province is generalized from few samples over a vast area. The relatively local influence of environment on the faunal assemblage is minimized in this broad treatment. It is well known that contemporaneous fossil faunas were different in different environments, and an attempt is made to examine these differences in one region from which data are available. It is shown that faunas are most varied (rapidly evolving) in areas of varied environments; that in certain environments particular families are persistently represented, i.e. are well adapted; such long-ranging forms are less useful than newly evolved types or migrants in determining age.

Data published since 1966 are used in this study, and a stimulus to undertaking it was provided by Whittington's visit to Australia in 1970. Few Ordovician trilobites from that continent have been described, and he is indebted to many kind friends for allowing him to examine collections in their charge, and for discussion of relevant matters: M. R. Banks, University of Tasmania; Dr K. S. W. Campbell, Australian National University; Miss J. Gilbert-Tomlinson and Dr J. H. Shergold, Bureau of Mineral Resources, Canberra; Dr O. P. Singleton, University of Melbourne; Dr B. D. Webby, University of Sydney. We are also indebted to Drs R. Sibson and N. Jardine of the King's College Research Centre, Cambridge, for much helpful advice on the analysis of the faunal data, to Dr A. Gilbert Smith, Department of Geology, Cambridge University, for his help in producing the maps, and to Mr John Lewis for his skill in preparing the figures. Tables of coordinates from which figures 1, 2, 4, 5, 7, 8, 10 and 11 were plotted, and tables of half matrices of dissimilarity indices for families and genera in the various samples (see appendix) are deposited in the archives of the Royal Society. The value of certain of these indices, within a particular range, is indicated in figures 1, 2, 4, 5, 7, 8, 10 and 11.

2. PROCEDURES

Williams (1969*a*, pp. 123–129) discussed procedures in studies of faunal provinces. We follow him in selecting for compilation the most complete, valid and well-dated taxonomic data available, and in accepting the genus as the lowest taxonomic category to be used. We differ in not employing cluster analysis, for reasons given below, and in analysing our data at both generic and familial rank. Fell (1968), using the *Treatise on Invertebrate palaeontology* as a principal source, compiled lists of genera present at any time during the Ordovician period in each present-day continent. These lists were analysed only as percentages in common between the continents. It is little wonder that such procedures led to results which bear virtually no relation to this or other work.

(*a*) *Compilation of data*

The data for the analyses consist of lists of families and contained genera of trilobites found in rocks of specified series in various areas. The sources for each list are given in the appendix. We have accepted the stratigraphical correlation used by Whittington (1966, table 1), and a division of the Ordovician System into Lower (Arenig, Llanvirn and Llandeilo series) and Upper (Caradoc and Ashgill series). World-wide correlation more closely than to series is not practicable; the boundary between Arenig and Llanvirn is difficult to determine in certain areas so that these series have been treated together. We have selected, wherever possible, localities or areas in which the fauna has been long collected and recently described. Each list is thus considered to contain the best available sample, expressed in up-to-date taxonomy. Imperfections have been partially overcome by combining, where the opportunity arises, the work of more than one author in a single list, and by using our first-hand knowledge of collections to reassign certain taxa. Taxonomic lists unsupported by descriptive work have not been used.

A particular list may be from a single locality, from an area of a few square kilometres, a state, province or larger portion of a continent. Difficulties have arisen in attempting to include such regions as south-east Asia, where much of the work was done many years ago, and the sampling is inadequate.

Since the index used in assessing dissimilarity between the faunas (see § 2 (*c*)) puts considerable weight on the smaller sample, the inclusion of very small samples may produce misleading results because the addition or subtraction of a single taxon produces a large percentage change in the value of the index. It was thus arbitrarily decided to omit from the analyses faunas composed of less than ten taxa (this limit being lowered to eight for the Llandeilo in order to obtain comparable faunas for analysis). The small faunas thus excluded are discussed in the appropriate places in § 3 (*a*, *b*), within the basic province framework provided by the analyses. Such faunas were also utilized in the compilation of the maps and are listed separately in the appendix. Particularly well-studied faunas may contain many taxa, including a considerable proportion of rare forms. It was found that omission of rare forms from such faunas had a negligible effect on the analyses, so that the full lists have been used.

(*b*) *Taxonomic level of data for analysis*

The genus is the lowest rank that is widely and objectively used in taxonomic work (Williams 1969*a*, pp. 124–126), so that conclusions on biogeography have been drawn by using data of this rank (Dean 1967*a*; Spjeldnaes 1967; Williams 1969*a*, *b*; Lochman-Balk 1970). Other authors (Hallam 1969) have used the family rank, and Whittington (1966) used a combination of both generic and familial distribution. We have made analyses at both levels, and the major features of trilobite distribution are shown at the family level (figures 1, 4, 7, 10). That provinces should be recognizable at a particular time at this level of analysis implies a considerable earlier history of genetic isolation. Analyses at the generic level (figures 2, 5, 8, 11) give a more detailed picture, and changes in time such as merging of provinces are more clearly brought out.

(*c*) *Assessment of dissimilarity*

The choice of methods of assessing similarity between faunas is considerable. Simpson (1960) reviewed, in an informal way, some possible indices and strongly favoured the index that he proposed in 1947 which has subsequently become known as Simpson's index—defined as the percentage of common taxa present in the smaller sample. Cheetham & Hazel (1969) have reviewed recently the properties of various indices.

The major difficulty in palaeontological work of this type is that the samples are frequently of different sizes, due not to any major primary difference in size of faunas sampled, but to differences in sampling errors. This means that any index putting equal weight on absences of taxa, as on presences, will be likely to give erroneous results. In the present study, where faunas are taken over relatively large areas over long time periods, it seems unlikely that the original faunas would have varied widely in size, although as shown in § 5 tropical faunas were somewhat more diverse. The differences in faunal size (which ranges from 10 to 67 within warm water areas), are thought more likely to reflect the thoroughness of study of the faunas. It was essentially because of these kinds of imperfections in palaeontological data that Simpson proposed his index. This index has been used in this study, with the minor modification that it has been converted to a *dissimilarity index* (Simpson 1960, p. 304, equation 6) in order that it may be treated as a distance measure (Sokal & Sneath 1963, pp. 143–153) in the analytical procedure and in the construction of the diagrams. In the calculation of the indices, taxa common to all samples have been omitted since they have no bearing on provincialism. Tables of indices are deposited in the archives of the Royal Society.† The range of values of certain indices are given in figures 1, 2, 4, 5, 7, 8, 10 and 11.

(*d*) *Analysis of dissimilarities*

Few palaeontologists have attempted to analyse relationships between fossil faunas. Kielan (1960, p. 23) illustrated in a simple manner some degree of the relationships between various European Ashgill trilobite faunas. Williams (1969*a*, *b*) conducted a more precise analysis of European and N. American brachiopods. A greater number of zoological studies have been made (e.g. Holloway & Jardine 1968), but most of these studies are able to make more complex analyses because the data are more detailed.

Recently in a series of articles Jardine, Jardine and Sibson (Jardine, Jardine & Sibson 1967; Jardine & Sibson 1968*a*, *b*; Sibson 1970) have shown that of cluster analysis techniques, the single link method is the least prone to give misleading results. Although their work was based on the assumption that the data were complete and that absences were as meaningful as presences, there is no reason to suppose that the same does not hold true for the rather less rigid data available for palaeontological work. However, all cluster analyses, whether using single link or other methods, assume an inherent hierarchic structure to the data which may or may not be present in reality. Further, these techniques assume the data to be reasonably portrayed in two dimensions. Because of these defects, cluster analysis techniques may produce very misleading results (Kaesler 1970). Since there is no theoretical reason to suppose that the distribution of past faunas should be hierarchic in nature, or that it can be represented adequately in two dimensions, it is here preferred not to use cluster analysis; instead a non-metric multi-dimensional scaling technique is used (see Kruskal 1964*a*, for a full theoretical background to this technique). It has the advantage over cluster analysis in that it gives the best representation on '*n*' related objects in a given number of dimensions such that the inter-point distances correspond as nearly as possible to the relationships between the objects—in this instance the dissimilarity indices between the faunas. In this study it has been found that a three-dimensional plot gives a reasonably good fit for the data, (ranging from 'excellent' to between 'fair' and 'good' in Kruskal's evaluation 1964*a*, p. 3), while still being reasonably easy to portray graphically. The analytical procedure used here is a slight modification of that of Kruskal (1964*b*), developed by Dr R. Sibson.

The configurations obtained by this technique are plotted (figures 1, 2, 4, 5, 7, 8, 10, 11) in two dimensions with an indication of the magnitude of the third coordinate. A graph of selected index values is then superimposed on the plot to make the actual values of linkages more obvious. This is thought to give a more easily comprehended picture than that obtained by plotting three separate diagrams of each possible pair of axes. Tables of coordinates are deposited in the archives of the Royal Society.†

(*e*) *Construction of maps*

A major aim of our work is an attempt to relate faunal provinces to possible geography in the Ordovician. A Lower Palaeozoic palaeogeography of the Atlantic area, and a reconstruction of Gondwanaland, have recently been proposed, but no world map. We have concocted a series

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† Copies may be purchased from the National Lending Library, Boston Spa, Yorkshire, LS 23 7 BQ, Great Britain. (Reference number SUP 10006.)

of four Ordovician palaeogeographical maps, using data on palaeomagnetism and suggestions on lithosphere plates, and the assumption that a faunal province extended through shallow seas around continental masses, and was bounded by barriers to migration that were either oceanic or temperature controlled. The great majority of trilobites were benthonic animals, inhabitants of shelf seas, so that the oceans were barriers to their dispersal throughout the Ordovician. The progressive merging of provinces during the period is thus ascribed to the breaking down of oceanic barriers, resulting from relative movements between continental masses, and the concomitant changes in latitude (and therefore temperature) and oceanic circulation. The masses adopted are listed and explained briefly below:

Gondwanaland
North America
Baltic, i.e. East European and Russian platforms and the Urals
Southern Europe
North-east Asia, including the Siberian platform, north-east U.S.S.R., and Kazakhstan
South-east Asia, including China and mainland south-east Asia, from Burma to Malaya.

Palaeomagnetic data from the Lower Palaeozoic were used by McElhinny & Luck (1970) to reconstruct Gondwanaland. Their reconstruction differs from that of Smith & Hallam (1970) principally in that Australia is more widely separated from Antarctica. We have taken the Smith & Hallam version for convenience, since we have used their computer programs to construct our maps. The North American mass includes the Arctic islands and has, following Wilson (1966), parts of Ireland, Scotland, western Norway and Spitsbergen added to the margin adjacent to Greenland. We have used the line ('consuming plate margin') of Dewey, Rickards & Skevington (1970, Fig. 1) to divide Norway, the British Isles, Newfoundland and north-eastern North America. We place the eastern portion of Newfoundland, and the detached part of north-eastern North America (termed the Maritime and New England portion), adjacent to the Iberian peninsula (cf. Wilson 1966). We do this so that we may use proto-Atlantic in Wilson's sense, though there is no evidence from trilobites in Ordovician rocks to support this procedure. The North American mass is bounded on the south across Mexico, and a portion encompassing Florida is detached and placed in Gondwanaland in the position suggested by Bullard, Everett & Smith (1965, Fig. 8). The Eurasian continent has been divided into five portions, one, peninsular India, being included in Gondwanaland. The Baltic mass includes the East European platform (Størmer 1967), together with the Russian platform, Ural Mountains, Pay Khoy and Novaya Zemlya, because Lower Ordovician faunas are similar over this area. South of the margin of the East European platform faunas are quite different, so we separate southern Europe, as a mass which included England, Wales and south-eastern Ireland and extended eastwards to Turkey and Syria. Hamilton (1970) and Kropotkin (in press) have suggested that the Russian and Siberian platforms were separate units during the Lower Palaeozoic, and Kropotkin also suggests a separate Chinese platform. The latter is bounded on the north by the present-day Tien Shan–Mongolia—Okhotsh mountain belts. We have taken approximately this line to divide Asia into two blocks. North-east Asia includes the Siberian platform, north-east U.S.S.R. and Kazakhstan, because of similar faunas. South-east Asia embraces China and mainland south-east Asia, including the Pamir, Himalayas, Burma and Malaya. The most difficult problems are over the possible divisions of Asia, and the procedure we adopt is tentative, based on inadequate knowledge of faunas and their distribution.

The maps have been plotted, using the computer programs of Smith & Hallam (1970), in hemispheres centred on the north and south geographical poles. Latitudinal placing of major units is based on palaeomagnetic data (Hamilton 1970; Irving 1964; McElhinny & Luck 1970), the longitudinal position on evidence derived from faunas. No palaeomagnetic data were available for South-east Asia, so that this mass is positioned tentatively on faunal grounds. The four successive maps show relative movements between the continental blocks, reasons for which are developed in the discussions of faunal provinces. McElhinny & Luck (1970) place the south pole in north-west Africa in the Ordovician, in South Africa in the Lower Devonian. We adopt the north-west Africa position in the Lower Ordovician, but suggest that a shift had taken place by the beginning of the Upper Ordovician. This suggested drift of Gondwanaland agrees with faunal evidence and the distribution of supposed glacial deposits of late Ordovician age.

The use of present-day continental outlines and names for these masses (except for Gondwanaland) is for simplicity and ease of understanding. Wilson (1966) used the term proto-Atlantic for the sea separating the North American from the Baltic and southern European masses. Tethys (Dean 1967*a*, p. 12) has been used to designate an 'ancestral Mediterranean' sea, but since this name was proposed for a Mesozoic sea we prefer proto-Tethyan (a use of this term apparently different from that of Dewey *et al.* 1970, p. 24). For the sea separating the Baltic and Southern European masses we use the name mid-European.

3. FAUNAL PROVINCES AND PALAEOGEOGRAPHY

(*a*) *Lower Ordovician*

(i) *Arenig and Llanvirn Series*

The sixteen faunas selected have all been analysed at the generic level, and thirteen of them at the family level. Their mutual relationships are expressed in figures 1, 2. Four distinct groupings emerge from the generic analysis, three of which belong respectively to the Bathyurid, Asaphid and Selenopeltis faunal provinces distinguished previously (Whittington 1966), a fourth constitutes the Asaphopsis province, defined below. The family analysis separates the Selenopeltis province, but draws China into it. The Asaphid and Bathyurid provinces have stronger internal links than the link between them. The South American and Australian faunas are less isolated and not linked to each other, but weakly to the Bathyurid faunas. The fauna of each of the four provinces is summarized in table 1, and the dissimilarities between them in table 2. Half or more of the genera in each province are endemic. The Bathyurid fauna is characterized by such endemic families as the Endymioniidae and Dimeropygidae, and the high proportion of endemic genera of Asaphidae, Bathyuridae, Cheiruridae and Pliomeridae. Within the Bathyurid province the five samples are linked (figure 2) at the generic index 60 value and lower, the strongest link being between faunas in the same area of western Newfoundland. There are also strong links between samples in this province in the family analysis (figure 1). In the Asaphid fauna (table 1) Bathyuridae and Pliomeridae are few in kinds and numbers, there is a high proportion of endemic asaphid and cheirurid genera, and distinctive endemic genera of Encrinuridae, Pterygometopidae and Odontopleuridae occur. Within the province the samples are linked at the generic index 45 or less; these links are stronger than those between most samples in the Bathyurid province. In the family analysis (figure 1), links between samples in each province are equally strong. In both analyses a relatively strong link is present between one sample in each province. In the generic analysis this link (between the Pay Choy and western Newfoundland (B) samples), is as strong as those between some samples within the Bathyurid province. These links suggest that the provinces were not completely isolated genetically from each other in the early Lower Ordovician, and their subsequent history of merging shows that migrations between them increased.

