

DISTRIBUTION OF BRACHIOPOD ASSEMBLAGES IN RELATION TO ORDOVICIAN PALAEOGEOGRAPHY

by ALWYN WILLIAMS

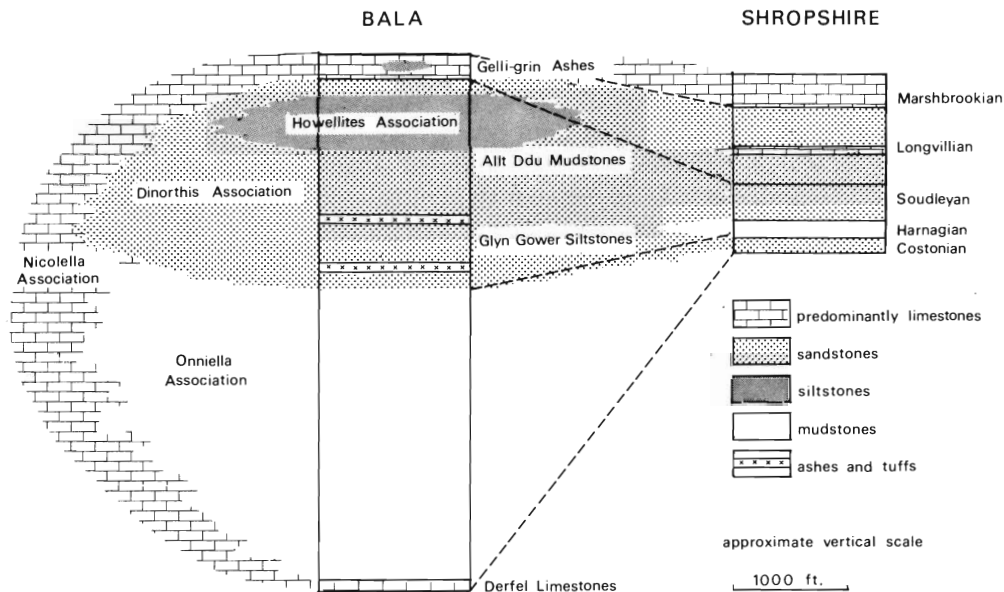
ABSTRACT. Cluster analyses of ninety assemblages of Ordovician brachiopod genera, from rocks of Arenigian, Llanvirnian, Early Caradocian, Later Caradocian, and Mid-Ashgillian age exposed throughout the world, indicate that the assemblages and smaller contemporaneous collections from several other localities belonged initially to at least five distinct provinces with a high proportion of endemic genera. This provinciality prevailed until Mid-Caradocian time, when a reduction in the number of provinces was accompanied by changes in their geographic distribution and increases in their pandemic and partially pandemic contents. Up to this time a reclusuring of the partially pandemic residues of the older provinces and unattached assemblages showed that nearly all groups could be unequivocally assigned to either an American or a European Realm. By Mid-Ashgillian time, however, despite the survival of some provinciality, the difference between the Realms no longer held, and an essentially cosmopolitan fauna began to emerge. A redistribution of continental shields with their attendant platform or miogeosynclinal facies can reasonably be achieved within the latitudinal constraints afforded by palaeomagnetism to satisfy brachiopod distributions. It suggests that, whereas the faunal boundary between the American and European Realms coincided with the northern eugeosynclinal basin of the British Isles and marked the site of a destructive continental plate margin, a constructive margin was simultaneously developed between the Kazakhstan boundary of the Siberian-Cathaysian Shields and the Texan edge of the Canadian Shield.

THE purpose of this paper is not to give an account of the distribution of brachiopod taxa in Ordovician rocks nor to conjure up past environments from their occurrences in time and space, but to determine whether the known record forms a pattern consistent with a geophysical restoration of Ordovician oceans and continents on a global scale. There are two ways of carrying out this comparison. One is to reconstruct a palaeontological model based on temporal and spatial relationships among Ordovician brachiopods and then decide whether the uncertainty and error attending estimates of palaeomagnetism and the identification of tectonic plate boundaries of the period are large enough to prompt acceptance of the model until the geophysical data are checked and refined. The other is to follow the procedure adopted for this symposium *viz.* to accept a regrouping of parts of continents with latitudinal constraints determined geophysically, and to assess the degree to which palaeontological data conform. The difference can be very important in problems where inference plays a vital role in so far as the information shaping a hypothetical model is usually less subject to continuous scrutiny than data of another kind being fitted to that model. It is therefore essential to the success of this exercise constantly to bear in mind that palaeontological evidence is at least as trustworthy as geophysical. One must not forget that not so long ago, the concept of continental drift, supported though it was by sound geological and geomorphological evidence, was a source of amusement for some eminent geophysicists and not a few geologists. In 1957 when the writer first attempted to present evidence for continuity of Ordovician faunal boundaries between Europe and North America, the most consistent criticism brooking no compromise was that fifteen million sq. miles of North Atlantic

made nonsense of the paper. Smith and Hallam (1970, p. 6), in their definitive study on the fit of the southern continents, paid tribute to Du Toit's restoration of Gondwanaland as follows: 'Many of the conclusions given here were first expressed by Du Toit; based as they were on limited data they appear to us as a triumph of imaginative synthesis.' They were right to be generous in their acclamation of Du Toit's brilliant synthesis (1937) but, as he would have been the first to agree, the geological evidence for it was incontestable by any unbiased standards of correlation.

The groundwork for the following review of the world distribution of Ordovician brachiopod assemblages (*sensu* Craig 1953, p. 547) is a study carried out by the writer (Williams 1969*a* and *b*) on brachiopod genera recovered from rocks of the western part of the Northern Hemisphere. The analysis indicated the existence of generic assemblages forming statistically related clusters that were largely independent of one another in time and space. The assemblages were composed of collections recorded from biostratigraphic units that were deliberately broadly defined to embrace a wide variety of rocks. The assumptions that could then be sustained were that such assemblages represented communities inhabiting different substrates, and that clusters of them constituted provinces in the ecological sense.