The Selenopeltis fauna (table 1) is characterized by a high proportion of endemic genera of Trinucleidae, Asaphidae, Nileidae, Cyclopygidae, Cheiruridae and Homalonotidae, and other peculiar genera including *Selenopeltis* (Odontopleuridae). The isolation of this province is shown

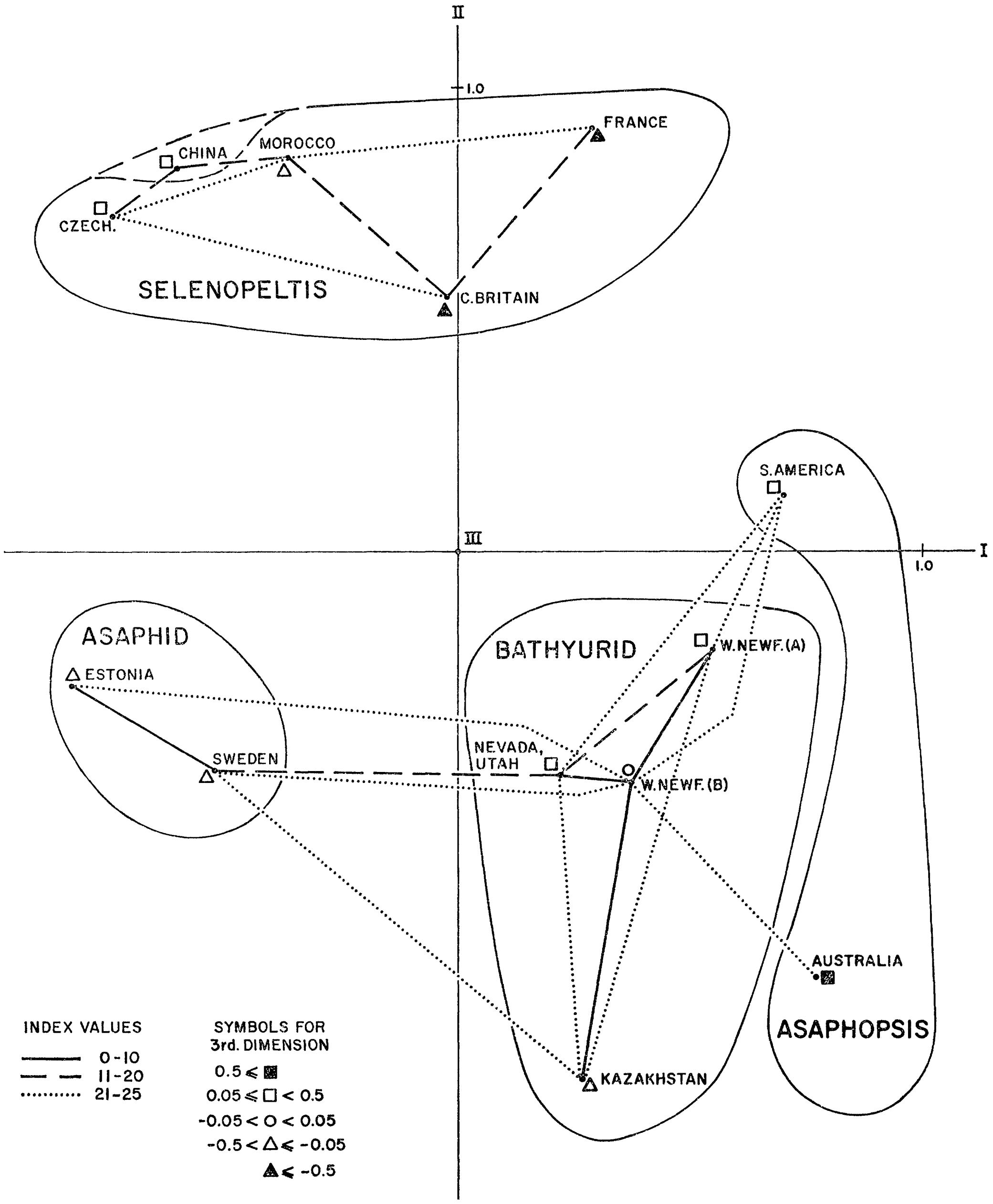

FIGURE 1. Arenig and Llanvirn Series: faunal provinces based on trilobite families. Three-dimensional plot (third axis perpendicular to page) of analysis of dissimilarity indices between samples (see §2 (*c*, *d*)). Selected dissimilarity index values superimposed, each province outlined and named. See appendix for explanation of geographical names.

by both analyses (figures 1, 2), but in neither are the links between samples as strong as corresponding links in the Bathyurid and Asaphid provinces. Only in the generic analysis is a weak link to another province, the Asaphid, shown. The suggestion is that there were some barriers to migration within the province and strong external barriers.

The Australian and South American faunas are linked to each other at index 58 in the generic analysis, and otherwise are almost completely isolated. The family analysis shows each fauna weakly linked to different samples in the Bathyurid province. Accordingly, we consider them to form part of a single province, and not to belong in separate provinces as believed earlier (Whittington 1966). The genus *Asaphopsis* (Hungaiidae) was first described from North Vietnam (Mansuy 1920), and is present in Tasmania and the Llanvirn of Argentina; it is selected for the name of the province. The fauna (table 1) includes endemic genera mainly from South America; because of the lack of detailed studies of the Australian faunas it is not possible to characterize this province further. In the family analysis the Chinese fauna appears

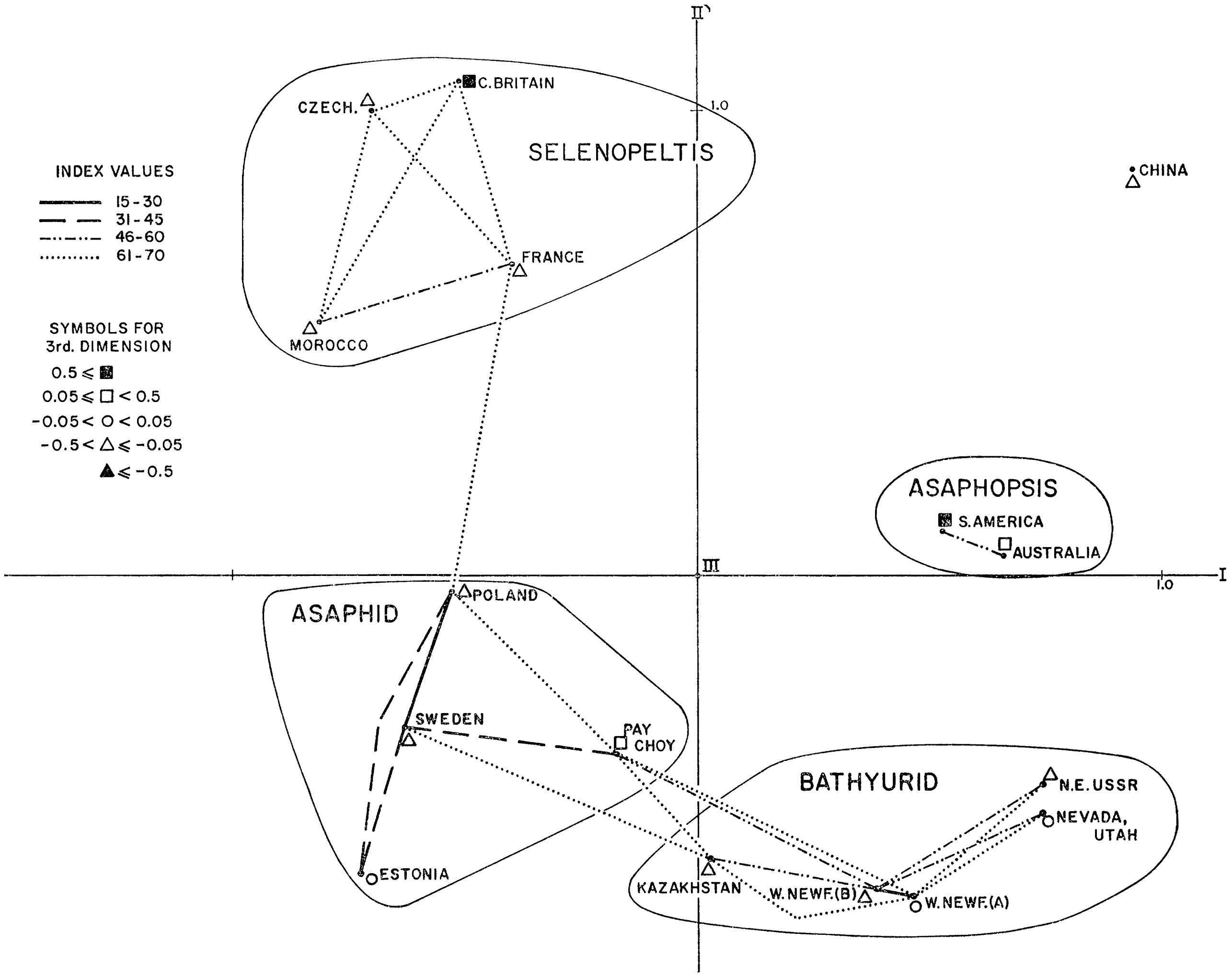

Figure 2. Arenig and Llanvirn Series: faunal provinces based on trilobite genera. Three-dimensional plot (third axis perpendicular to page) of analysis of dissimilarity indices between samples (see §2 (*c*, *d*)). Selected index values superimposed, each province outlined and named. See appendix for explanation of geographical names.

to belong in the Selenopeltis province, but in the generic analysis is extremely isolated. These uncertainties reflect the inadequate data, and this fauna, together with a small one from the Pamir, cannot be placed in any one of the provinces. It has been shown recently (Dean 1966, 1971; Brenchley, Harper & Skevington 1967) that *Hanchungolithus* and *Taihungshania*, genera first described from south China, are widespread in the Selenopeltis province. On the other hand, *Asaphopsis* and other hungaiids are known from Korea and south China (Sheng 1934,

Table 1. Arenig and Llanvirn Series: families and numbers of genera of trilobites in the four provinces and from China

Cosmopolitan refers to the provinces only; numbers of endemic genera in parentheses. See appendix for sources.

family	Selenopeltis	Asaphid	Bathyurid	Asaphopsis	China
Agnostidae	4 (2)	2 (2)	2 (1)	1	—
Harpididae	—	2 (1)	1	—	—
Harpidae	1 (1)	1	1	—	—
Raphiophoridae	1	3 (1)	8 (4)	2 (1)	—
Trinucleidae	11 (10)	—	—	2 (1)	4 (3)
Orometopidae	—	1 (1)	—	—	—
Hapalopleuridae	—	—	—	1 (1)	—
Alsataspididae	1 (1)	—	—	—	—
Endymioniidae	—	—	1 (1)	—	—
Dionididae	2 (1)	1	—	—	—
Shumardiidae	—	1	2 (1)	1	—
Olenidae	1	1 (1)	2	2	—
Hystricuridae	—	—	2 (1)	1	—
Dimeropygidae	—	—	2 (2)	—	—
Celmidae	—	1 (1)	—	—	—
Proetidae	—	—	1 (1)	—	—
Otarionidae	1 (1)	—	—	—	—
Isocolidae	—	—	2 (2)	—	—
Glaphuridae	—	1	2 (1)	—	—
Asaphidae	13 (7)	19 (13)	15 (13)	12 (8)	3 (?)
Hungaiidae	1 (1)	—	—	1 (1)	2 (1)
Taihungshaniidae	1	—	—	—	1
Nileidae	6 (5)	2	3 (1)	1	1
Komaspididae	—	1	2 (1)	1	—
Telephinidae	—	—	1 (1)	—	—
Remopleurididae	2 (1)	6 (1)	9 (4)	1	1
Cyclopygidae	8 (7)	1	—	—	—
Bathyuridae	—	1 (1)	18 (18)	1 (1)	—
Scutelluidae	1 (1)	3 (2)	2 (1)	—	—
Illaenidae	2 (2)	3 (2)	3 (2)	1 (1)	1
Cheiruridae	5 (4)	9 (7)	7 (5)	1	—
Pliomeridae	3 (1)	1	14 (9)	3 (1)	1 (1)
Pilekiidae	—	2 (2)	2 (2)	—	—
Encrinuridae	2 (2)	3 (2)	1	—	—
Calymenidae	4 (2)	2 (1)	—	2 (1)	2 (1)
Homalonotidae	5 (5)	—	—	—	—
Dalmanitidae	2 (2)	—	2 (2)	—	—
Pterygometopidae	1	3 (1)	—	—	—
Odontopleuridae	1 (1)	4 (3)	3 (2)	—	—
Lichidae	2 (1)	3 (2)	2 (2)	—	—
other genera	6 (5)	2 (1)	5 (5)	4 (4)	—
totals					
all genera	87	79	115	38	17
cosmopolitan	1	1	1	1	0
endemic	63 (72%)	43 (55%)	82 (71%)	19 (50%)	6+?

1958). Not only are the data inadequate to assess the affinities of faunas from South-east Asia, but the continental block so designated here (figure 3) is speculative (see §2 (*e*)). *Taihungshania* has been described (Kobayashi 1940*a*) from the south island of New Zealand. The material is poor and distorted, and Cooper (1968, p. 86) and Wright (1968) have doubted the identification and questioned the supposed Arenig age.

The present-day areas in which faunas of the four provinces, and the China–Korea faunas, are known (figure 3) have been drawn from previous (Whittington 1966) and subsequent work (see Appendix). The Selenopeltis and Asaphopsis faunas appear to have been inhabitants of shallow seas around the margins of Gondwanaland (using this term for the major, central part of late Palaeozoic Gondwanaland of Smith & Hallam 1970, Fig. 1). The Selenopeltis fauna is also present in south-eastern Ireland, Britain, from the Lake district southwards to Shropshire and south Wales, Brittany, Czechoslovakia, southern France, Spain, Portugal and Turkey. The division of Europe corresponds to the boundary between the Asaphid and Selenopeltis provinces, and southern Europe is placed near North Africa because of the faunal similarities in the proto-Tethyan region. In the previous map (Whittington 1966, Fig. 2) the Czechoslovakian faunas were shown in error as an Asaphid province; Bednarczyk (1968) has demonstrated that Asaphid faunas extended as far south as north-eastern Poland. A single trilobite from a boring in north-west Florida (Whittington 1953) is of Selenopeltis faunal type; this is consistent with the position of Florida adopted here (see §2 (*e*)). The northern half of Europe including the Baltic area and eastwards to the Ural Mountains (here referred to as the Baltic mass) was occupied by the Asaphid province. This region is here separated by some 30° of latitude from southern Europe; this gap, the mid-European sea, was the barrier to faunal migrations between the provinces. The Bathyurid fauna of North America is also known in north-western Ireland and Scotland, western Norway and Spitsbergen, a distribution which is consistent with the reconstruction adopted (figure 3). The proto-Atlantic ocean acted as the barrier to faunal migrations between the Bathyurid province and the Asaphid and Selenopeltis provinces.

Table 2. Arenig and Llanvirn Series: half matrices of trilobite genera in common and dissimilarity indices between the four provinces of table 1

	genera in common					dissimilarity indices			
	Selenopeltis	Asaphid	Bathyurid	Asaphopsis		Selenopeltis	Asaphid	Bathyurid	Asaphopsis
Selenopeltis	—	—	—	—	Selenopeltis	—	—	—	—
Asaphid	18	—	—	—	Asaphid	77	—	—	—
Bathyurid	6	20	—	—	Bathyurid	92	74	—	—
Asaphopsis	6	7	11	—	Asaphopsis	84	82	71	—

In the North-east Asian block, Bathyurid faunas have been recognized on the Siberian platform, and in north-eastern U.S.S.R. The Llanvirn faunas of Kazakhstan (Apollonov 1968) are like those of North America, that is, also of Bathyurid type. Faunal evidence thus suggests a position for this portion of Asia adjacent to south-western North America, a different position from that proposed by Ross & Ingham (1970, Fig. 5). The faunas of the South-east Asia mass are of uncertain affinity, but it is placed nearer to Gondwanaland than to the Baltic block. It is

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known that there are similarities between late Cambrian faunas of China and those of Australia, and the position adopted may help to explain the link revealed at the family level (figure 1) between the Chinese sample and the Selenopeltis fauna.

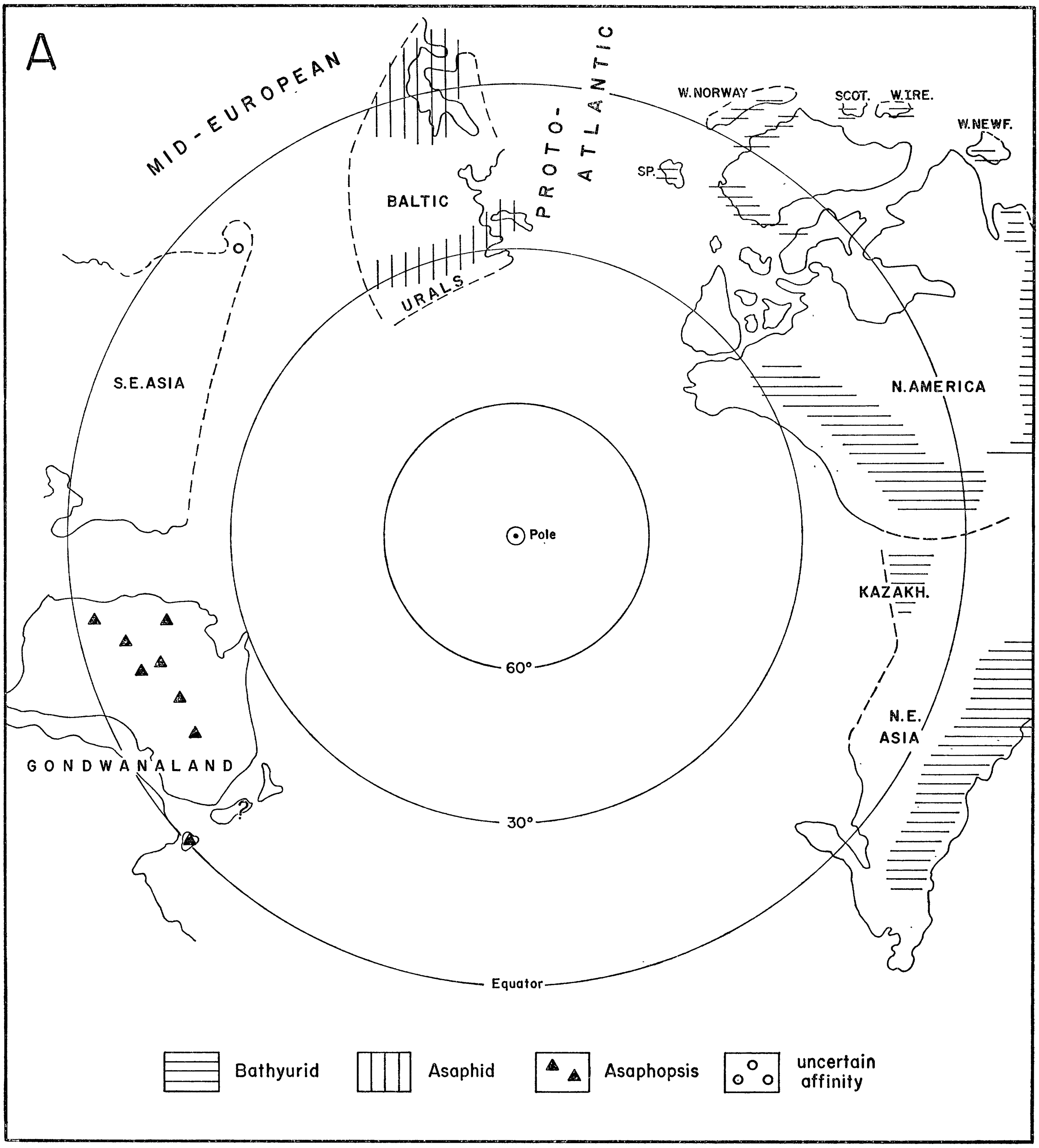

FIGURE 3. For legend see facing page.