The relation between provinces and communities as understood by the writer is illustrated by the distribution of brachiopods in the Caradocian successions of Bala and Shropshire (text-fig. 1). There is evidence to suggest that three associations dominated the brachiopod communities of those times (Williams 1963, pp. 340-344). They were: a *Dinorthis* association (with *Bicuspina*, *Dalmanella*, *Heterorthis*, and *Leptaena*), a *Nicolella* association (with *Eoplectodonta*, *Leptestiina*, *Platystrophia*, *Rhactorthis*, and *Strophomena*), and an *Onniella* association (with *Sericoidea* and



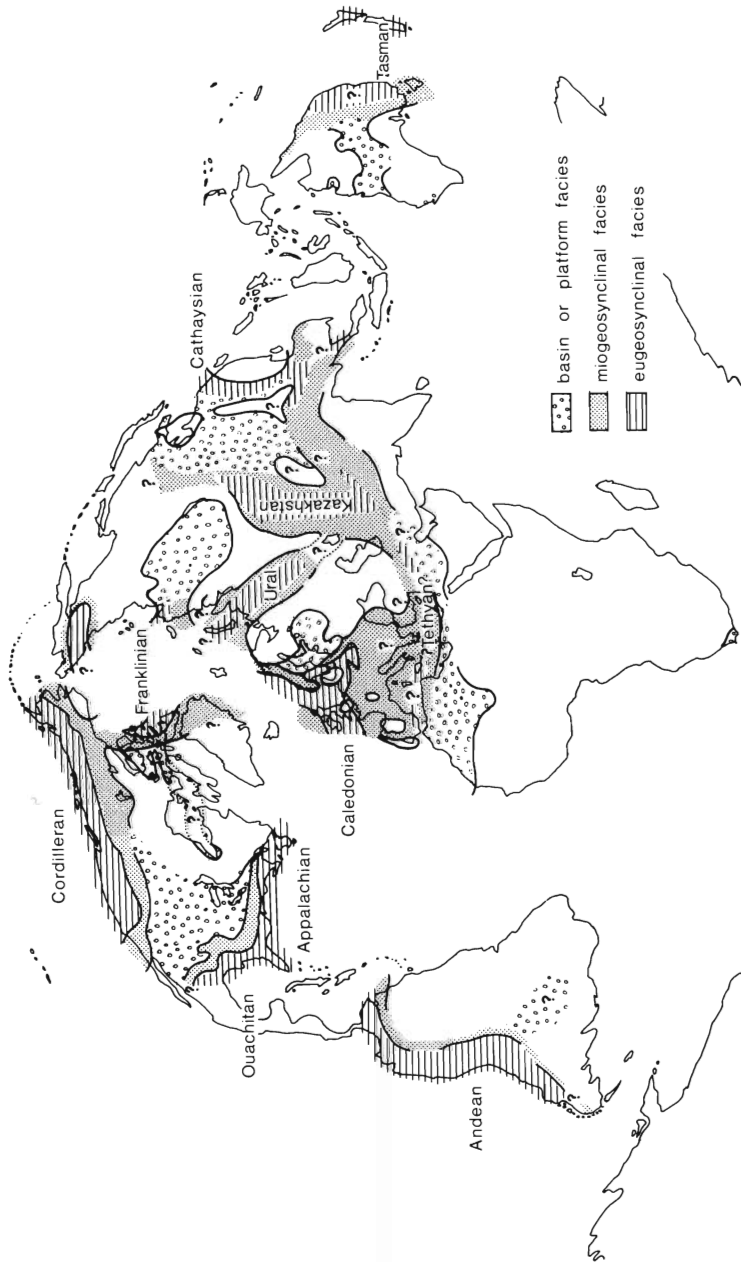
TEXT-FIG. 1. Inferred distribution of brachiopod associations in the Lower Caradocian successions of Bala and Shropshire.

Paracraniops). A silty substrate supported all three associations and especially a fourth including *Howellites* with *Sowerbyella*; but the first three were prevalent on sandy, carbonate-rich, and muddy sediments respectively. Yet so great is the variability of Caradocian lithofacies in the Anglo-Welsh area, that all genera composing these associations are included in assemblages of Longvillian age for both Bala and Shropshire. Consequently differences between the two assemblages may be attributable to factors other than the texture and composition of the substrate. Bretsky (1970) demonstrated similar relationships between communities and the nature of the substrate in the Upper Ordovician facies of the Central Appalachians.

Some colleagues seem reluctant to accept such an orthodox definition of a province as that given above (see Middlemiss and Rawson 1971, p. 201), because there is no immediately obvious connection between clusters of benthic organisms and lithofacies. They have apparently overlooked the fact that the nature of the substrate is only one of many controls (thermal, chemical, or biological) that may be stratigraphically undetectable yet decisive in determining the organic constitution of a complex of communities making up a province.

This incompleteness of the geological record prompts an open admission that the clusters identified in this paper may not represent provinces as understood by zoogeographers (e.g. Udvardy 1969). Yet they do have an individuality in time and space that would surely not have emerged in cluster analysis unless they reflected evolving ecosystems akin to provinces. Thus in 1969 three distinct clusters of brachiopod assemblages, designated the American, Baltic, and Anglo-Welsh Provinces, were demonstrated to have occupied more or less the same parts of the western Northern Hemisphere from Arenigian to Early Caradocian times. By the Mid-Caradocian epoch, however, assemblages began to show profound changes in composition and palaeogeographic distribution including an increase in pandemic genera and a diminution in the area of the American Province. These changes were the prelude to a new faunal balance struck during Mid-Ashgillian times when a 'North European fauna', consisting essentially of a greatly enlarged Baltic assemblage, became established throughout most of the western Northern Hemisphere. Reciprocally, the American Province had, by that time, been reduced to the western and middle region of the continent only; while a Bohemian cluster, based on Czechoslovakian assemblages that had always tended to have a low intercorrelation with the Anglo-Welsh Province, indicated a third provincial centre. The emergence of a North European Province was obviously precursory to the extraordinary spread of such a compact assemblage as the Hirnantian fauna (Wright 1968) which is known to extend not only throughout Europe but into the Himalayan area (Temple 1965, p. 417; Bergström 1968) and the Southern Appalachians (Amsden 1971). The ubiquity of the Hirnantian fauna, in turn, anticipates the essentially cosmopolitan nature of the Silurian brachiopod assemblages demonstrated by Berry and Boucot (1970, pp. 29-33) and now reviewed by L. R. M. Cocks and W. S. McKerrow for this symposium.

It seems, therefore, that the Ordovician period was a time of abnormal changes in the provinciality, distribution, and composition of brachiopod faunas. All three aspects are linked to one another. Changes in composition can result not only from evolution of endemic stocks but also through recruitment from other provinces which was an important factor in the enlargement of the North European Province.



TEXT-FIG. 2. A reconstruction of the principal Ordovician facies as inferred from the main present-day distribution of Ordovician rocks.

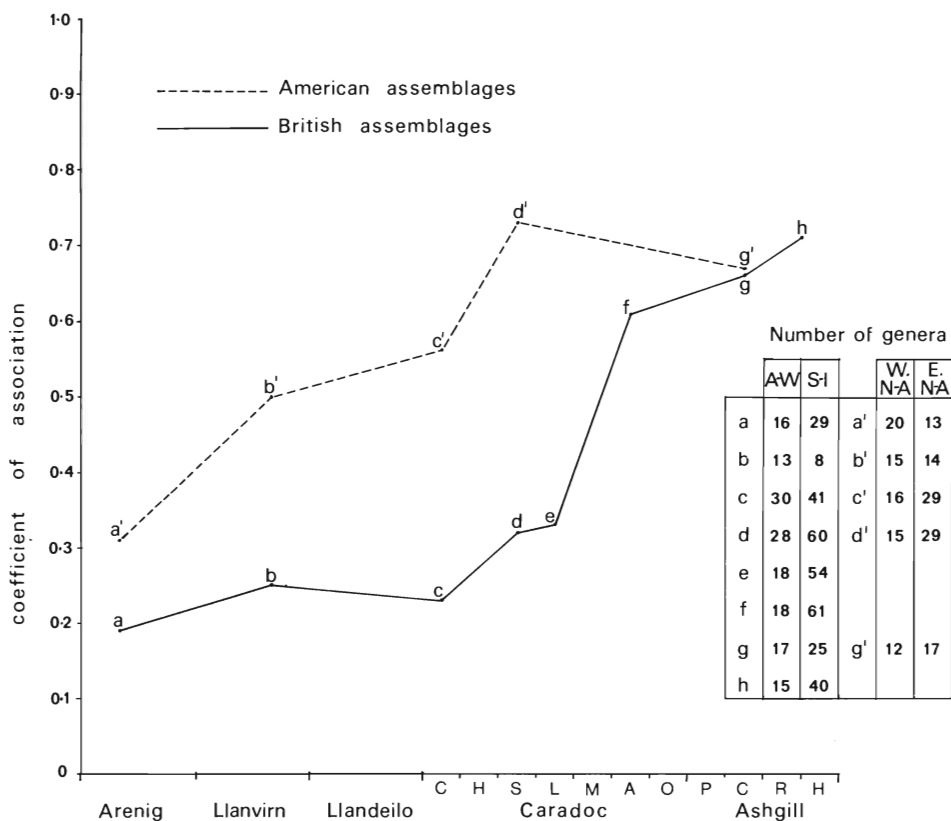
Such recruitment, whether by climatic changes modifying selection pressures (Spjeldnaes 1961), reorientation of sea currents responsible for species dispersion (Williams 1969*a*), or by marine transgression establishing new channels of communication between communities, affect at least the provincial flavour of clusters. But significant changes in any of the three agents cited above ultimately involve readjustments in the earth's crust. Hence changes in faunal composition may be a guide to tectonic disturbances. In particular, attention should be given to those areas where differences between assemblages taken from two currently adjacent areas changed dramatically during the Ordovician. Text-fig. 2 shows the inferred maximum distribution of Ordovician sediments broadly interpreted relative to the environment of deposition as eugeosynclinal, miogeosynclinal, or platform facies. According to present-day distributions, the distance between western Ireland-south-western Scotland, and west and north-western England is only about one-tenth that between Nevada-Idaho and the mid-Appalachians-Newfoundland areas. Yet the coefficients of association calculated as:

$$\frac{\Sigma \text{ genera in common to both assemblages}}{\Sigma \text{ all genera in smaller assemblage}}$$

for correlated assemblages recovered from stated horizons for each set of compared areas, are differently distributed (text-fig. 3). The plot for the British and Irish successions shows a trend away from an insignificant communality in Arenigian times to a high degree of similarity by Late Ashgillian times with the steepest rise occurring during the Caradocian. In contrast, although the oldest compared assemblages from the American continent are not much more alike than those of the British Isles, all younger faunas show a high but variable degree of similarity comparable with that displayed by collections from one horizon in an area of less than 100 sq. miles (Williams 1969*a*, p. 124). Gradients signifying faunal changes on the scale of those in British Ordovician successions are undeniable clues to gross environmental modifications. In terms of plate tectonics, the breakdown of provinciality which such a gradient represents may be interpreted as indicating the existence of destructive margins, with each approaching plate originally supporting a distinctive benthic fauna. Thus, appraisal of any relationship that may exist between the distribution of brachiopod faunas and plates with their attendant platform and miogeosynclinal facies, rests not only on exploring the individuality of provinces, but also on identifying those zones where acceleration in faunal changes took place.

The procedure adopted for the collation and analysis of data concerning brachiopod distribution is that used in 1969 with some minor refinements.

The genus remains the taxonomic unit used for calculations because it is less subjectively defined than the species. Indeed most palaeontologists concede that the great majority of genera are reliably identifiable from illustrations alone which afford checks on faunal lists, especially when collections from particular regions are not available for study. Moreover, as Ekman pointed out (1953, p. 371), not only are endemic taxa more important than pandemic taxa in the delineation of a province but that genera are more diagnostic of sustained regional differences than species.



TEXT-FIG. 3. Coefficients of association for assemblages of brachiopod genera recorded in England and Wales (A-W) and Scotland and Northern and Western Ireland (S-I) in contrast to those for American assemblages from Nevada and Idaho (W.N.A) and the Appalachians and Newfoundland (E.N.A). *a*, Mytton Flags and Tourmakeady Limestone; *b*, Ffairfach Group and Lower Mweelrea grits; *c*, Costonian beds and Lower Barr Series; *d*, Soudleyan beds and Balclatchie Group; *e*, Longvillian beds and Lower Ardwell Group; *f*, Actonian beds and Upper Ardwell Group; *g*, Lower Cautleyan mudstones and Lower Drummuck Group; *h*, Upper Rawtheyan and Hirnantian mudstones and shales and Upper Drummuck Group (s.l.). *a*¹, Lower Pogonip Group and Ninemile Formation, Nevada, and Upper Canadian dolomites and limestones of Alabama, Virginia, and Maryland; *b*¹, *Orthidiella* and *Anomalorthis* Zones, Nevada, and Table Head Formation, Newfoundland; *c*¹, Yellow Limestone Formation, Nevada, and Middle Pinesburg Formation, Pennsylvania; *d*¹, Shales with *Reuschella*, Nevada, and Oranda Formation, Virginia; *g*¹, Saturday Mountain Formation, Idaho, and Middle Richmond Group, Ohio.

The assemblages used in the cluster analyses have been drawn from five horizons corresponding to the Arenig, Llanvirn, basal Caradoc (about Costonian), Middle Caradoc (about Longvillian), and Middle Ashgill (about Late Cautleyan–Early Rawtheyan) of the standard succession. These horizons have been determined solely by the availability of adequate material to ensure intercontinental comparison. In the preparation of matrix tables of intercorrelation based on coefficients of association, any genus recorded in every assemblage used to represent a particular horizon has been omitted, and no assemblage of fewer than eight genera has been included. Care has been taken to ensure that compared assemblages were contemporaneous although it has been demonstrated that precision finer than the time-stratigraphic equivalent of a stage is not essential to the identification of the kind of basic compositional differences characterizing provinces (Williams 1969a, p. 127).

Although cluster analysis is a less elegant method of identifying the essential links in intercorrelated data than other methods of analysis, it is reliable enough for the data at hand and has been retained for this study. Since, however, up to twenty assemblages may be used in one analysis, the drop in the value of the B-coefficient signalling termination of a cluster has not been standardized as in the previous exercise (Williams 1969a, p. 128). Instead, the critical value of the reduction has been inversely related to the number of assemblages within a cluster as advocated by Holzinger and Harman (1941, pp. 28–34). The difference in approach turned out not to be important except in the identification of Late Ordovician clusters when distinctions between earlier defined provinces were becoming blurred. Graphically the results have again been presented by plotting an average profile for each cluster based on the mean coefficient of association between each assemblage in an analysis and all assemblages in a cluster (Williams 1969a, p. 128).