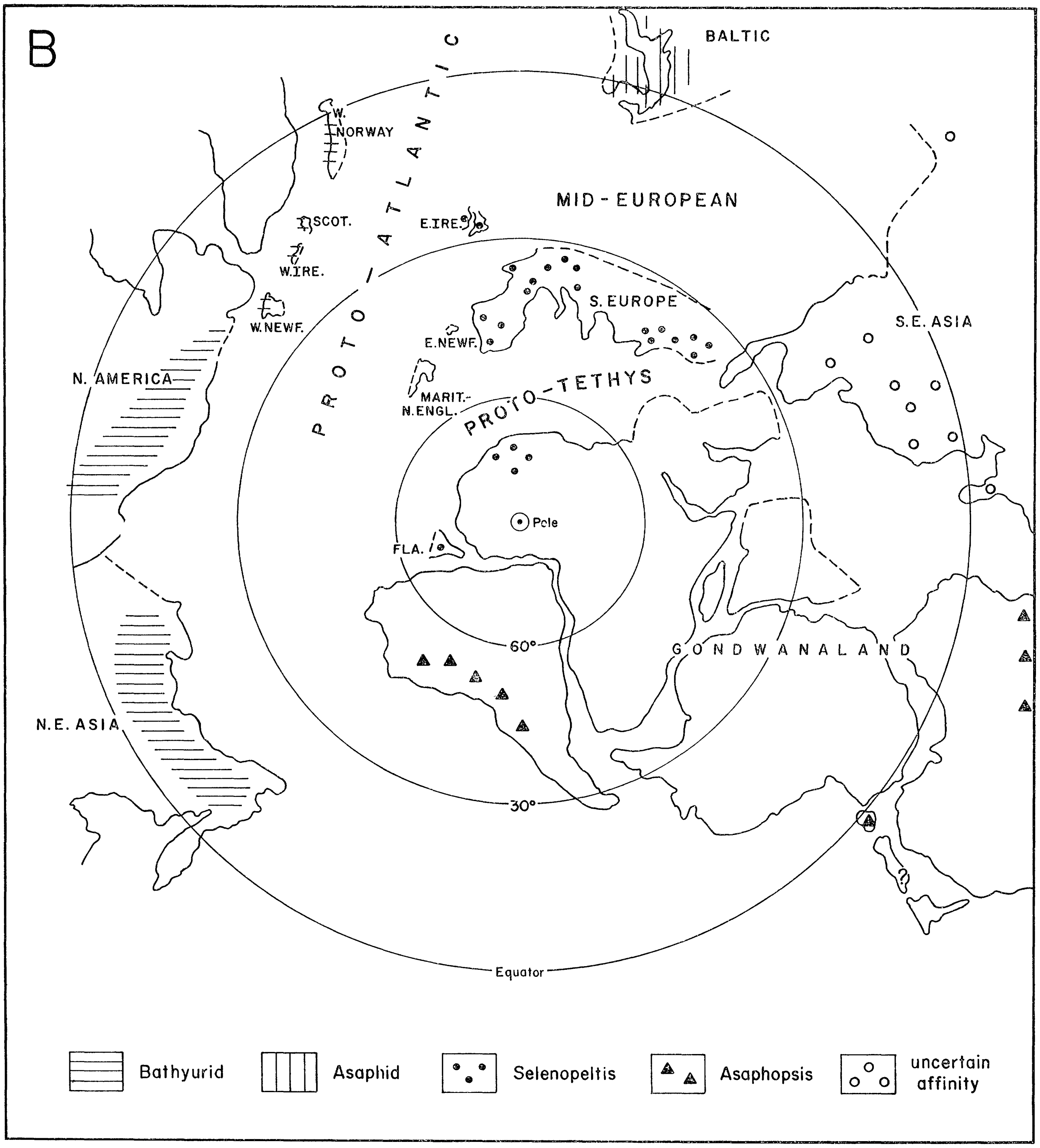

Figure 3. Arenig-Llanvirn Series: palaeogeography and trilobite faunal provinces. Stereographic projections of the northern (A) and southern (B) hemispheres. See § 2 (*e*). Abbreviations for geographical areas: E. Ire., South-eastern Ireland, with England and Wales adjacent to it; E. Newf., eastern Newfoundland; Fla., state of Florida, U.S.A.; Kazakh., Kazakhstan, U.S.S.R.; Marit.-N. Eng., parts of the Maritime provinces of Canada and New England states of U.S.A.; Scot., Scotland; Sp., Spitsbergen; W. Ire., north-western Ireland; W. Newf., western Newfoundland; W. Norway, western Norway.

(ii) *Llandeilo Series*

Ten faunas of this age have been analysed at the generic level, and eight of them (each including eight or more families) analysed at the family level. Their mutual relationships are expressed in figures 4, 5. In these diagrams three provincial groupings are apparent, each a direct successor of an Arenig and Llanvirn province. The Selenopeltis province is again the most isolated, the Asaphid and Bathyurid provinces closer together and with links between them stronger than links from either to the Selenopeltis province. The faunas of the three provinces are summarized in table 3, and the dissimilarities between them in table 4. The Selenopeltis fauna retains its distinctive character, the high percentage of endemic genera belonging to the same families as earlier, together with the Agnostidae, Dionididae, Calymenidae and Dalmanitidae; *Selenopeltis* is also present. The sample from central Britain stands considerably apart from the others in the province, being linked relatively weakly only to that of

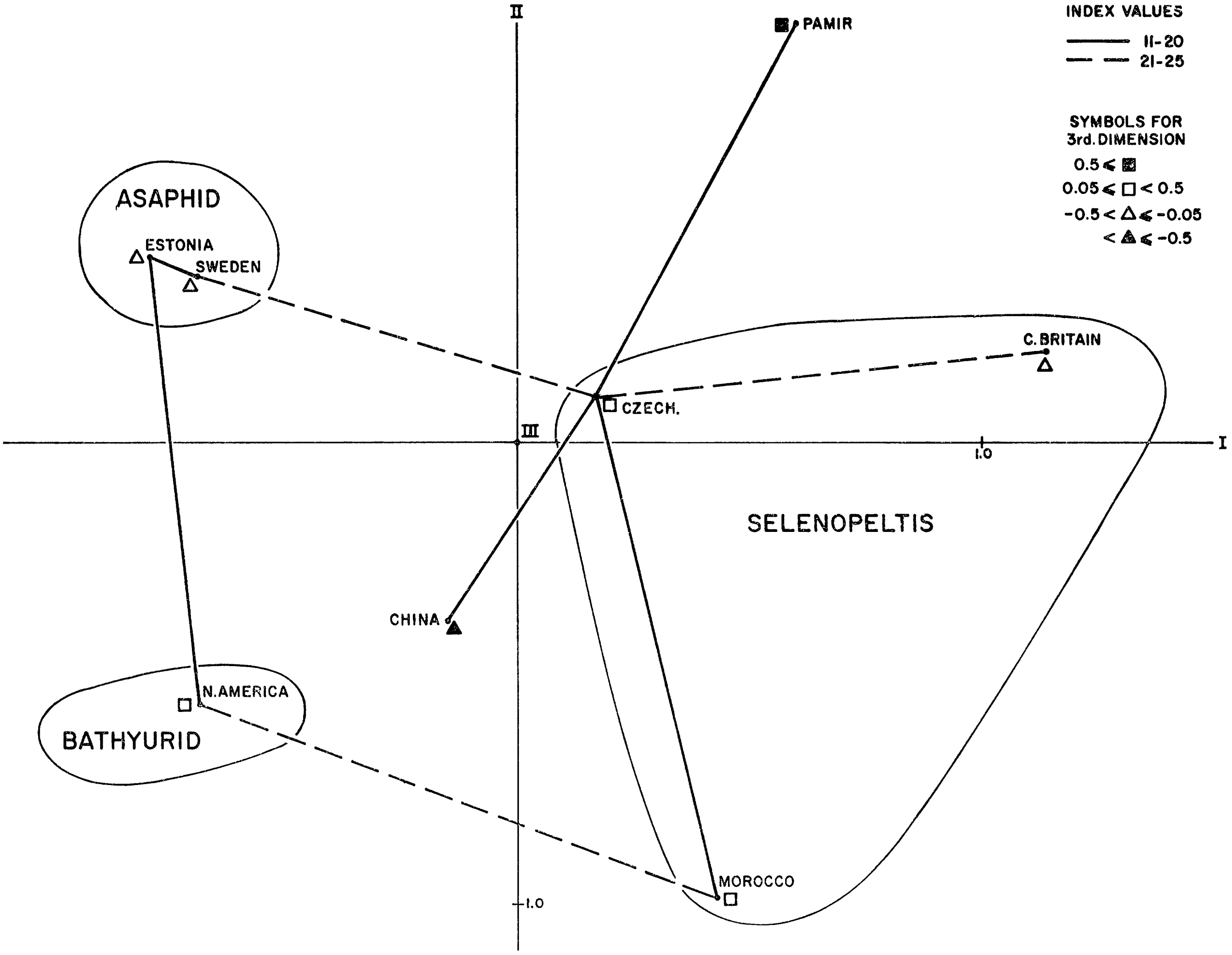

FIGURE 4. Llandeilo Series: faunal provinces based on trilobite families. Three-dimensional plot (third axis perpendicular to page) of analysis of dissimilarity indices between samples (see § 2 (*c*, *d*)). Selected index values superimposed, each province outlined and named. See appendix for explanation of geographical names.

Czechoslovakia. Faunas of the Asaphid province have a lower percentage of endemic genera, but these include, as earlier, Asaphidae, Encrinuridae and Pterygometopidae. The Bathyurid fauna (table 3), composed largely from the recently described Chazy Group trilobites, has a high percentage of endemic genera, including as before Dimeropygidae, Asaphidae, a bathyurid, Cheiruridae and a pliomerid.

Two faunas from South-east Asia have been included in the analyses, though they contain few genera (table 3). Faunas of Llandeilo age are reported from Pay Khoy, Kazakhstan, the Siberian platform and north-eastern U.S.S.R., but contain too few genera for inclusion. No faunas of this age are known from Australia or South America. The fauna from China, at the generic level (figure 5), is as strongly linked to Swedish faunas as the sample from the Pamir is to the Czechoslovakian sample. A less strong link runs between the Chinese and Czechoslovakian samples. At the family level (figure 4) the links are only to Czechoslovakia. In both analyses the China and Pamir samples are remote from any of the three provinces, but without a mutual link. The affinities of these South-east Asian faunas are problematical; the sample from China resembles older faunas in that area in containing a hungaiid, aff. *Prosopiscus*, and calymenid genera. In

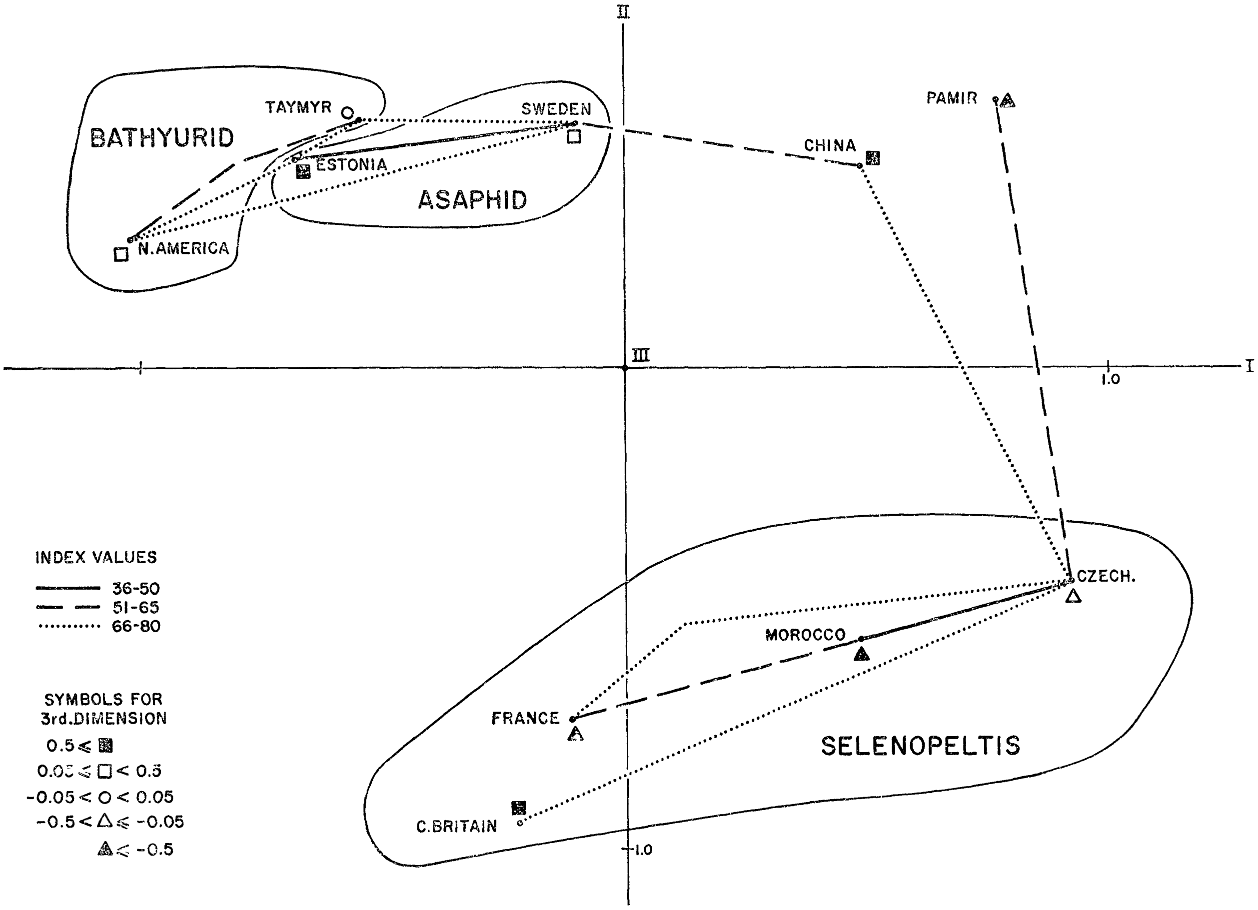

Figure 5. Llandeilo Series: faunal provinces based on trilobite genera. Three-dimensional plot (third axis perpendicular to page) of analysis of dissimilarity indices between samples (see § 2 (*c*, *d*)). Selected index values superimposed, each province outlined and named. See appendix for explanation of geographical names.

the map (figure 6) the continental blocks have been left in essentially the same positions as in the Arenig–Llanvirn map, except that the North American–North-east Asia mass and Baltic block have been brought closer to each other to suggest that the barrier to migration was beginning to break down. This implies that closure of the proto-Atlantic began in late Lower Ordovician time.