The analysis of faunas on a world-wide scale permits a further refinement in procedure leading to estimates of the degree of communality existing between provincial clusters. By excluding all endemic or ubiquitous genera, each cluster is reduced to partially pandemic residues. These are then subjected to a second-order cluster analysis in the same way as regional assemblages. As will be shown below, such residual clusters, which are essentially pandemic indices of provinces, fall into a few large groups herein called realms (*sensu* Schmidt 1954, p. 326). Assemblages, which for reasons of size or, more rarely, imprecise correlation do not figure in the matrix tables, may then be reviewed to determine whether they decisively belong to one realm or another. In this way 348 genera recorded from 117 different regions and horizons have contributed to the delineation of the realms and provinces described below.

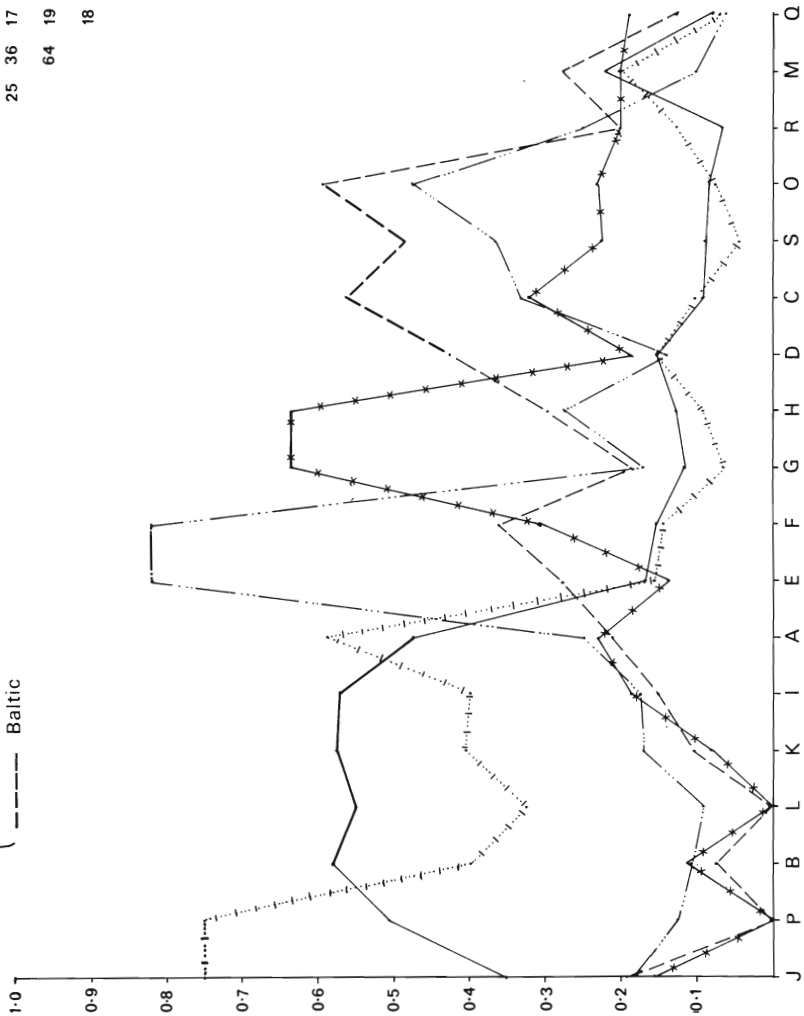
ARENIGIAN FAUNAS

Eighteen assemblages varying in size from 8 to 43 genera and involving 125 genera have been used in a cluster analysis of Arenigian faunas (text-fig. 4). The analysis resulted in the identification of five clusters and three assemblages which remained unattached.

A well-defined cluster, which may be described as the Scoto-Appalachian Province, included faunas from SW. Ireland, Quebec, the Appalachians, Oklahoma, and Texas. The province is characterized by such endemic forms as *Calliglypha*, *Clarkella*, *Diaphelasma*, *Finkelburgia*, *Oligorthis*, *Polytoechia*, *Pomatotrema*, *Syntrophinella*,

	A	B	C	D	E	F	G	H	I	J	K	L	M	O	P	Q	R	S
41	18	37	27	22	18	27	48	55	61	36	30	10	62	12	10	18	A	
12	12	09	12	13	09	65	29	61	64	40	06	50	13	00	00	B		
50	27	39	19	45	09	20	08	00	40	64	00	25	30	54	C			
09	19	19	18	19	31	08	00	30	50	00	13	10	27	D				
82	09	18	18	18	18	18	09	00	46	13	00	20	27	E				
25	36	17	17	15	09	20	50	13	30	45	F							
64	19	13	08	00	20	19	00	13	20	18	G							
18	18	09	00	20	27	00	25	20	27	H								
30	61	54	40	14	50	13	13	18	I									
31	27	40	15	75	13	25	09	J										
45	00	15	50	00	10	09	K											
00	00	37	00	00	00	L												
30	00	13	30	10	M													
00	13	30	64	O														
00	00	00	P															
13	00	Q																
10	R																	
10	S																	

Realms {
 American {
 Provinces {
 N.W. American
 Scoto-Appalachian
 European {
 Celtic
 Anglo-French
 Baltic



Tetralobula, *Xenelasma*, and *Xenorthis*. A second cluster, consisting solely of faunas from Nevada and British Columbia, the North-western American Province, has no endemic forms and although it is numerically distinguishable from the Scoto-Appalachian Province, the trends of average correlations seen in text-fig. 4 show the close links between the two provinces.

A third cluster embracing faunas from S. Norway, S. Sweden, the Estonia-Leningrad area, the Holy Cross Mountains, all comprising the Baltic Province, had a relatively high proportion of endemic genera with *Apomatella*, *Clitambonites*, *Eostrophomena*, *Inversella*, *Iru*, *Ladogiella*, *Lycophoria*, *Oslogonites*, *Paurorthis*, *Productorthis*, *Progonambonites*, and *Rauna*, occurring in two or more localities.

A fourth cluster defining a Celtic Province included the Arenigian faunas of Anglesey and SE. Ireland. Only *Rhynchorthis* was endemic and the coincidence of the cluster with a secondary peak of intercorrelation for the Baltic cluster (text-fig. 4) indicates the close connection between the two provinces.

The fifth cluster of faunas from Shropshire and the Montagne Noire, the Anglo-French Province, contains *Dalmanella* and *Monobolina* as endemic stocks. In addition, small assemblages from Bohemia, S. China, and Turkey showed no significant correlation with one another or with any cluster.

In a second-order cluster analysis of the partially pandemic contents of these clusters and independent assemblages (only *Lingulella* proved to be cosmopolitan), the first two clusters combined and may be appropriately described as the American Realm. It was characterized in particular by the widespread occurrence of *Diparlasma*, *Hesperonomia*, *Leptella*, *Nanorthis*, *Schizambon*, *Syntrophia*, *Syntrophopsis*, *Taffia*, and *Trematorthis*. In relation to these and other endemic constituents of the American Realm, the Arenigian faunas of NW. Scotland (Williams 1969a), Utah (Ross 1951, 1968), NE. U.S.S.R. (Balashov *et al.* 1968), Spitzbergen (Hallam 1958), Novaya Zembla (Andreeva 1967, Bondarev *et al.* 1965), Kazakhstan (Nikitin and Apollonov 1968), S. Korea (Kobayashi 1934), and Tasmania (Brown 1948, Banks 1962) belong to this group.

The second-order cluster analysis also identified another equally distinctive

TEXT-FIG. 4. Coefficients of association between eighteen Arenigian brachiopod assemblages, and graphs showing the degree of association between faunas included in each defined province (indicated by a thickening of the correlation line) and all other faunas. a, Tourmakeady Limestones, Co. Mayo (Williams MS.); b, El Paso Formation and Ellenberger Group, W. Texas (Cloud 1948); c, *Expansus* Beds, Norway (Öpik 1939, Bergström, pers. comm.); d, Holy Cross Mountains and Peribaltic Depression, Poland (Bednarczyk 1964, Biernat and Williams 1970); e, Arenig rocks of Tagoat, Co. Wexford (Brenchley *et al.* 1967); f, Arenig grits, Anglesey (Bates 1968); g, Mytton Flags, Shropshire (Williams MS.); h, Arenig sandstones and mudstones, Montagne Noire (Williams MS.); i, Lévis Shale and Upper Beekmantown Group, Quebec, and NW. Vermont (Ulrich and Cooper 1938); j, Lower Pogonip Group and Ninemile Formation, Nevada (Ulrich and Cooper 1938, Ross 1964); k, Upper Canadian dolomites and limestones of Alabama, Virginia, Maryland, and Pennsylvania (Ulrich and Cooper 1938); l, Kindblade, Cool Creek and West Spring Creek Formations, Oklahoma (Ulrich and Cooper 1938, Cooper 1952); m, Klabava Formation, Czechoslovakia (Havlíček and Vaněk 1966); o, Onitakan sandstones and limestones (B1 to B111 α), E. Baltic (Rubel 1961, Goryansky 1969); p, Lower Skoki Formation, British Columbia (Aitken and Norford 1967, Norford 1969); q, Ur. Panho and Lr. Chaochiapa Formations, W. Tapashan (Wang 1955, 1956; Lu 1959); r, Seydisheir Shale and Sobova Formation, Turkey (Dean and Monod 1970); s, *Expansus-raniceps* Beds, Öland (Bergström, pers. comm.).

complex, the European Realm, composed of the Baltic, Celtic, and Anglo-French Provinces, and at this stage in analysis assimilated the Bohemian assemblage. The realm was characterized by *Ahtiella*, *Antigonambonites*, *Estlandia*, *Glossorthis*, *Orthis*, *Panderina*, and *Ranorthis* occurring in two or more provinces; and having regard for the endemic properties of the realm, the Arenigian brachiopods of Mid Sweden (Tjernvik 1956), Bavaria (Sdzuy 1971), Morocco (Havlíček 1971, and the C. Sahara (Legrand 1971), can be considered European.

A number of genera are recorded from both realms and presumably represent evidence of pre-Arenigian communication. They include: *Acrotreta*, *Archaeorthis*, *Camarella*, *Conotreta*, *Lingulella*, *Hesperonomiella*, *Ingria*, *Nothorthis*, *Obolus*, *Orthambonites*, *Orthidiella*, *Paterula*, *Porambonites*, *Scaphelasma*, *Siphonotreta*, *Torynelasma*, *Tritoechia*, and *Westonia*. None the less, the general impression of Arenigian brachiopod distribution is of a strong provinciality subordinate to at least two realms on a supracontinental scale. The exclusion of the Turkish and Chinese assemblages from these realms may be significant in that they are from areas within a large part of the earth's crust, comprising south and east Asia and parts of Australia, where the faunas are not as well known as they are in N. America, Europe, and the U.S.S.R. Consequently a third realm may have existed in that region although the composition of younger faunas found there do not support this prospect.

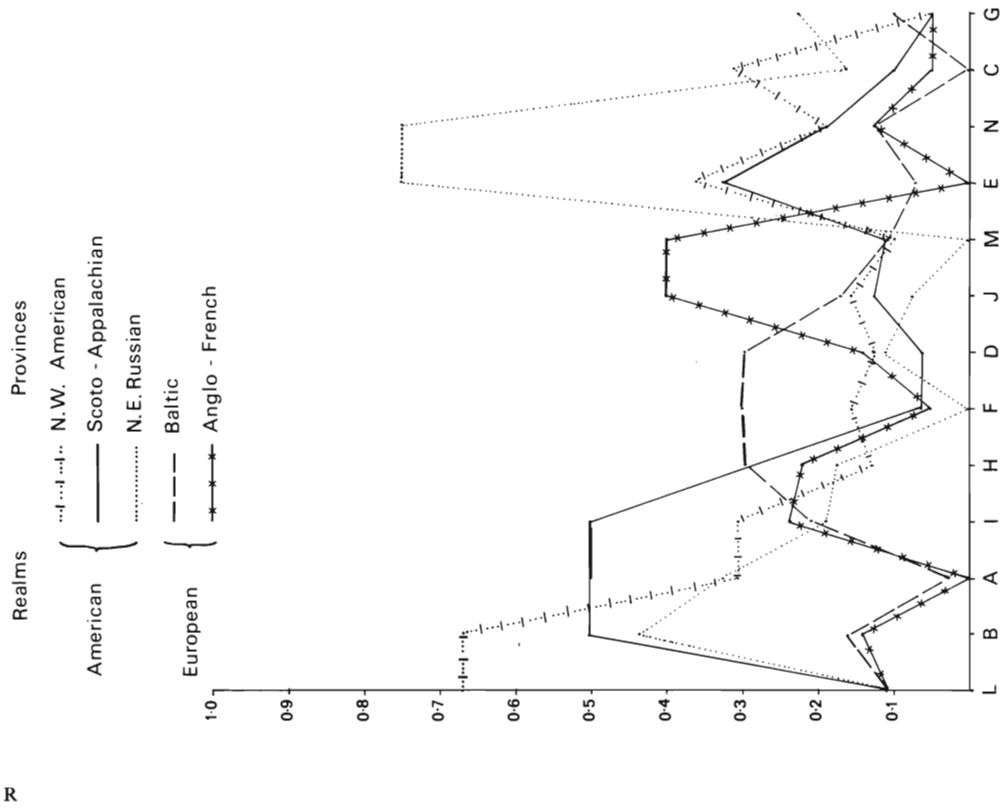
LLANVIRNIAN FAUNAS

The Llanvirnian faunas available for study are more restricted in content and distribution than the Arenigian brachiopods, because only thirteen regional assemblages varying in size from eight to seventeen constituents and involving ninety genera were available for cluster analysis. The analysis, however, confirmed the provinciality evident in Arenigian faunas because five clusters and two independent assemblages are identifiable (text-fig. 5).