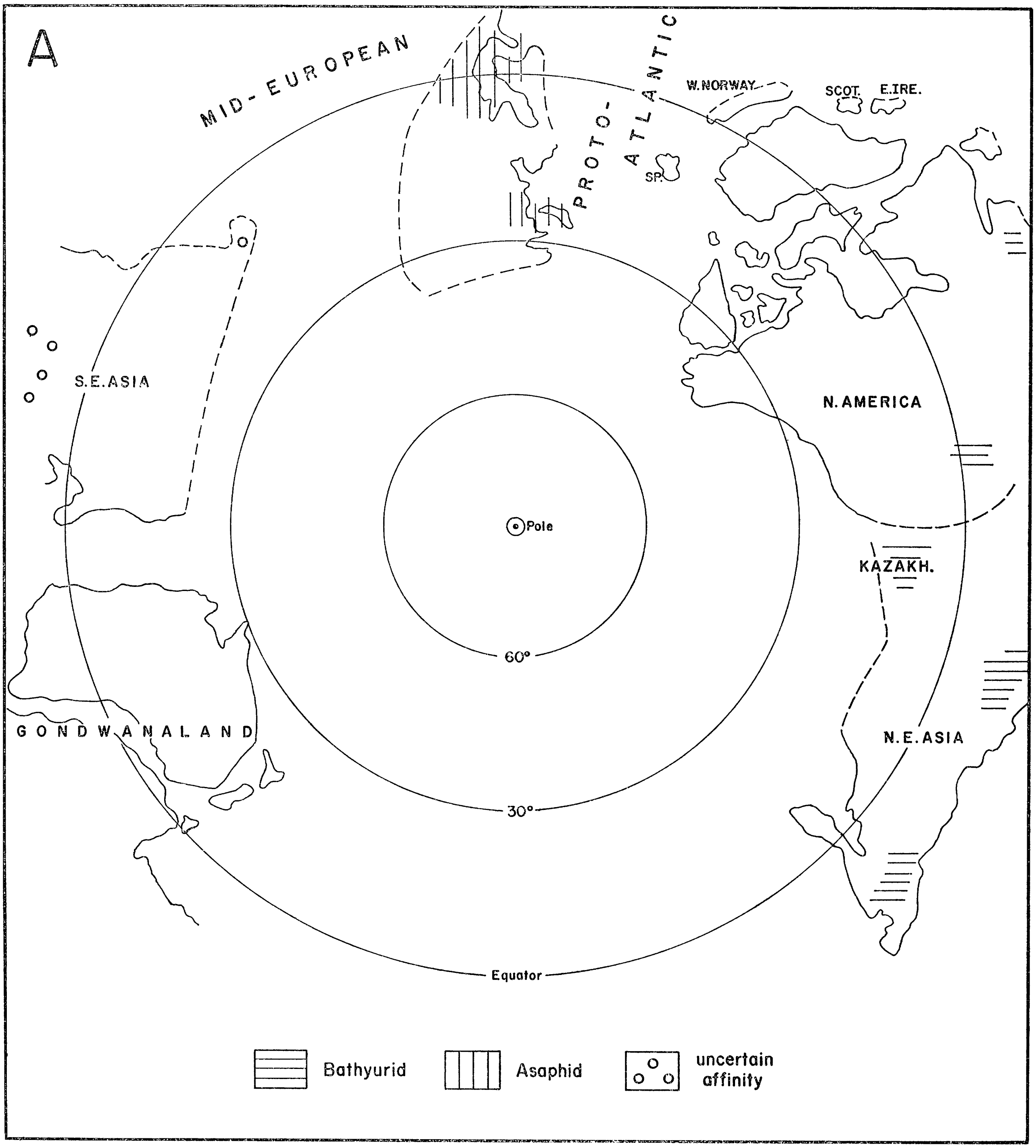

FIGURE 6. For legend see facing page.

(*b*) *Upper Ordovician*

(i) *Caradoc Series*

Analyses have been made of genera (figure 8) in fifteen samples of early Caradoc age, and of families (figure 7) from twelve of these samples. A Selenopeltis province is isolated from the

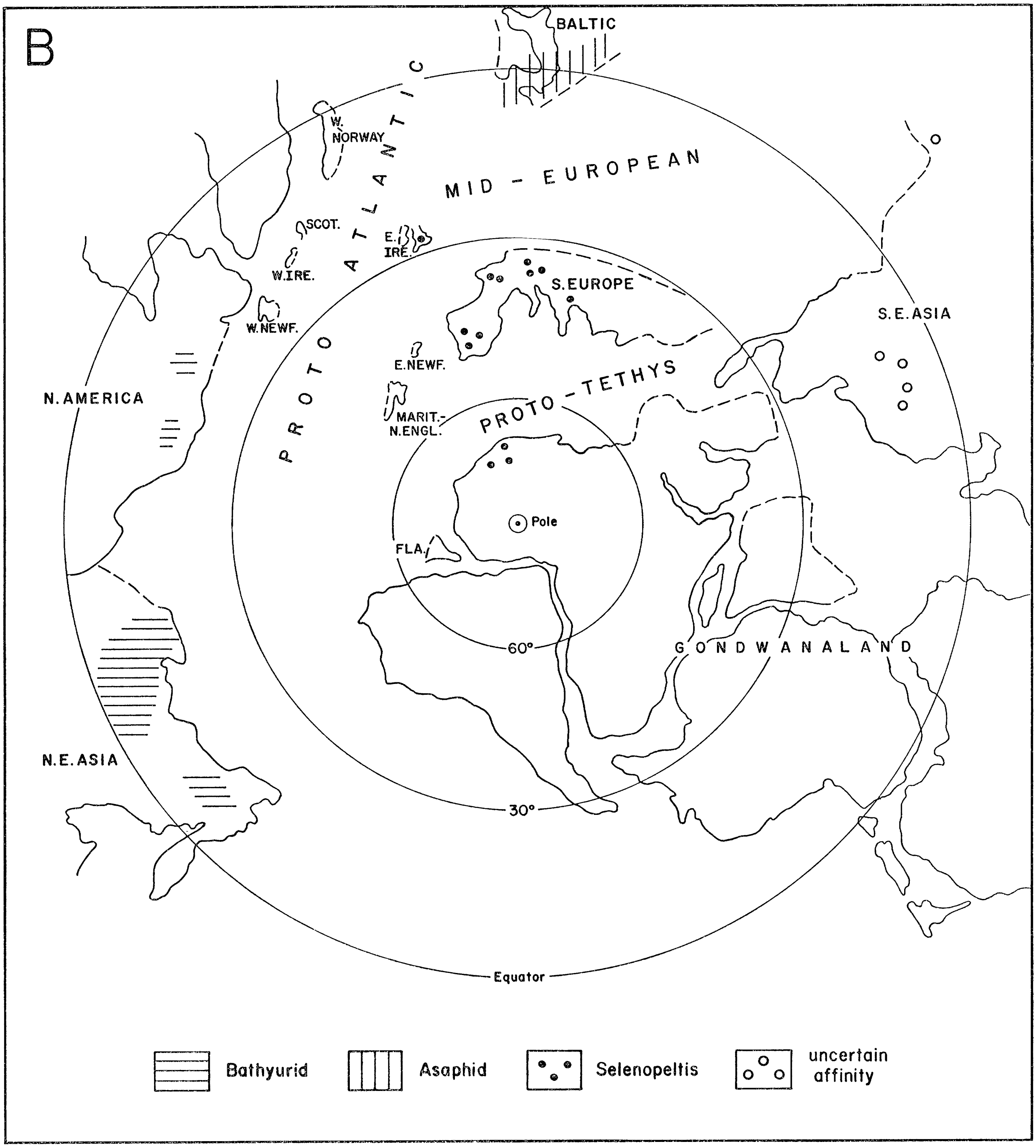

Figure 6. Llandeilo Series: palaeogeography and trilobite faunal provinces. Stereographic projections of the northern (A) and southern (B) hemispheres. See § 2 (*e*) and explanation of figure 3 for abbreviations of geographical names.

Table 3. Llandeilo Series: families and numbers of genera of trilobites in the three provinces, China and the Pamir Mountains

Numbers of genera endemic to province or area in parentheses. See appendix for sources.

family	Selenopeltis	Asaphid	Bathyurid	China	Pamir
Agnostidae	4 (4)	1 (1)	—	—	—
Harpidae	1 (1)	—	2 (2)	—	—
Trinucleidae	7 (7)	—	—	—	1 (1)
Dionididae	3 (2)	—	—	—	1
Raphiophoridae	2 (2)	2	4 (1)	1	1
Hapalopleuridae	1 (1)	—	—	—	—
Shumardiidae	1 (1)	—	—	—	—
Dimeropygidae	—	—	1 (1)	—	—
Proetidae	1 (1)	—	—	—	—
Otarionidae	—	—	1 (1)	—	—
Glaphuridae	—	—	2 (2)	—	—
Aulacopleuridae	—	—	—	—	1
Asaphidae	4 (2)	9 (7)	4 (3)	—	—
Hungaiidae	1	—	—	1 (1)	1
Nileidae	5 (4)	1	—	—	—
Komaspididae	—	—	1 (1)	—	—
Telephinidae	—	1 (1)	—	1	—
Remopleurididae	—	1	2 (1)	—	—
Cyclopygidae	6 (5)	—	—	—	1
Bathyuridae	—	—	1 (1)	—	—
Scutelluidae	1 (1)	1 (1)	2 (2)	—	1 (1)
Illaenidae	2 (2)	1	7 (6)	1	—
Cheiruridae	4 (4)	5 (1)	11 (7)	—	1 (1)
Pliomeridae	1 (1)	—	1 (1)	—	—
Encrinuridae	2	2 (1)	2 (2)	—	1
Calymenidae	4 (4)	—	—	2 (1)	—
Homalonotidae	3 (3)	—	—	—	—
Dalmanitidae	6 (6)	—	1 (1)	—	—
Pterygometopidae	—	3 (3)	—	—	—
Lichidae	3 (2)	2 (1)	1 (1)	1	—
Odontopleuridae	3 (3)	—	2 (2)	—	—
uncertain	3 (3)	1 (1)	1 (1)	1 (1)	1 (1)
totals					
all genera	68	30	46	8	10
endemic genera	59 (87%)	17 (57%)	36 (78%)	3 (37%)	4 (40%)

Table 4. Llandeilo Series: half matrices of trilobite genera in common and dissimilarity indices between the three provinces of table 3

genera in common

	Selenopeltis	Asaphid	Bathyurid
Selenopeltis	—	—	—
Asaphid	3	—	—
Bathyurid	1	7	—

dissimilarity indices

	Selenopeltis	Asaphid	Bathyurid
Selenopeltis	—	—	—
Asaphid	90	—	—
Bathyurid	98	79	—

remainder, but samples from central Britain, north Wales and eastern Ireland no longer lie within it, as the faunas from these areas did in the Lower Ordovician. Already in the Llandeilo Series the fauna from central Britain was somewhat removed from others in the same province, and by the early Caradoc the change had proceeded further. The earlier history of central

British faunas is shown by the presence of a cyclopygid and *Selenopeltis* in the Caradoc sample. The Selenopeltis fauna (table 5) continues to be characterized by a high proportion of endemic Cyclopygidae, Cheiruridae, Homalonotidae and Dalmanitidae, and in addition endemic Illaenidae as well as *Selenopeltis* itself. In the Llandeilo there were some links between faunas of the Bathyurid and Asaphid provinces, in the Caradoc there were stronger links, such as between the Oslo and Estonian faunas and Scotland at the generic level, and Estonia to Scotland at the family level. It seems evident from the analyses (figures 7, 8) that only one province other than the Selenopeltis can be recognized at either level. This province is here named Remopleuridid. It includes faunas from areas formerly in the Bathyurid and Asaphid provinces (Scotland, Virginia, Mississippi, Oslo and Estonia), linked at both taxonomic levels of analysis. Two faunas from areas formerly in the Selenopeltis province (North Wales (B), east Ireland) are strongly linked to them. Two additional faunas (North Wales (A), Central Britain), also from areas formerly in the Selenopeltis province, appear remotely linked at the generic level to other faunas in the province, and have weak links to Selenopeltis faunas, but that from North Wales

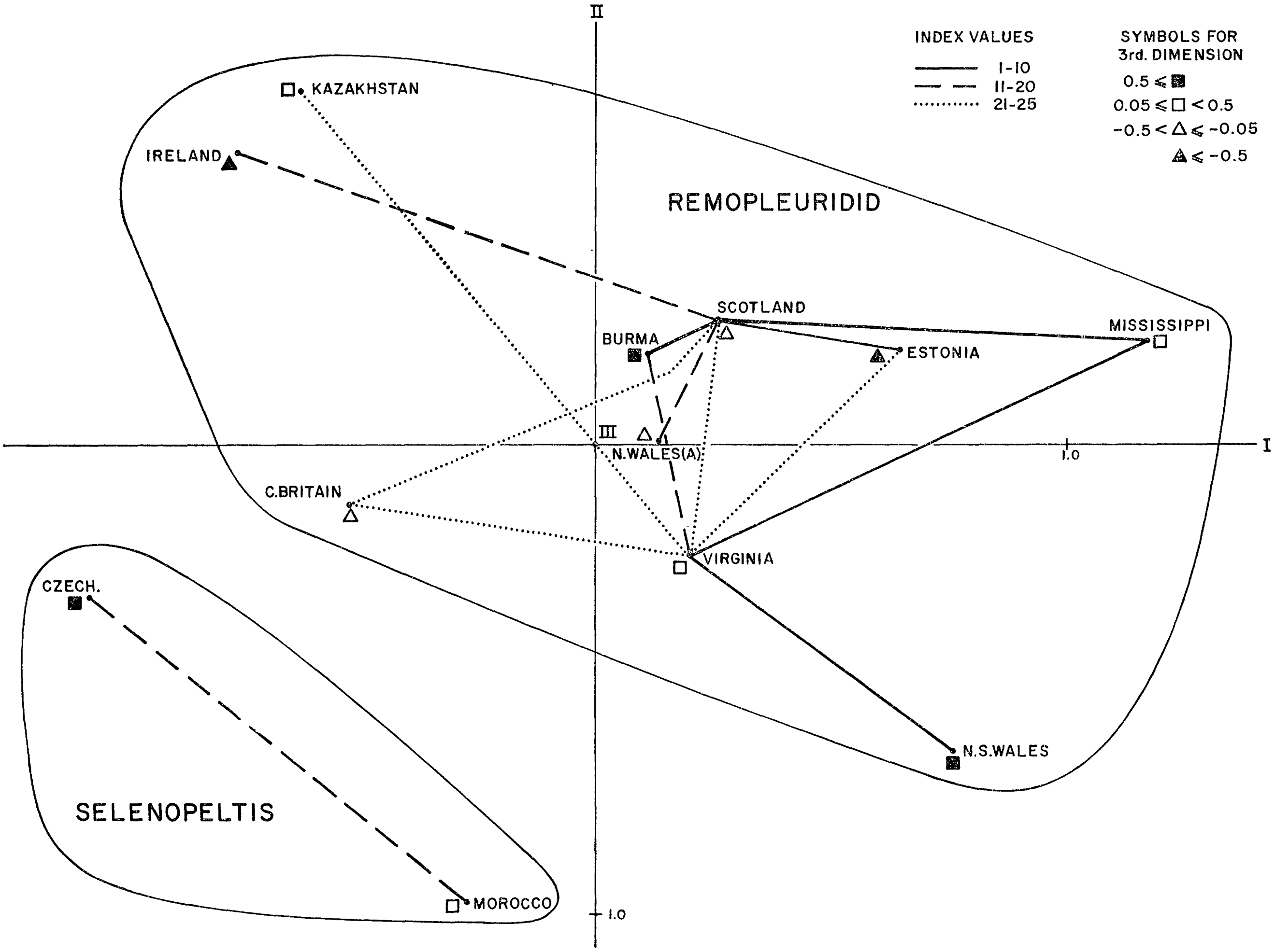

FIGURE 7. Caradoc Series: faunal provinces based on trilobite families. Three-dimensional plot (axis perpendicular to page) of analysis of dissimilarity indices between samples (see § 2 (*c*, *d*)). Selected index values superimposed, each province outlined and named. See appendix for explanation of geographical names.

(A) is better linked at the family level. The Kazahkstan sample appears to lie within the province, but is weakly linked to other faunas. In the Arenig and Llanvirn, faunas from Australia were interpreted as being within an Asaphopsis province. The Caradoc sample from New South Wales is linked to American and Scottish faunas of the Remopleuridid province, as is that from Burma, situated in the South-east Asia region. The Remopleuridid province thus extended over a vast area, and the fauna was large (table 5), though little more so than the Bathyurid fauna of the Arenig and Llanvirn. It contains a high proportion of endemic families and genera, and one of the former is selected for the provincial name.

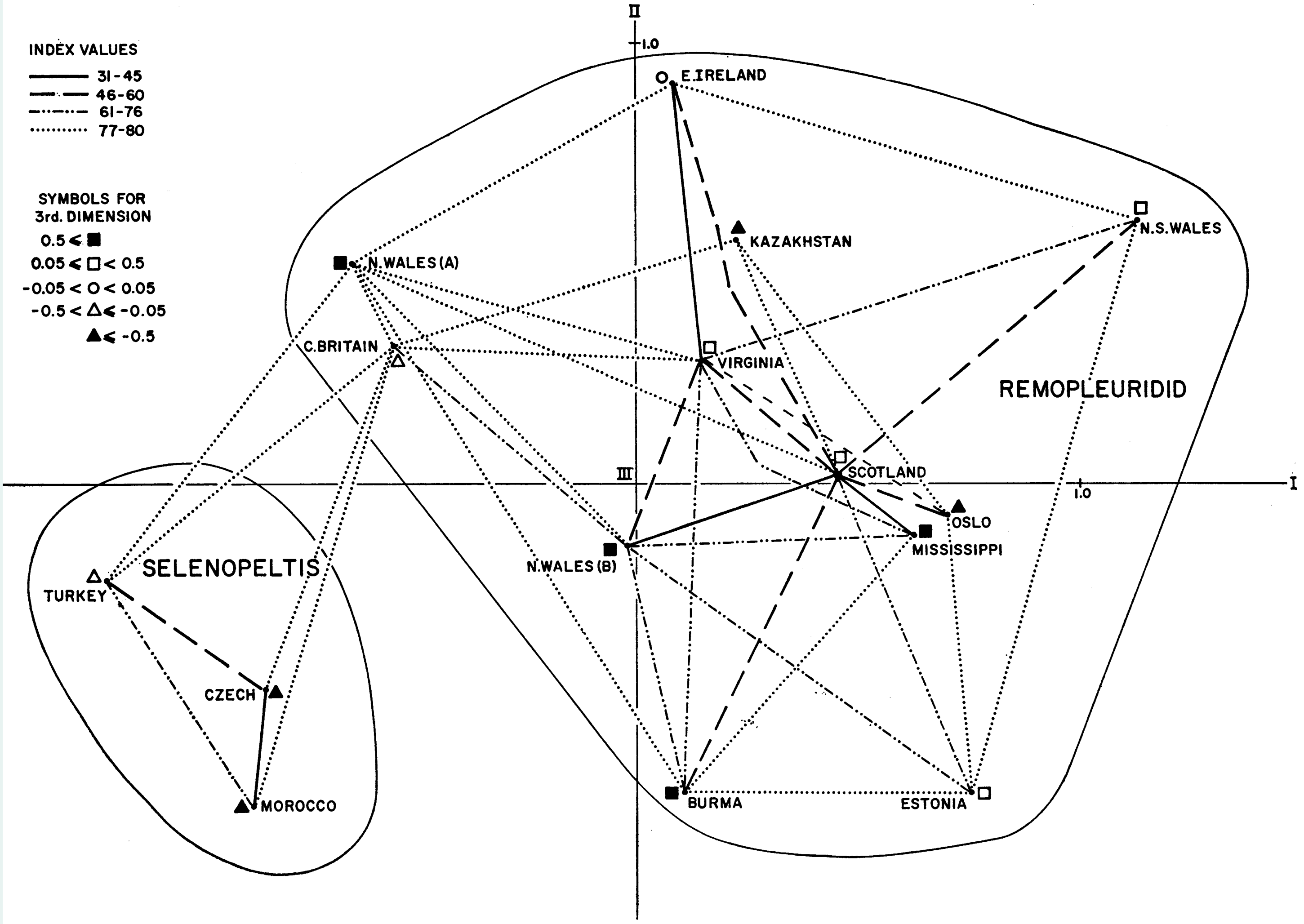

Figure 8. Caradoc Series: faunal provinces based on trilobite genera. Three-dimensional plot (third axis perpendicular to page) of analysis of dissimilarity indices between samples (see § 2 (*c*, *d*)). Selected index values superimposed, each province outlined and named. See Appendix for explanation of geographical names.