One cluster characterized by an endemic *Anomalorthis* includes the Llanvirn faunas of Nevada and the Rocky Mountains, i.e. the North-western American Province; another with *Pleurorthis* as the endemic stock links W. Newfoundland and SW. Ireland and is clearly a manifestation of the Scoto-Appalachian Province. A third cluster involving assemblages from Estonia, Anglesey, and Maine, and including *Ahtiella*, *Apomatella*, *Platystrophia*, *Productorthis*, and *Ranorthis* as endemic in at least two stations is an interesting extension of the Baltic Province

TEXT-FIG. 5. Coefficients of association between thirteen Llanvirnian brachiopod assemblages, and graphs showing the degree of association between faunas included in each defined province (indicated by a thickening of the correlation line) and all other faunas. A, Table Head Formation, Newfoundland (Cooper 1956); B, *Orthidiella* and *Anomalorthis* Zones, Nevada (Ross and Ingham 1970); C, Kopaly and Karakan Horizons, Kazakhstan, U.S.S.R. (Nikitin and Apollonov 1968); D, Lower Purtsean beds (B111β-C1a), E. Baltic (Rubel 1961, Goryansky 1969); E, Elgenchak Stage, NE. U.S.S.R. (Balashov *et al.* 1968); F, Llanvirn grits and siltstones, Anglesey (Bates 1968); G, *Yangtzeella* Formation, Hupeh (Wang 1955, 1956, Lu 1959); H, Shinbrook Formation, New Brunswick and Maine (Neuman 1971); I, Lr. Mweelrea grits, Co. Mayo (Williams 1972); J, Ffairfach Group, S. Wales (Williams 1953); L, Ur. Skoki Formation, British Columbia (Aitken and Norford 1967, Norford 1969); M, Llanvirn shales and volcanics, Shropshire (Williams MS.); N, Labistakhs kaya Stage, Sette-daban, NE. U.S.S.R. (Rozman *et al.* 1970).

Realms	Provinces	A	B	E	D	E	F	G	H	I	J	L	M	N
American	N.W. American	50	20	00	40	00	10	07	50	00	11	00	25	A
	Scoto - Appalachian	40	13	50	20	10	14	50	20	67	08	37		B
European	N.E. Russian	00	20	00	00	00	00	00	00	10	22	00	13	C
	Baltic	10	30	20	29	13	20	11	08	13				D
	Anglo - French	00	20	10	25	00	22	00	75	E				
		00	30	13	10	11	00	00	F					
		10	00	10	00	00	25	G						
		37	20	11	25	25	H							
		25	11	22	13	I								
		11	40	25	J									
		11	00	L										
		00	M											
			N											



already hinted at in the high correlation between the Baltic and Celtic faunas of Arenig age. A fourth cluster consisting of assemblages from W. England and SW. Wales with endemic *Macrocoelia* and *Sowerbyella* is undoubtedly part of the Anglo-French Province. Sufficient data have been obtained also to identify a fifth cluster in the NE. U.S.S.R. with *Xenelasmella* as the sole endemic genus. Assemblages from Hupeh and Kazakhstan did not cluster with any other group.

A second-order analysis of the clusters and independent assemblages identified above again resulted in the emergence of the American and European Realms. The former included the Scoto-Appalachian, Western-North American, and NE. U.S.S.R. Provinces as well as the Kazakhstan and, on balance, the Hupeh assemblages, and was characterized by the widespread appearance of *Apothophyla*, *Camarella*, *Desmorthis*, *Hesperonomia*, *Idiostrophia*, *Leptella* (or *Petroria*), *Orthidiella*, *Orthidium*, *Rhysostrophia*, and *Valcourea*. The Llanvirn fauna of Oklahoma (Cooper 1956, Ross and Ingham 1970) belongs to this Realm.

The European Realm with *Dalmanella*, *Glyptorthis*, and *Paurorthis* as well-distributed endemic stocks, embraced the Baltic, Celtic, and Anglo-French Provinces. Llanvirn brachiopod assemblages found in Spain (Tamain 1971) and, on balance, those of Bohemia (Havlíček and Vaněk 1966) and Poland (Bednarczyk 1966) belong to the European Realm.

Pandemic genera common to both realms include *Eremotoechia*, *Hesperonomiella*, *Hesperorthis*, *Lingulella*, *Onychoplecia*, *Orthambonites*, *Plectorthis*, *Polytoechia*, and *Porambonites*; but as in Arenig times, these are well outweighed by endemically occurring taxa.

EARLY CARADOCIAN FAUNAS

The definition of the base of the Caradocian Series in relation to the standard graptolitic succession is currently being reviewed on evidence from two sources. Mr. R. Addison of the Queen's University, Belfast, has demonstrated that, although the shelly faunas of the Llandeilo Series in SW. Wales are older than those of Costonian age occurring in the base of the Caradocian Series in the type area, *Nemagr. gracilis* occurs in rocks in SW. Wales which are correlatives of the Middle Llandeilo at Llandeilo. Bergström (1971, p. 109) has demonstrated a similar correlation on conodont faunas. These important finds prompt a reappraisal of the correlation of the Llandeilo-Caradoc boundary in different regions now that it no longer coincides with the first appearance of *Nemagr. gracilis*. Such a review, however, will not affect the relative estimates of intercorrelation on which the following analysis of the distribution of Early Caradocian faunas has been based. Apart from the negligible adverse effects of imprecise correlation already referred to (Williams 1969a, p. 126), all assemblages used here are either direct correlatives of the shelly Costonian assemblages or associated with well-developed *gracilis* faunas. Furthermore, whether the assemblages compared are Late Llandeilian or Early Caradocian in the sense of the revised correlation, is immaterial because in all areas, where there is continuity in shelly faunas from one series to another, the provincial nature of the fauna is essentially maintained.

In all, twenty regions yielded 161 taxa, in assemblages varying from eleven to

sixty-three genera in size, for cluster analysis. The resultant pattern (text-fig. 6) clarifies the picture of extreme provincialism of Arenigian and Llanvirnian brachiopods in that the assemblages now congregate into four well-defined clusters.

The principal grouping which can immediately be identified as the American Realm consists of ten regions: Nevada, Oklahoma, Alabama, Tennessee, Virginia, Pennsylvania, SW. Scotland, Kazakhstan, the Siberian Platform, and NE. U.S.S.R. Sixty-two genera are endemic to this Realm with the following occurring in four or more regions: *Bimuria*, *Dactylogonia*, *Laticrura*, *Mimella*, *Plectorthis*, *Protozyga*, and *Valcourea*.

A second cluster involving a number of assemblages is obviously a continuation of the earlier formed Baltic (and Celtic) Province, because it includes six regions in SE. Ireland, N. Wales, and Estonia. Twenty-three members of the provincial fauna are endemic including *Actinomena*, *Clitambonites*, *Leptestia*, *Leptestina*, *Nicolella*, *Pseudocrania*, *Sericoidea*, and *Vellamo* recorded in three or more areas.

The third cluster, composed of assemblages from W. England and SW. Wales (with six endemic genera), is part of the Anglo-French Province. But the fourth cluster to emerge as a distinct province is new because Bohemia, which previously shared low faunal correlations with other European stations, is found to be closely linked with Morocco, although only one of the six endemic genera of the fauna, *Aegiromena*, is found in both areas.

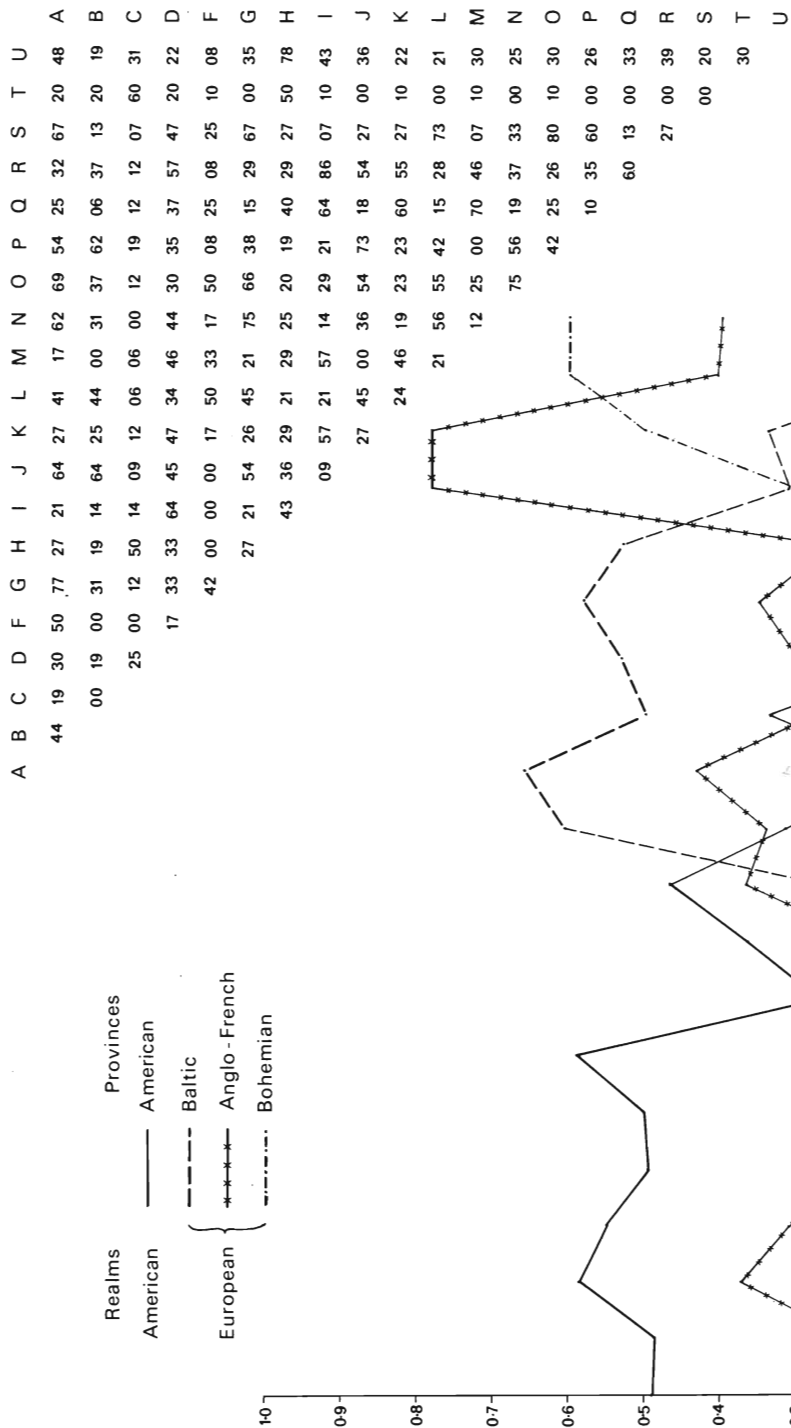
A second-order cluster analysis of the partially pandemic genera of these clusters simply confirms the first cluster as the American Realm and the remaining three as the European Realm. Within the latter *Bicuspina*, *Dalmanella*, *Dolerorthis*, *Drabovia*, *Heterorthis*, *Orderleyella*, *Howellites*, *Onniella*, *Orbiculoidea*, *Platystrophia*, and *Salopia* occur in two or more provinces.

In relation to this regrouping, the W. Urals (Ivanov 1955), E. U.S.S.R. the Altai Mountains (Petrunina and Severgina 1962), NE. U.S.S.R. at Sette Daban (Rozman *et al.* 1970), E. U.S.S.R. at Turukhan (Petra-kov 1963), W. Thailand (Hamada 1964), New South Wales (Packham 1967, Semeniuk 1970, Webby and Semeniuk 1971), and Tasmania (Banks 1962) belong to the American Realm; and Sweden (Jaanusson 1962, 1964), Spain (Tamain 1971), and, on balance, Norway (Spjeldnaes 1957*a, b*) in the European Realm.

As is to be expected the pandemic elements had greatly increased by Early Caradocian times and the following genera have been recorded from both realms. *Anisopleurella*, *Atelelasma*, *Bilobia*, *Camarella*, *Christiania*, *Conotreta*, *Cyclospira*, *Cyrtonotella*, *Dinorthis*, *Ectenoglossa*, *Glossella*, *Glyptorthis*, *Hesperorthis*, *Isophragma*, *Kullervo*, *Leptaena*, *Lingulella*, *Macrocoelia*, *Metacamarella*, *Multispinula*, *Obolus*, *Opikina*, *Orthambonites*, *Palaeostrophomena*, *Paterula*, *Paurorthis*, *Petrocrania*, *Philhedra*, *Porambonites*, *Productorthis*, *Pseudolingula*, *Ptychoglyptus*, *Ptychopleurella*, *Rafinesquina*, *Rostricellula*, *Schizotreta*, *Siphonotreta*, *Skenidioides*, *Sowerbyella*, *Strophomena*, *Trematis*, and *Triplexia*.