No faunas adequate for inclusion in the analyses are known from the Siberian platform or North-eastern U.S.S.R., but such genera as are recorded are like those in the Remopleuridid province. In addition, genera of Monorakidae are varied in these areas, and the position of this continental block adjacent to the North American block is supported by the occurrence of a single monorakid genus in the western United States (Whittington 1966). The distribution of monorakid genera may signify a subprovince within the Remopleuridid province. The single fauna from South-east Asia large enough to include in the analyses is within the Remopleuridid province. However, the genus *Pliomerina* was first described from late Llanvirn rocks of south-west China, but has since been recognized in Caradoc strata in South Korea and Kazakhstan, as well as Australia. Peculiar calymenids such as *Reedocalymene* and *Vietnamia* occur in South-east Asia and Australia, and hungaiids such as *Birmanites* and *Birmanitella* are known from Kazakhstan and South-east Asia, reflecting an ancestry reaching back to the Asaphopsis province. Thus Kazakhstan, South-east Asia and Australia also show indigenous characters, and increased knowledge may permit further subdivision of the Remopleuridid province. Few trilobites of Caradoc age are known from South America or New Zealand, so that their affinities cannot be assessed.

Table 5. Caradoc Series: families and numbers of genera of trilobites in the two provinces

Numbers of endemic genera in parentheses. See appendix for sources.

family	Selenopeltis	Remopleuridid
Agnostidae	1 (1)	2 (2)
Harpidae	—	3 (3)
Trinucleidae	4 (2)	11 (9)
Dionididae	1	1
Raphiophoridae	1	8 (7)
Endymioniidae	—	2 (2)
Hapalopleuridae	—	1 (1)
Shumardiidae	—	1 (1)
Olenidae	—	1 (1)
Dimeropygidae	—	4 (4)
Proetidae	—	5 (5)
Otarionidae	—	1 (1)
Isocolidae	—	1 (1)
Asaphidae	—	11 (11)
Hungaiidae	1	2 (1)
Nileidae	—	2 (2)
Komaspididae	—	1 (1)
Telephinidae	—	1 (1)
Remopleurididae	—	4 (4)
Cyclopygidae	3 (3)	1 (1)
Bathyuridae	—	1 (1)
Scutelluidae	1	5 (4)
Illaenidae	4 (3)	5 (4)
Cheiruridae	2 (2)	12 (12)
Pliomeridae	1 (1)	5 (5)
Encrinuridae	—	9 (9)
Calymenidae	3 (1)	4 (2)
Homalonotidae	5 (5)	—
Dalmanitidae	6 (6)	2 (2)
Pterygometopidae	—	3 (3)
Lichidae	—	6 (6)
Odontopleuridae	2	7 (5)
uncertain	—	1 (1)
totals		
all genera	35	123
endemic	24 (69%)	112 (91%)

dissimilarity index between provinces: 69

The faunal evidence suggests that further relative movements between continental masses had occurred by Caradoc time (figure 9). Progressive narrowing of the proto-Atlantic would have facilitated migrations and thus the merging of the former Bathyurid and Asaphid provinces. The continued existence of the Selenopeltis province suggests that the proto-Atlantic and mid-European seas were the barriers that isolated it. However, faunas from England, Wales and

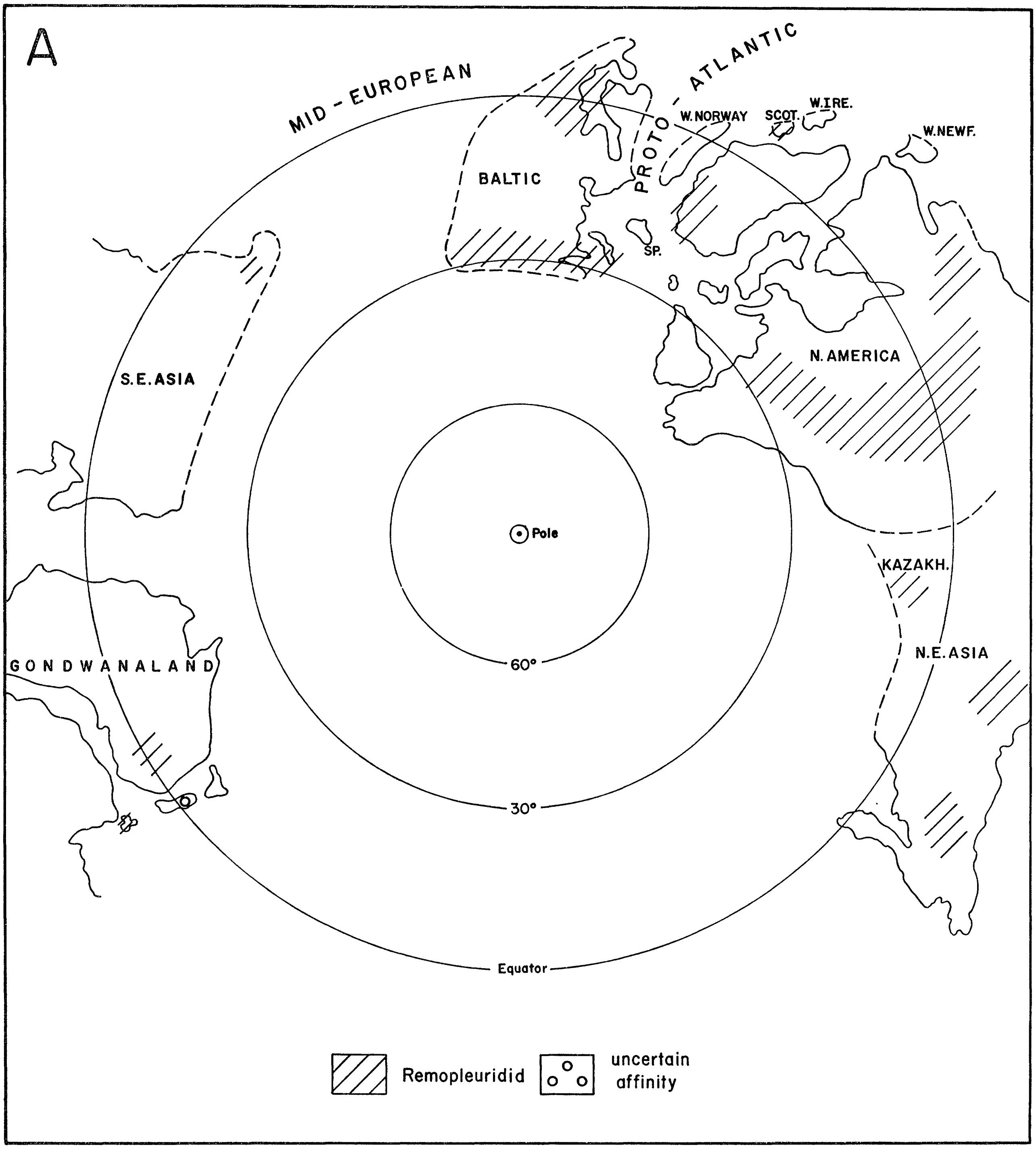

FIGURE 9. For legend see facing page.

south-east Ireland no longer belonged within it, so that we suggest that these areas moved relatively away from the remainder of southern Europe, nearer to Scotland and north-west Ireland. Such a narrowing of the proto-Atlantic may have facilitated migration of elements of

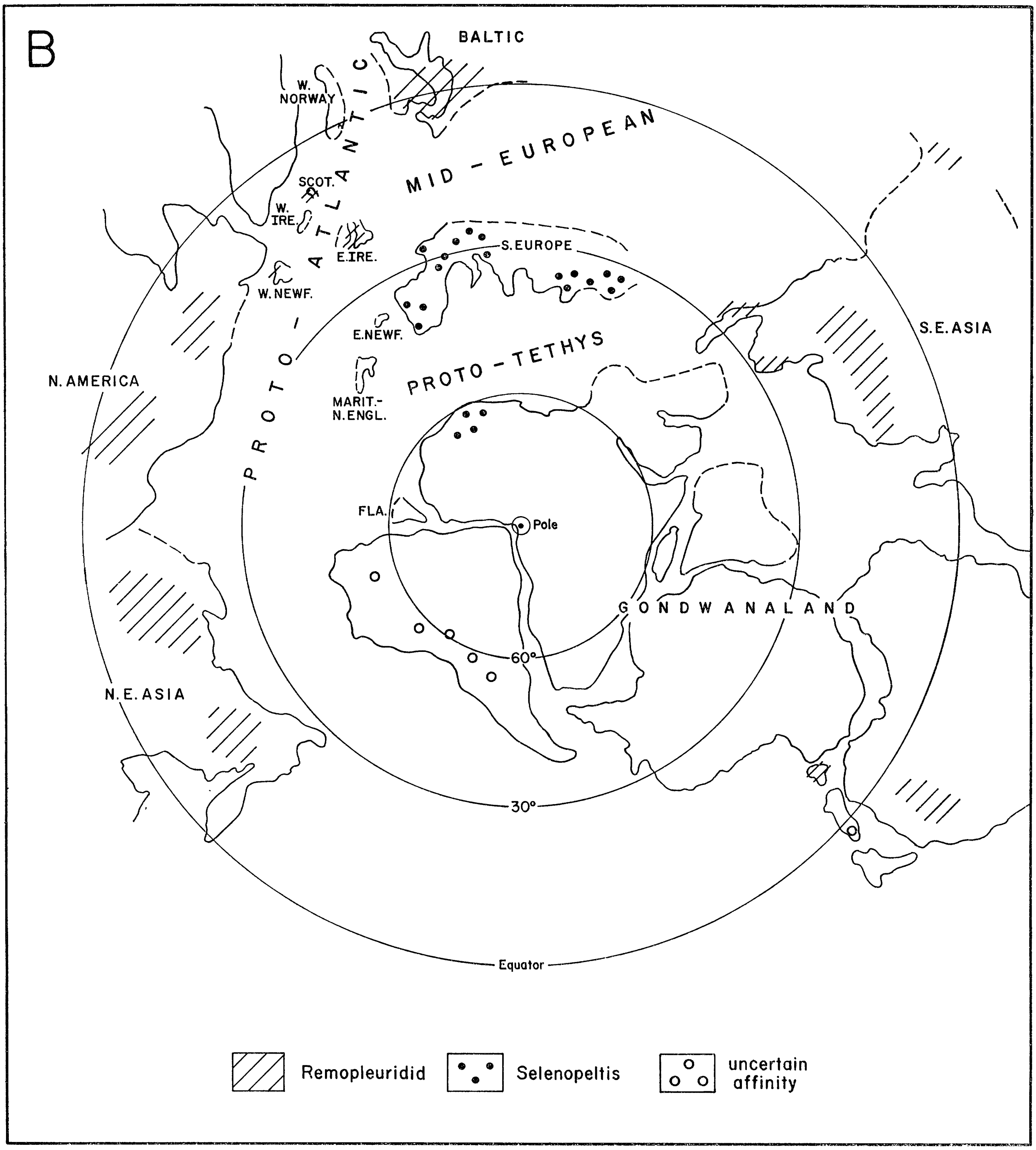

FIGURE 9. Caradoc Series: palaeogeography and trilobite faunal provinces. Stereographic projections of the northern (A) and southern (B) hemispheres. See § 2 (*e*) and explanation of figure 3 for abbreviations of geographical names.

the Remopleuridid fauna into England, Wales, and south-east Ireland, so that they replaced almost entirely the earlier Selenopeltis faunas of these areas. A movement of Gondwanaland relative to the pole is suggested on other grounds (see § 2 (*e*)), and the North American–North-east Asia mass has been rotated to effect a partial closure of the gap between North-east Asia and Gondwanaland. Because of the lack of contrary evidence, we continue to place South-east Asia closer to Gondwanaland than to the Baltic mass. Migrations in the tropical and subtropical

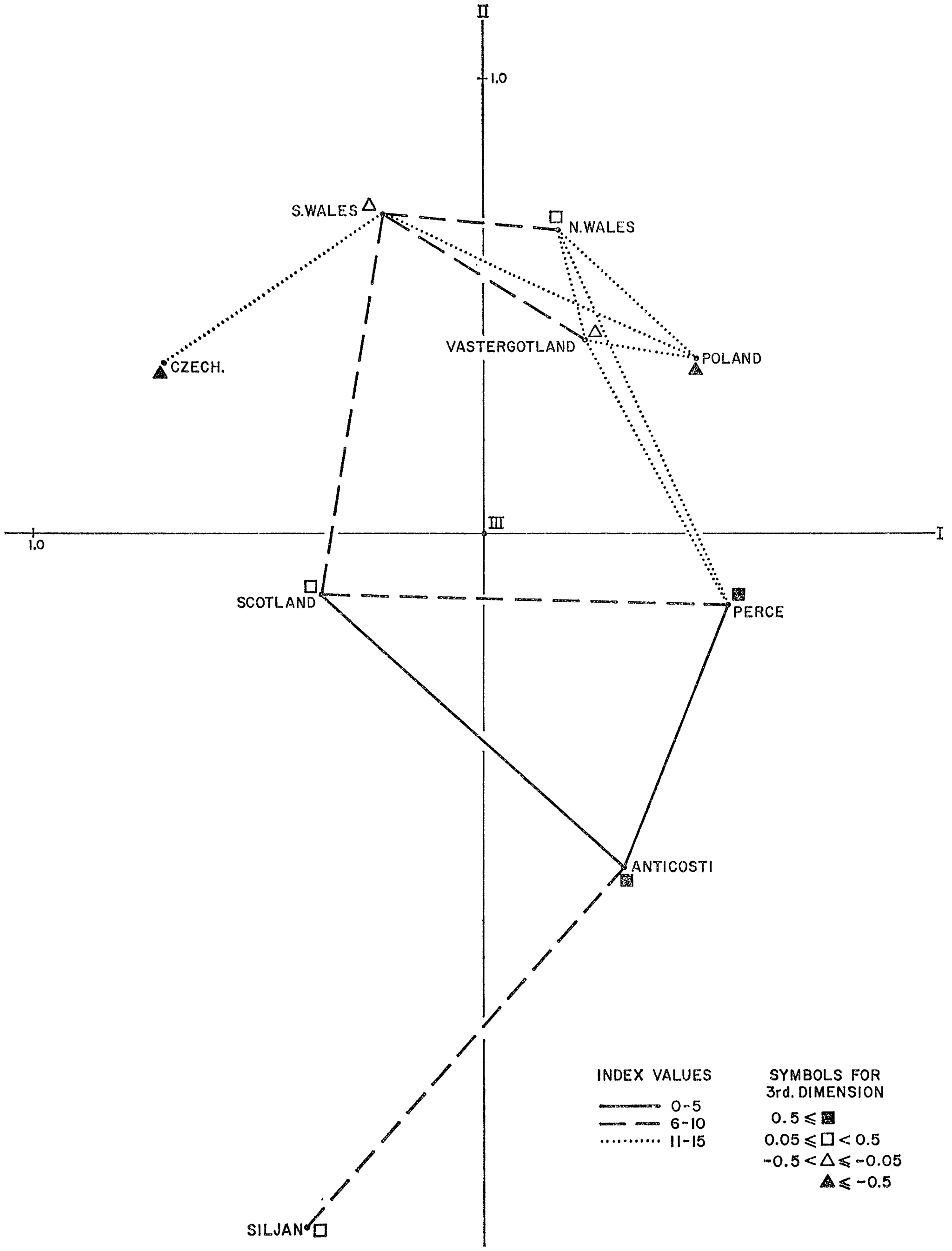

FIGURE 10. Ashgill Series: relationships between trilobite faunas based on families. Three-dimensional plot (third axis perpendicular to page) of analysis of dissimilarity indices between samples (see § 2 (*c*, *d*)). Selected index values superimposed. See Appendix for explanation of geographical names.

regions between continental masses may have produced the broad similarity within the Remopleuridid province. The possible subprovinces in North-east Asia, South-east Asia and Australia hint at partial barriers to migration and independent evolution in these areas.

(ii) *Ashgill Series*

Fourteen lists of genera have been analysed (figure 11), nine being acceptable for analysis at family level (figure 10). In the generic analysis the two provinces of the early Caradoc are still recognizable, but hardly so in the family analysis. The proportion of endemic genera is low in both provinces (table 6), and the dissimilarity index is the lowest between any two provinces during the period. The increased intermingling of faunas is thus clearly revealed. In the generic analysis, faunas from Great Britain, Sweden, Poland and North America are linked at indices

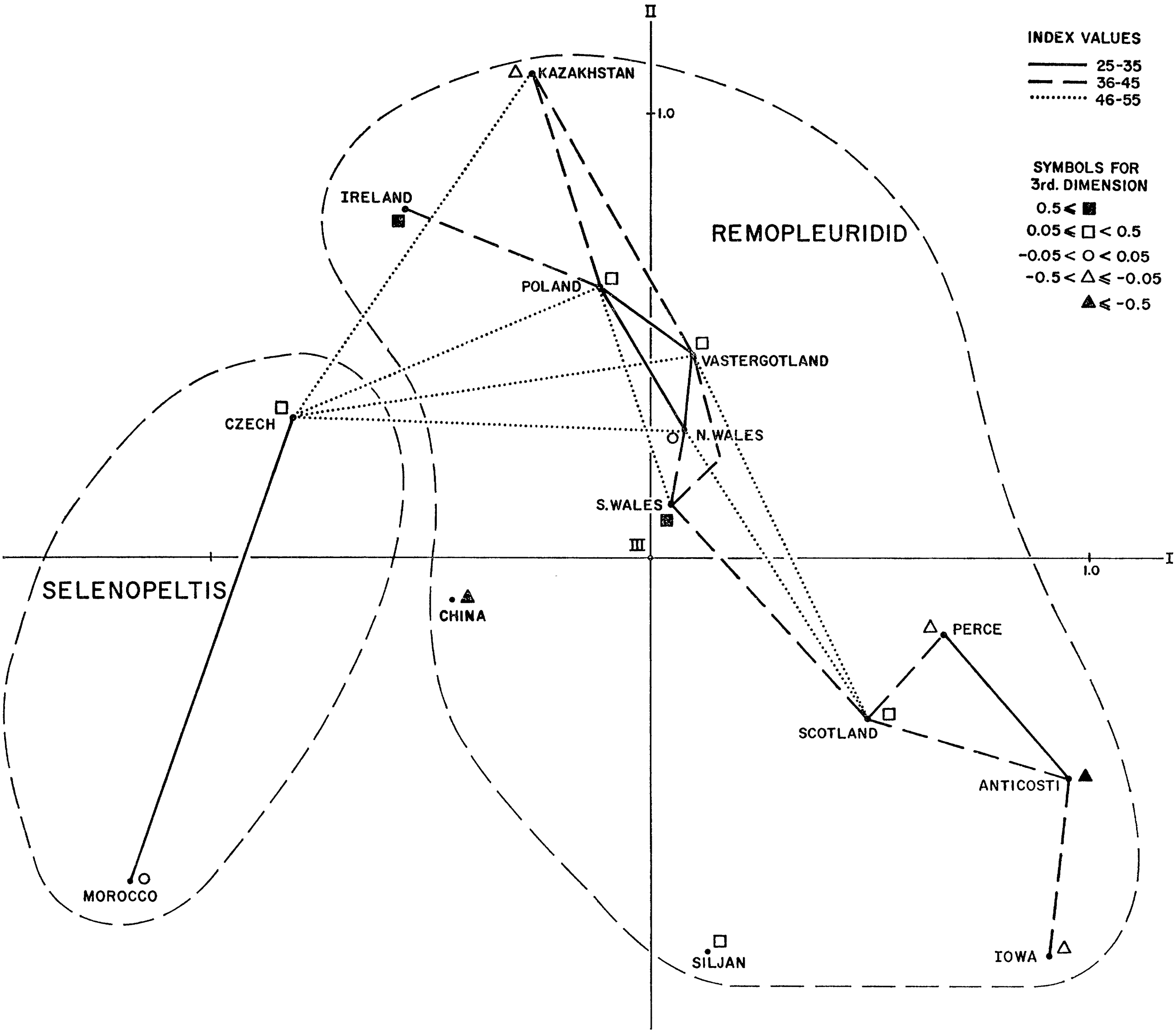

FIGURE 11. Ashgill Series: faunal provinces based on trilobite genera. Three-dimensional plot (third axis perpendicular to page) of analysis of dissimilarity indices between samples (see § 2 (*c*, *d*)). Selected index values superimposed, the two provinces indicated. See Appendix for explanation of geographical names.

25 to 45, and, as in the early Caradoc, they contain a variety of Trinucleidae, Asaphidae, Cheiruridae, Encrinuridae, Calymenidae, Lichidae and Odontopleuridae (table 6). The Czechoslovakian and Moroccan samples are closely linked at index 27, and these Selenopeltis faunas contained, as earlier, endemic Cyclopygidae, Illaenidae, Homalonotidae and Dalmanitidae, together with *Selenopeltis* (table 6). Thus the provinces reflect their ancestry of greater isolation, but, on the other hand, the remopleuridid *Amphitryon* was present in both provinces, as were

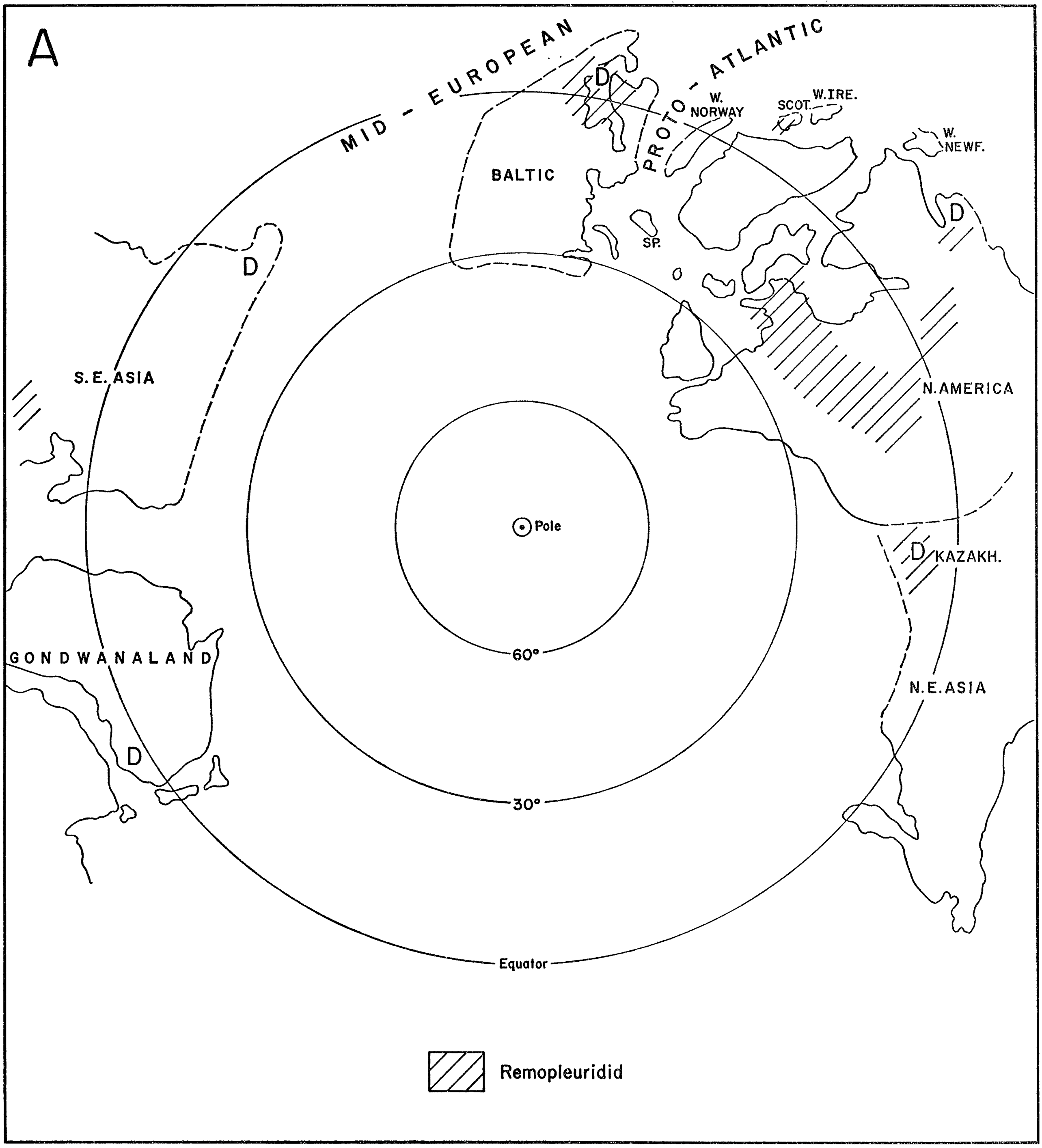

FIGURE 12. For legend see facing page.

various Cyclopygidae. The faunas from China and Siljan (table 6) are linked at levels 60 to 65 to only one fauna each in the Remopleuridid province. The sample from China is small, and that from the Siljan district is in an unusual white reef limestone facies. It contains a number of endemic genera, but the family analysis reveals its relationship to Remopleuridid faunas.

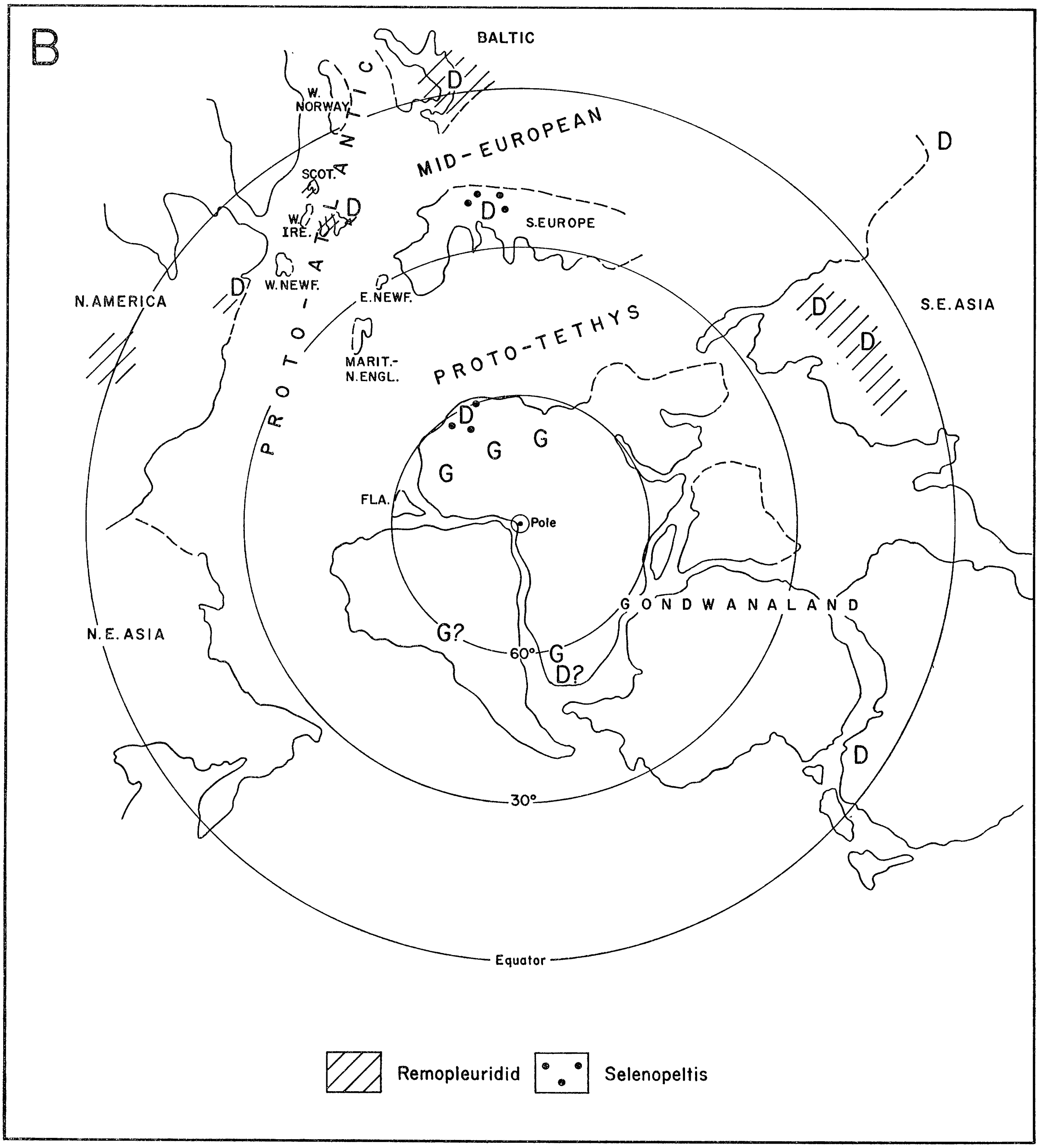

Figure 12. Ashgill Series: palaeogeography and trilobite faunal provinces. D, occurrence of late Ashgill genus *Dalmanitina*; G, evidence of glaciation. Stereographic projections of northern (A) and southern (B) hemispheres. See § 2 (*e*) and explanation of figure 3 for abbreviations of geographical names.

The world-wide occurrence of the late Ashgill trilobite *Dalmanitina* (figure 12) is paralleled by the wide distribution of brachiopod faunas of the same age (Cocks, Brunton, Rowell & Rust 1970; Ingham & Wright 1970). This absence of provinciality appears to be the culmination of the trends revealed in post-Llanvirn time. To account in part for the apparent lack of barriers to migration, we suggest (figure 12) further closure of the proto-Atlantic sea and that the southern European mass was relatively closer to the North American block.

4. IMPLICATIONS OF THE PALAEOGEOGRAPHICAL RECONSTRUCTIONS

The analyses of the faunas (figures 1, 2, 4, 5, 7, 8, 10, 11) show a progressive reduction in provinciality of Ordovician faunas with time, which resulted from the progressive breakdown of barriers to migration between provinces. The Arenig–Llanvirn map (figure 3) shows such

TABLE 6. ASHGILL SERIES: FAMILIES AND NUMBERS OF GENERA OF TRILOBITES IN THE TWO PROVINCES

Faunas from China and Siljan, Sweden, are given separately from those of remainder of the Remopleuridid province because of their isolated position. Numbers of endemic genera in parentheses. See appendix for sources.

	Selenopeltis	Remopleuridid		
family	Czech., Morocco	China	Siljan	all other
Agnostidae	1	1	—	4 (2)
Harpidae	—	—	1	1
Ityophoridae	—	—	1 (1)	—
Trinucleidae	3 (1)	1 (1)	—	3 (1)
Dionididae	1	—	—	1
Raphiophoridae	2	2 (1)	—	2
Shumardiidae	—	—	—	1 (1)
Dimeropygidae	—	—	1 (1)	—
Proetidae	—	—	2 (1)	2 (1)
Phillipsinellidae	1	—	—	1
Otarionidae	—	1	1	1
Isocolidae	—	—	1 (1)	1 (1)
Holotrachelidae	—	—	1	1
Asaphidae	—	—	1	4 (3)
Hungaiidae	1	—	—	1
Telephinidae	1	1	1	1
Remopleurididae	1	—	1	2
Cyclopygidae	4 (1)	—	—	6 (3)
Scutelluidae	1	—	2 (1)	2
Illaenidae	5 (2)	—	3	7 (2)
Cheiruridae	5 (1)	2 (1)	6 (2)	10 (2)
Pliomeridae	—	—	—	1
Encrinuridae	1	1	2	6
Staurocephalidae	1	—	—	1
Calymenidae	2 (1)	—	1	4 (2)
Homalonotidae	3 (3)	—	—	—
Carmonidae	1	—	—	1
Dalmanitidae	5 (4)	—	—	3 (2)
Pterygometopidae	—	1	—	3 (2)
Lichidae	1	1	5 (1)	4 (1)
Odontopleuridae	3 (2)	—	5 (2)	7 (4)
uncertain	1 (1)	—	—	5 (5)
totals				
all genera	44	11	35	86
endemics	16 (36%)	3 (37%)	10 (29%)	32 (27%)

dissimilarity index between provinces: 39

seas as the proto-Atlantic, mid-European, proto-Tethys, and that between North-east Asia and Gondwanaland, which separated major continental masses. We consider that the isolation of provinces in the Arenig–Llanvirn was effected by a combination of factors related to the extent and depth of these ancient seas, and the temperature and current pattern. The duration of the floating larval and earliest developmental stages in trilobites is unknown, but presumably it was measured in days or 1 or 2 weeks at most, so that a wide, deep ocean would have constituted a barrier to migration. The maps of succeeding series (figures 6, 9, 12) portray a progressive closure during post-Llanvirn time of the proto-Atlantic, and narrowing of the mid-European sea, as well as relative movement of Gondwanaland. We consider that these processes would have facilitated migrations of benthonic faunas, because of narrowing and/or shallowing of parts of the seas, production of islands, and changes in patterns of ocean currents. Thus the Asaphid and Bathyurid provinces lose their individuality at the beginning of the Upper Ordovician, and before the end of the period the Selenopeltis province is no longer recognizable.

Over continental shelves presumably temperature was an important factor controlling latitudinal distribution. Throughout the Ordovician period we presume equatorial waters were warmer than polar, the difference becoming greater in the Upper Ordovician because of the evidence for late Ordovician glaciation (figure 12; Appendix). The prevalence of limestones, and presence of gypsum-bearing evaporite deposits (particularly in the Upper Ordovician), is characteristic of the regions here regarded as tropical (cf. Whittington 1966, Text-figs. 2, 16, p. 731). The Selenopeltis faunas may owe their peculiarity, which extends over most of the Ordovician period, not only to having evolved in isolation, but also to having inhabited colder waters on the margin of Gondwanaland. Other marginal parts of Gondwanaland appear to have been submerged by warmer waters, and this temperature difference, combined with isolation, may help to explain the Asaphopsis province (figure 3). Closure of the proto-Atlantic is believed to have led to merging of the Bathyurid and Asaphid provinces by early Caradoc time. The resulting Remopleuridid province (figure 9) extended also over South-east Asia and Australia. The implication is that migration was possible between all parts of this vast area of warm waters, though indications of subprovinciality suggest the existence of partial barriers. We are not aware of compelling geological evidence for closure of other seas that separated continental masses. We have suggested some drift and rotation of North American–North-east Asia to effect a narrowing of the sea separating North-east Asia and Gondwanaland (figures 9, 12).

The mid-European sea acted as an effective barrier to isolate the Selenopeltis province, this effect being supplemented presumably by the cooler temperatures consequent on the geographical position of the province. A problem is presented by the faunas of England, Wales and south-east Ireland, which are within this province in the Lower Ordovician, but clearly in the Remopleuridid province by early Caradoc time. We suggest (figure 9) that these British areas moved relatively away from the remainder of southern Europe, closer to the North American block. By late Ashgill time (figure 12) this gap may have narrowed again by southern Europe moving relatively closer to the North American mass.

5. Faunal diversity in Ordovician trilobites

Some measure of faunal diversity is given by numbers of genera, drawn from the samples we have analysed, present in particular areas during each selected interval (table 7). The maps suggest that the Selenopeltis province was in cooler waters throughout the period, other provinces in warmer waters. The time intervals represented by the series are unlikely to be equal, for example the Arenig and Llanvirn was probably far longer than any of the other three; thus comparisons of one with another may be misleading. Although the data for the Llandeilo are poor, it appears that cooler water faunas were less diverse throughout the Ordovician (cf. Stehli, McAlester & Helsley 1967; Valentine 1967). The particularly large difference in diversity of faunas in warm and cool waters in the Caradoc may reflect the diversity that resulted from the development of subprovinces in the Remopleuridid province (see § 3*b* (i)).

We have shown that the Ordovician history of trilobite distribution was one of progressively decreasing provinciality. Valentine (1967) contended that decreasing provinciality reduces total diversity. The figures for total diversity (table 7) appear in general to support this claim, although the possibility that the four time intervals are widely disparate must be borne in mind. The apparent rise in diversity of the Remopleuridid province of the Caradoc over its predecessor in time may reflect the inadequate data on the Llandeilo, or a real increase in diversity consequent upon the development of sub-provinces within the Remopleuridid province. Valentine (1967) also advanced cogent reasons for believing that during climatic deterioration diversity increases. Supposedly the Ordovician period was a time of deteriorating climate, if late Ordovician glaciation was widespread. The trend toward decreasing diversity with time shown by Ordovician trilobites implies that decreasing provinciality was the dominant factor affecting diversity, and not climatic deterioration.

6. Facies and subfaunas within provinces

The survey of biogeography of Ordovician trilobites is necessarily generalized, so that each province is portrayed as having covered a large area and persisted for millions of years. Clearly the species constituting a fauna were not uniformly distributed throughout the province at any one time, enlargement or contraction of areas occupied took place in time, as well as evolutionary changes. The palaeoecological conditions, reflected in part in the enclosing rock, also varied in time and space within a province. The analysis of such complex patterns offers challenging problems, some of which are briefly outlined below.

(*a*) *Bathyurid and Remopleuridid faunal provinces*

Rodgers (1968) has given clear expression to the idea that the Arenig (Upper Canadian) deposits of eastern North America were part of an extensive carbonate bank, which at its outer margin sloped abruptly into deeper waters, where clastic deposits accumulated. Similarly, in western North America, the carbonate bank on which deposits of similar age were formed may

Table 7. Numbers of trilobite genera in warm and cool waters in the series of the Ordovician system, together with total numbers of different genera in each series

The Selenopeltis province was in cool waters throughout the period. The named provinces, and areas of uncertain affinity (except South America during the Caradoc), were in warm waters.

	warm	cool	total
Arenig and Llanvirn	201	87	263
Llandeilo	69	68	130
Caradoc	130	35	154
Ashgill	99	44	115

have sloped equally abruptly at the western and southern margins into deeper waters (Ross & Berry 1963, pl. 14; Jackson 1966; Ross & Ingham 1970). We here refer to the region surrounding central North America, on which carbonate deposits accumulated in shallow waters, as the *platform*, and the marginal declivity as the *slope*.

During Arenig time the deposits of the platform are shallow-water carbonates, with algal banks and mounds, contemporaneous lime-breccias and lenses of lime-sand, non-depositional breaks being a characteristic feature. Because of structural complexities at and adjacent to the original declivity, deposits of the slope are difficult to recognize when preserved. The boulders of the Cow Head Group, western Newfoundland, appear to provide a sample of upper slope carbonate deposits, for they include fragments of reefs, lime sands and lime muds, which were moved down-slope to form boulder beds interbedded with graptolite shales (Kindle & Whittington 1958). In table 8 Bathyurid faunas of the platform are contrasted with those of the slope. The platform fauna belongs within nine families, there being a variety of genera of Asaphidae, Bathyuridae and Pliomeridae, so that it contains more genera than the slope fauna. The families present on the platform are also present on the slope, with one exception, but half of the genera are different. The slope fauna also contains genera of eleven additional families, and so is more diverse, presumably reflecting adaptation to the wider variety of slope environments. The Cow Head boulder beds afford a sample of these environments, but may also include boulders of rocks originally deposited on the platform. It is thus uncertain that all the genera in common between the two faunas were inhabitants of slope environments.

Table 8. Bathyurid faunas of Arenig age in two environments in North America

1, platform, St George Formation (Whittington 1968*b*, p. 52); Garden City Formation and Pogonip Group, zones G to J, Utah and eastern Nevada (Ross, 1951; Hintze, 1953). 2, slope, boulders in Cow Head Group, beds 8a–10, Western Newfoundland (Whittington 1968*b*, Table 4.1, and C. P. Hughes, in preparation).

	numbers of genera		
family	(1) platform	(2) slope	in common
Agnostidae	—	2	—
Harpidae	—	1	—
Raphiophoridae	—	1	—
Alsataspididae	—	1	—
Shumardiidae	—	1	—
Hystricuridae	2	2	2
Dimeropygidae	1	1	—
Isocolidae	—	1	—
Glaphuridae	—	1	—
Asaphidae	11	3	1
Komaspididae	1	2	1
Remopleurididae	3	4	1
Bathyuridae	10	5	5
Scutelluidae	1	1	—
Illaenidae	—	1	—
Cheiruridae	1	—	—
Pilekiidae	—	1	—
Pliomeridae	6	2	—
Odontopleuridae	—	1	—
uncertain	—	1	—
totals			
genera	36	32	10
families	9	19	—

Dissimilarity index (genera): 69.

Table 9, columns 2 to 5, gives, for overlying younger formations in western Newfoundland, a summary of faunas in a greater variety of slope environments. The dissimilarity indices (table 10) show that the reef fauna of table 9, column 2, is unlike that of other slope environments, reflecting the niche-diversification characteristic of reefs. There is a strong resemblance between the remaining slope faunas, which come from muddy and nodular limestones exhibiting slump structures, dark, platy limestones interbedded with shales, and of boulders of these limestones. These are typical slope environments, and the restricted fauna (table 9, column 4) of certain platy limestones is presumably that of deeper, muddy waters, and interbedded shales contain abundant graptolites, as do certain of the muddy limestones (Whittington & Rickards 1968). The platform fauna (table 9, column 1) is taken from Utah and eastern Nevada because rocks of this facies and age are not present in western Newfoundland. The platform sample is derived from a variety of rocks—quartzites, shales, calcarenites, sponge beds, calcilutites and dark, muddy limestones, so that the fauna given is a mixture from various environments. As the dissimilarity indices (table 10) show, this sample is different from any on the slope.

Tables 8 and 9 also reveal that Agnostidae, Harpididae, Harpidae, Raphiophoridae, Endymioniidae, Alsataspididae, Shumardiidae and Odontopleuridae make their first appearance in slope environments, some subsequently invading the platform. Glaphuridae and Isocolidae are peculiar to the presumed reef environment (table 9, column 2), and Lichidae make their first appearance there, accompanied by peculiar Bathyuridae, Illaenidae and Cheiruridae.

The trilobites of the younger Chazy Group (Llandeilo) have been described by Shaw (1968) and these are from reef, lime sand and other facies of presumably the upper slope. Shaw's results (1968, Table 5, pp. 12 to 14) show the variety of the reef fauna, that *Glaphurus* and other genera are confined to the reefs, and that certain additional genera are large in size or abundant in this rock. In the non-reef facies some different genera are present, and Harpidae and Raphiophoridae are present only in non-reef facies.

Similar features are shown in the early Upper Ordovician (tables 11, 12) by faunas from the continental interior platform region of North America and from slope environments in Virginia and Scotland. The reef fauna is poorly known, but includes the isocolid *Tiresias* (Dean 1962), a glaphurid, and *Hyboaspis*, a genus of uncertain affinity also known in Chazy reefs (Shaw 1968, p. 63). It is unlike other faunas on the slope or platform. Of the remaining slope faunas, the Scottish examples are similar to each other and more like the platform fauna of Virginia than the non-reef slope fauna. Raphiophoridae are varied in the slope faunas and in the Virginia example (table 11, column 3) Agnostidae, Endymioniidae, Trinucleidae, Dionididae and Olenidae are also present in the muddy limestones interbedded with graptolite-bearing shales. The platform fauna contains a harpid, a dalmanitid and lichids, families which appeared first (tables 8, 9) in Lower Ordovician slope deposits.

This generalized analysis of Lower and early Upper Ordovician faunas from North America suggests that the following conclusions may be drawn:

(i) The families peculiar to each environment—platform, reef, lime sands, dark shales with interbedded muddy limestones—tended to persist in that environment, though there is some evidence of invasion of the platform by groups which first appeared on the slope.

(ii) In each environment evolution was continuous, so that the generic (and specific) composition of a fauna in a particular environment was constantly changing with time. Thus the Llandeilo age reefs (Shaw 1968, Table 5) have no species and only three genera in common with the older Lower Head reef rock (table 9, column 2), and boulders of Llanvirn age (table 9,

Table 9. Bathyurid faunas of late Arenig and Llanvirn age, on the platform and in various slope environments, North America

1, platform, Kanosh Shale and Lehman Formation, Utah (Hintze 1953) and Antelope Valley Limestone, Nevada (Whittington in Kay 1962; Ross 1967). 2, slope, reef limestone boulder at Lower Head, Western Newfoundland (Whittington 1963). 3, slope, muddy limestones and interbedded shale, displaying slump structures, type middle Table Head Formation, western Newfoundland (Whittington 1965, pp. 284–285). 4, slope, platy limestones interbedded with black shale yielding graptolites, Black Cove, western Newfoundland (Whittington 1965, p. 286). 5, slope, boulders in Cow Head Group conglomerates, Portland Creek and Daniel's Harbour, western Newfoundland (Whittington 1965, pp. 286–287).

	numbers of genera				
		slope			
family	(1) platform	(2) reef	(3) slumped, muddy, lime-stones	(4) platy limestones with black shale	(5) boulders
Agnostidae	1	1	2	1	1
Harpididae	—	—	1	—	—
Harpidae	1	1	—	—	—
Raphiophoridae	—	—	3	2	3
Endymioniidae	—	—	1	1	1
Shumardiidae	1	—	2	—	1
Olenidae	1	—	2	1	1
Dimeropygidae	1	3	1	—	—
Proetidae	—	1	1	—	—
Isocolidae	—	2	—	—	—
Glaphuridae	—	1	—	—	—
Asaphidae	1	—	2	2	2
Nileidae	2	1	3	2	2
Komaspididae	1	—	—	1	—
Telephinidae	—	—	1	1	1
Remopleurididae	1	1	3	1	2
Bathyuridae	2	3	—	—	—
Scutelluidae	1	1	1	—	1
Illaenidae	1	2	1	—	1
Cheiruridae	3	4	3	—	—
Pliomeridae	4	3	1	—	1
Encrinuridae	1	—	2	—	1
Calymenidae?	1	—	—	—	—
Dalmanitidae	—	—	—	—	1
Lichidae	—	1	—	—	—
Odontopleuridae	1	1	—	—	—
uncertain	2	—	—	—	—
totals					
families	18	15	18	9	14
genera	26	26	31	12	19

Table 10. Bathyurid faunas of late Arenig and Llanvirn age

Half matrices of genera in common and dissimilarity indices between environments 1 to 5 of table 9.

genera in common

5	—	—	—	—	—
4	9	—	—	—	—
3	16	9	—	—	—
2	3	0	6	—	—
1	5	2	7	8	—
	5	4	3	2	1

dissimilarity indices

5	—	—	—	—	—
4	18	—	—	—	—
3	11	18	—	—	—
2	83	100	76	—	—
1	72	82	72	68	—
	5	4	3	2	1

column 5) no species and only four genera in common with the boulders of Arenig age (table 8, column 2).

(iii) The long range in time of certain genera, or of closely related genera, may give a superficial similarity between faunas of quite different age. This may be especially so if they were inhabiting similar environments, and hence contain genera belonging to the same families. For example, the muddy limestones and interbedded black shales of early Llanvirn age in

TABLE 11. REMOPLEURIDID FAUNA OF EARLY CARADOC AGE, IN PLATFORM AND SLOPE ENVIRONMENTS, NORTH AMERICA AND SCOTLAND

1, platform, Platteville Group, Upper Mississippi valley (De Mott, personal communication). 2, slope, reef limestones in McNutt quarry (Cooper 1944, p. 63; Butts 1940, p. 153; Raymond 1925, p. 173) and Porterfield quarry (Butts 1940, p. 153; Cooper 1953, p. 9), Virginia. These quarries are in the Effna Limestone (Cooper 1944) and include reef-like masses (Butts 1940, Pl. 31B). No study has been made of the trilobites of the reef masses, and some of the genera listed may be from associated calcarenites, so that this list is of doubtful validity. The list given by Cooper (1953, Table 1) includes forms from a variety of rock types. 3, slope, Liberty Hall and Athens, black shale and black limestone, Virginia (Raymond 1925; Cooper 1953; Whittington 1959). 4, slope, calcareous sandstones, mudstones and silts, Confinis Flags, Scotland (Tripp 1962). 5, slope, platy limestones, Upper Stinchar Limestone, Scotland (Tripp 1967; personal communication). 6, slope, calcareous siltstones, nodular limestones, Albany Mudstone, Scotland (Tripp 1965; Ross & Ingham 1970).

	numbers of genera					
		slope				
family	(1) platform	(2) reef	(3) muddy limestone and shale	(4) calcareous sandstones and silt	(5) platy limestone	(6) calcareous silts, nodular limestones
Agnostidae	—	—	1	—	—	1
Harpidae	1	—	—	—	—	1
Raphiophoridae	—	—	5	2	1	3
Endymioniidae	—	—	1	—	—	—
Trinucleidae	—	—	2	—	—	—
Dionididae	—	—	1	—	1	—
Olenidae	—	—	1	—	—	1
Dimeropygidae	—	—	1	—	2	3
Proetidae	—	—	1	1	1	—
Otarionidae	—	—	—	1	1	1
Isocolidae	—	1	—	—	—	—
Glaphuridae	—	1	—	—	—	—
Asaphidae	2	2	1	2	—	1
Nileidae	—	1	—	—	—	2
Komaspididae	—	—	—	—	1	1
Telephinidae	—	—	1	—	1	—
Remopleurididae	1	—	3	2	2	4
Bathyuridae	1	—	—	—	—	1?
Scutelluidae	—	—	1	3	2	3
Illaenidae	3	3	—	2	2	2
Cheiruridae	2	2	2	4	6	3
Pliomeridae	1	—	—	—	1	—
Encrinuridae	2	1	—	3	4	6
Calymenidae	—	—	—	1	1	1
Dalmanitidae	1	—	1	2	1	—
Lichidae	2	1	—	2	2	2
Odontopleuridae	—	—	1	1	1	2
uncertain	—	1	—	—	—	1
totals: genera	16	13	23	26	30	39
families	10	9	15	13	17	19

western Newfoundland (table 9, column 3) and early Caradoc strata of Virginia and Tennessee (table 11, column 3) both yield the raphiophorids *Ampyx* and *Lonchodomas*, the olenid *Triarthrus*, the scutelluid *Raymondaspis*, and the cheirurid *Ceraurinella*. The dissimilarity index is 65, and no species are in common between them, evidence of the evolution that has taken place in the long time separating these faunas. The persistence of Isocolidae in reef limestones, from Arenig (table 8) to late Ordovician (Boda Limestone, Whittington 1966, Table 6) age, is another example of this phenomenon.

(iv) Tables 8 to 12 indicate the wide variety of genera in the varied environments of the slope, and the few that are in common with the contemporaneous platform fauna. Few, if any, species are known to be in common between any of these environments. Thus the slope, with its many niches, especially the upper slope where reefs and lime-sands occur, is the prime region of evolutionary diversification. Genera and species peculiar to one locality in a particular environment, and thus limited in space and time in known distribution, are characteristic of upper slope environments.

TABLE 12. REMOPLEURIDID FAUNAS OF EARLY CARADOC AGE

Half matrices of genera in common and dissimilarity indices between environments 1 to 6 of table 11.

genera in common

6	—	—	—	—	—	—
5	18	—	—	—	—	—
4	18	17	—	—	—	—
3	13	7	8	—	—	—
2	4	3	5	1	—	—
1	9	9	9	2	5	—
	6	5	4	3	2	1

dissimilarity indices

6	—	—	—	—	—	—
5	40	—	—	—	—	—
4	31	35	—	—	—	—
3	50	70	65	—	—	—
2	67	77	62	92	—	—
1	44	44	44	87	62	—
	6	5	4	3	2	1

(v) Dissimilarity indices between the faunas of tables 8, 9, 11, are given (tables 10, 12), and over half range between 65 and 92. This range of indices is similar to that between faunal provinces (tables 2, 4, 5). It should not be concluded, however, that the supposed faunal provinces are merely a reflexion of the differences between, for example, platform and slope facies. In compiling the lists for the Bathyurid faunal province, faunas from all facies in particular areas, over a longer period of time, have been combined, for example in the Arenig and Llanvirn. The faunal province analysis is thus more generalized, but does give a consistent pattern. It is clear, however, that dissimilarity indices (or their converse) cannot be used uncritically in an attempt to date a particular fauna. Facies as well as provincial differences must be taken into account.

These conclusions reveal the complex pattern of evolution and migration in time and space within a province. Studies by Ross (1964, 1967, 1970) show the difficulties of correlation and dating of faunas over a large area in which environments changed laterally and vertically. Detailed studies of the type undertaken by Shaw (1968) show that the complications resulting from different modes of preservation of fossils make the unravelling of the history more difficult. Some of the most challenging problems awaiting analysis are in this field of environmental history and evolution. The problem of dating a particular fauna is not new to geologists, and it has long been realized that the evolution of new species and genera, and their first appearance in a fauna, are critical in dating.

The Toquima–Table Head faunal realm proposed by Ross & Ingham (1970) corresponds to the slope, as used here, in the Bathyurid faunal province. We do not consider that these slope faunas indicate the margin of *any* Ordovician continent, but the margin of a particular continent, that here (figure 3) composed of the North American and North-east Asian blocks (cf. Ross & Ingham 1970, Fig. 5). The contemporaneous faunas around the margins of Gondwanaland are manifestly different, as are the Asaphid faunas around the margin of the Baltic mass. Thus the 'Toquima–Table Head' faunas are dispersed in different environments around the margin of one continent, and owe their broad similarity to migration and dispersal in these waters.

The age of the 'Toquima–Table Head' faunas ranges from Arenig to early Caradoc (Ross & Ingham 1970, p. 395), the age span of the slope faunas of tables 8, 9, 11. As our discussion indicates, the age of a particular fauna may be difficult to determine, and there has been controversy as to the age and correlation of these faunas (cf. Ross 1970). For example, Ross & Ingham (1970, p. 397) raise the question of why the Albany Mudstone fauna (table 11, column 6) resembles that of the middle Table Head Formation (table 9, column 3). The resemblance is because of the presence of long-ranging genera in both faunas (those listed as 'Whiterock' by Ross & Ingham 1970, Table 2). Other genera in the Albany Mudstone have evolved in post-Table Head time, and indicate the younger age.

(*b*) *Asaphid and Remopleuridid faunal provinces*

Faunas of Arenig age in the platform region are well known, from the Oslo district eastwards through southern Sweden and Estonia to the Leningrad area. These platform deposits are relatively thin and predominantly of limestones containing discontinuity surfaces, and extend south to Bornholm (Poulsen 1965) and north-eastern Poland (Bednarczyk 1968). Slope environments appear to be exposed only to the west in the allochthonous belts of Norway (Størmer 1967) where trilobite faunas are little known. Hence no analysis of the type made for the Bathyurid province can be attempted. The platform limestones are different in character from those of North America, for there are interbedded graptolite shales (e.g. Størmer 1967, Fig. 9), indicating a wider variety of environments in space and time. Possibly as a reflexion of this, Agnostidae, Harpidae, Raphiophoridae and Shumardiidae are present in platform faunas of the Asaphid province during Arenig time, but not in those of North America.

Williams (1969*b*, Fig. 10) has portrayed a pre-middle Caradoc Baltic province in brachiopod faunas extending through Anglesey, south-eastern Ireland to northern Maine. During the Arenig (Williams 1969*a*, pp. 129 to 131) this Baltic fauna contained brachiopods like those from Estonia, an area included in our Asaphid trilobite faunal province. Arenig and Llanvirn trilobite faunas indicate that Anglesey (Bates 1968), south-eastern Ireland (Brenchley, Harper & Skevington 1967) and the Lake District of northern England (Whittington, study of collections), were part of the Selenopeltis province during the Lower Ordovician. Trilobites from northern Maine (Whittington *in* Neuman 1964), of late Arenig or early Llanvirn age, appear to belong to the Bathyurid fauna. Thus in trilobites we are not able to recognize Baltic (i.e. Asaphid) faunas in the same regions in the Lower Ordovician as Williams does, but such elements do appear in English and American trilobite faunas in the Caradoc (Whittington 1966, pp. 720, 726). The combination of factors controlling the distribution of trilobites may not be the same as that for brachiopods, and these differences are to be expected. We point out that our Asaphid and Bathyurid provinces were seemingly not genetically isolated in the Arenig and Llanvirn (figure 2), and in the Llandeilo they are closer together (figure 5).

(*c*) *Selenopeltis province*

This was the most distinctive and longest lasting Ordovician province, recognizable in the Arenig and apparently losing its individuality only in the late Ashgill. Throughout this time it extended over southern Europe and Morocco, but over England, Wales and south-east Ireland only during the Lower Ordovician. Rocks in these latter areas were deposited in the Caledonian geosyncline; geographical changes opened these areas to migrations from the Bathyurid and Asaphid provinces in the late Lower Ordovician, so that the Selenopeltis faunal character was progressively blotted out. The remainder of the province was isolated from such migrations. The deposits are clastic, transgressive on to older rocks, some were laid down in isolated deep basins, and volcanic ridges and islands were formed in different areas at varying times. A pattern of varied environments, constantly changing in time and space, appears to be typical of the province (Spjeldnaes 1967, Fig. 1; Babin *et al.* 1968, Figs. 1, 2). An analysis of the platform-slope type does not appear applicable, for there is no well-defined margin between two such different regions revealed by either rock types or structure (cf. Spjeldnaes 1967, p. 49).

Appendix

Sources of data for analyses

For each selected portion of the Ordovician system, a series of faunal lists from particular localities or areas was compiled, subject to the qualifications discussed in § 2 (*a*). An abbreviated name for each area or locality is used in figures 1, 2, 4, 5, 7, 8, 10, 11. These names are listed below with an explanation and references to sources. Family names are employed as in Whittington (1966), Hungaiidae including *Asaphopsis*, *Birmanites* Sheng, 1934, *Nobiliasaphus* Přibyl & Vaněk, 1965 (= *Pamirotchechites* Balashova, 1966) and *Opsimasaphus*. Calymenidae and Homalonotidae have been used in a conservative manner, rather than employing four additional family names as advocated by Dean (1966). In counting total number of genera in a fauna, indeterminate genera have been included; in counting numbers of genera in common between two faunas they have been excluded. Additional references used in compiling the maps are given below; the maps are partly based on earlier work (Whittington 1966; Dean 1967*a*).

Arenig and Llanvirn Series

W. Newf. (A): Newfoundland, St George and Table Head formations (Whittington 1965, 1968*b*).

W. Newf. (B): Newfoundland, boulders of Cow Head Group (Whittington 1963, 1965, 1968*b*; C. P. Hughes, in preparation).

N. E. U.S.S.R.: north-east portion of U.S.S.R. (Chugaeva, Rozman & Ivanova 1964).

Nevada, Utah: Nevada and Utah, zones G to N (Ross 1951, 1967; Hintze 1953; Whittington *in* Kay 1962).

Sweden: Sweden and Bornholm, Denmark (Bohlin 1949, 1955, 1960; Bruton 1966; Jaanusson 1960, 1963; Poulsen 1965; Tjernvik 1966).

Estonia (Schmidt 1907; Rõõmusoks 1970).

Morocco: Anti-Atlas Mountains (Destombes 1967).

C. Britain: Shelve district, Shropshire, England (Whittard 1966).

Czech.: Czechoslovakia, Klabava and Šárka formations (Havlíček & Vaněk 1966).

S. America: Argentina and Bolivia (Branisa 1965, collections from Bolivia in the U.S. National Museum include aff. *Prosopiscus*, a form discussed below under Australia; Harrington & Leanza 1957).

Australia: compiled by Whittington from study of collections in Universities of Melbourne, Sydney and Tasmania, Bureau of Mineral Resources, Canberra, and Australian National University.

In central Australia (Amadeus and Georgina basins and western New South Wales) faunas of late Arenig or Llanvirn age contain agnostids, hystricurids, *Lonchodomas*, *Carolinites*, *Annamitella* and possibly other bathyurids (Hill, Playford & Woods 1969, Pl. OV, Figs. 5, 6), asaphids, a pliomerid genus resembling *Encrinurella*, a *Neseuretus*-like calymenid, and a genus of uncertain affinity here termed aff. *Prosopiscus*. *Prosopiscus* Reed, 1912, has a glabella with three pairs of subparallel glabellar furrows, the eye lobe situated close to the anterior glabellar lobe, a conspicuous eye ridge running forward and outward to the eye lobe, and a pitted fixed cheek. The original material is flattened and from a poorly localized early collection from Spiti, Kangra district, northern India. It is associated with a *Neseuretus* type calymenid, a pliomerid and a cheirurid. The age may be Llandeilo or even early Caradoc, and so apparently younger than the Australian form. In the Canning Basin of northwestern Australia some of the genera mentioned are known, and in addition a possible hapalopleurid, an endymioniid, *Triarthrus*, and a pliomerid pygidium like that of *Ectenonotus*. The faunas of a similar age in Tasmania are distinctive in containing *Asaphopsis*, endemic genera such as *Tasmanocephalus* and *Etheridgaspis* (Kobayashi 1940*b*, *c*), as well as an agnostid, the widespread *Carolinites*, *Hystricurus*, a scutelluid and pliomerids. Some of these latter resemble *Encrinurella* Reed, 1915, and the fragment from Vietnam (Mansuy 1920, Pl. 2, Fig. 6).

China: Central and southwest China (Lu 1959, 1964; Reed 1917; Sheng 1934, 1958).

Kazakhstan: U.S.S.R. (Nikitin, Apollonov & Tsay 1968).

France: Southern France (Dean 1966).

Poland: North-east Poland (Bednarczyk 1968).

Pay Khoy: Arkhangelskaya, U.S.S.R. (Burskyi 1970).

References since 1966 used in compiling the map (Balashova 1967; Bates 1968; Bondarev, Burskyi & Nekhorosheva 1968; Brenchley, Harper & Skevington 1967; Burskyi 1966 *a–d*; Dean 1967*b*, 1971; Koroleva 1967). Collections from the Lake District, northern England, in the Sedgwick Museum, Cambridge, studied by Whittington.

Llandeilo Series

C. Britain: Shelve district, Shropshire, and Builth district, Central Wales (Whittard 1966; Hughes 1969, 1971, and in preparation).

Czech: Czechoslovakia: Dobrotívá Formation (Havlíček & Vaněk 1966).

France: Brittany (Babin *et al.* 1968; Henry 1970).

Morocco: Anti-Atlas Mountains (Destombes 1967).

N. America: Chazy Group, New York State, U.S.A. (Shaw 1968).

Estonia: division C_{1b-c} (Rõõmusoks 1970).

Taymyr: Eastern Taymyr peninsula, U.S.S.R. (Balashova 1960).

Sweden: Folkesunda and Furudal limestones (Jaanusson 1960, 1963).

China: south China, Shihtzupu Formation (Lu 1959; Sun 1931).

Pamir: Tadzhikistan, U.S.S.R. (Balashova 1966).

Additional reference (Burskyi 1970).

Caradoc Series

Virginia: rocks of Porterfield Stage, Virginia, U.S.A. (Cooper 1953; Whittington 1959).

Central Britain: Shelve district, gracilis and multidens zones, Shropshire (Whittard 1966); Builth district, central Wales (Hughes 1969, 1971, and in preparation).

Czech: Czechoslovakia, Libeň, Letná and Vinice formations (Havlíček & Vaněk 1966).

Morocco: Anti-Atlas Mountains (Destombes 1967).

N. S. Wales: East Central New South Wales, Australia, strata of Porterfield and Wilderness age; Webby, Moors & McLean (1970) have described *Encrinuraspis* and *Malongullia* (which we believe to belong in Endymioniidae); Campbell & Durham (1970) *Parkesolithus*; Whittington identifies the following from collections at the University of Sydney: asaphids, *Remopleurides*, *Eobronteus*, *Pliomerina*, *Sphaerocoryphe* and *Amphilichas*. From collections in the University of Tasmania, Whittington identifies: from the Gordon Limestone, an harpid, asaphids, illaenids, *Eobronteus*, *Pliomerina*, a second pliomerid resembling *Encrinurella*, *Ceraurinella* and *Amphilichas*; from the highest Ordovician strata in Tasmania, the Westfield beds, a trinucleid, an asaphid of *Brachyaspis* type, cf. *Neseuretinus* Dean, 1967*b*, and *Pliomerina*. Whittington (1966, p. 723, Fig. 16) used the name Encrinurella for a faunal province extending through south-east Asia to Australia, based on the supposed occurrence of this genus. Webby, Moors & McLean (1970) have shown that the Australian form is different from the Burmese, so that this name for the province is unsuitable.

Turkey (Dean 1967*b*).

Estonia: C_2 beds (Rõõmusoks 1970).

Kazakh: Kazakhstan, U.S.S.R. (Apollonov 1968; Nikitin, Apollonov & Tsay 1968).

Burma: Naungkaungyi beds (Reed 1915).

Mississippi: Platteville Group, Upper Mississippi Valley, U.S.A. (personal communication from L. L. De Mott to Whittington).

Scotland: Girvan district, Ayrshire, Scotland (Tripp 1962, 1965, 1967; Ross & Ingham 1970).

N. Wales (A): Derfel Limestone, North Wales (Whittington 1968*a*).

N. Wales (B): Anglesey (Bates 1968).

E. Ireland: Grangegeeth, southeastern Ireland (Brenchley, Harper, Romano & Skevington 1967; Harper & Romano 1967).

Oslo: Oslo district, Norway; Ampyx Limestone 4aβ (Henningsmoen 1960; Nikolaisen 1961, 1963; Skjeseth 1955; Størmer 1953).

Additional references (Branisa 1965; Cooper 1968; Hughes & Wright 1970; Wolfart 1968).

Ashgill Series

N. Wales: North Wales, Bala district, Rhiwlas Limestone (Whittington 1968*a*).

Poland: Middle Ashgill (Kielan 1960; Whittington 1968*a*).

Västergöt: Västergötland, Sweden, Upper Jonstorp Formation (Kielan 1960; Whittington 1968*a*).

Czech: Czechoslovakia, Králův Dvůr Formation (Havlíček & Vaněk 1966; Whittington 1968*a*).

Siljan: Boda Limestone, Siljan district, central Sweden; list compiled in Whittington 1966, p. 724.

Percé: Quebec, Canada, *Remipyge* fauna (Lespérance 1968).

Morocco: Anti-Atlas Mountains (Destombes 1967).

Kazakhstan, U.S.S.R. (Apollonov 1968).

China: Southwest China, Wufengian (Sheng 1964).

Anticosti: Anticosti Island, Quebec, Canada; English Head, Vauréal and Ellis Bay Formations (Twenhofel 1928; Lespérance 1968).

Iowa: Maquoketa Formation, Iowa, U.S.A. (Whittington 1954).

Scotland: Girvan district, Ayrshire, Upper Drummuck Group (personal communication from R. P. Tripp 1971).

Ireland: Co. Clare, Eire, Ballyvorgal Group (Weir 1959).

S. Wales: South Wales, Sholeshook Limestone; Whittington, study of collections in Institute of Geological Sciences and Sedgwick Museum, Cambridge.

Additional references used in compiling the map are: *Dalmanitina* from Quebec (Lespérance 1968); North Africa (Destombes 1967); Kazakhstan (Apollonov 1968); Europe and Burma (Temple 1952); Estonia (Männil 1966); Pamir (Balashova 1966); China (Sheng 1964); Victoria, Australia (personal communication from K. S. W. Campbell 1971). Late Ordovician glaciation (Branisa 1965; Cocks *et al.* 1970; Destombes 1968; Fairbridge 1971; Schermerhorn 1971); further references in latter two articles.

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