LATER CARADOCIAN FAUNAS

Analysis of Mid-Caradocian assemblages reveals that by Longvillian time discernible changes were beginning to affect distributions that had persisted throughout the earlier part of the Ordovician. The analysis involved 139 taxa recorded from nineteen regions in assemblages varying in size from nine to forty-seven genera. The



assemblages congregated into four clusters (text-fig. 7). The largest, best regarded as an extension of the Baltic Province, was based on collections from N. Wales, W. England, Sweden, Estonia, the Carnic Alps, Portugal, the Chorhoti Pass, and the Shan States. Twenty-five genera were endemic to this Province but only *Porambonites* occurred in three or more regions. A second Bohemian Province, seemingly surviving within the first because it is based on assemblages from Bohemia and Morocco had a relatively high endemic content of ten genera, three of which, *Drabovia*, *Drabovinella*, and *Gelidorthis*, are common to both regions. The third cluster brought together faunas from Alabama, Tennessee, Virginia, Iowa, Minnesota, New York State, and Ontario, and confirmed the persistence of the American Province with fourteen endemic genera including *Didymelasma* and *Zygospira* common to two or more regions. However, the boundaries of the American Province were already undergoing contraction because a fourth cluster appeared. It included assemblages from Maine, N. Ireland, SW. Scotland, and NE. U.S.S.R. with *Bimuria*, *Catazyga*, *Christiania*, and *Cyclospira* of the twenty-three recorded endemic genera occurring in two or more regions. The cluster is interesting because it embraces geographically disjunct areas that have two features in common. First, all except Maine had previously been peripheral but integral parts of the American Province. Secondly, as consideration of the endemic forms listed above as well as some others like *Campylorthis*, *Craspedelia*, *Eremotrema*, *Laticrura*, *Leangella*, *Liostrongia*, *Mimella*, *Metacamarella*, *Parastrophinella*, *Sampo*, *Sowerbyites*, and *Titanambonites* shows, the individuality of the faunas is compounded of relict American and Baltic-European stocks.

In view of the emergence of this transitory 'Circum-American Province', it is not surprising to find that a second-order cluster analysis of these four provinces leads to the identification of the American Realm composed of the American Province and the peripheral stations of Maine, N. Ireland, SW. Scotland, and NE. U.S.S.R., and of the European Realm based on the Baltic and Bohemian Provinces. Recourse to the endemic contents of these realms indicates that the assemblages from New South Wales (Semeniuk 1970) is American, whereas those from France (W. I. Mitchell, pers. comm.), Turkey (Dean 1967), and the Central Himalayas (Reed 1912) are

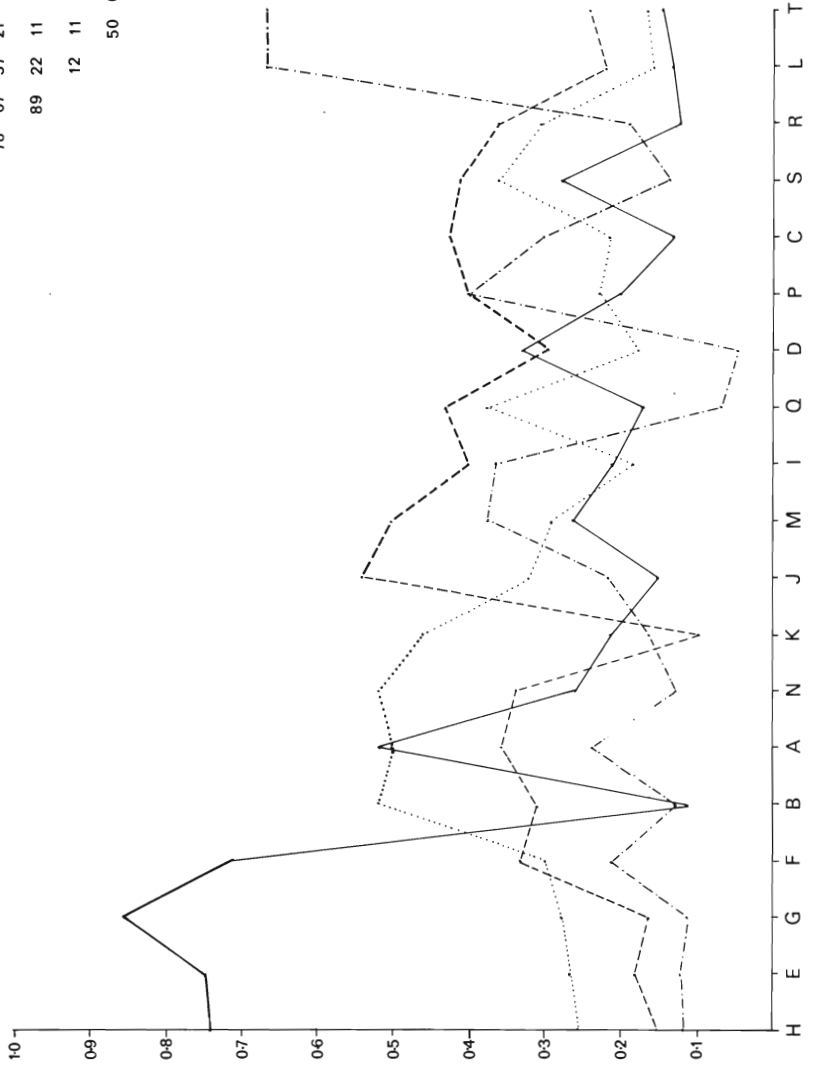
TEXT-FIG. 6. Coefficients of association between twenty Early Caradocian brachiopod assemblages, and graphs showing the degree of association between faunas included in each defined province (indicated by a thickening of the correlation line) and all other faunas. A, Pratt Ferry and Little Oak Formations, Alabama (Cooper 1956); B, Mangaseya Stage, Siberian Platform (Nikiforova and Andreeva 1961); C, Cernin shales, Czechoslovakia (Havlíček and Vaněk 1966); D, Grangegeeth Tuffs, Co. Meath (Harper and Rast 1964, W. I. Mitchell, pers. comm.); F, Ur. Tselinograd and Erkebidai Horizons, Kazakhstan, E. U.S.S.R. (Nikitin and Apollonov 1968); G, Arline Formation, Tennessee (Cooper 1956); H, Spywood grit, Shropshire (Williams MS.); I, Courtown Formation, Co. Wexford (Mitchell *et al.* 1972); J, Darpeer Stage, NE. U.S.S.R. (Chugaeva *et al.* 1964); K, Kukruse limestones and shales (C11), E. Baltic (Rõõmusoks 1970); L, Me. Pinesburg Formation, Pennsylvania (Cooper 1956); M, Lr. Caradocian conglomerates, grits, and shales, Anglesey (Bates 1968); N, Yellow Limestone Formation, Nevada (Cooper 1956); O, Stinchar Limestone, SW. Scotland (Williams 1962); P, Mountain Lake Formation, Oklahoma (Cooper 1956); Q, Derfel Limestone, N. Wales (Whittington and Williams 1955); R, Tramore Limestone, Co. Wexford (H. Carlisle, pers. comm.); S, Ward Cove Formation, Virginia (Cooper 1956); T, Lr. Ktaoua Group, Morocco (Havlíček 1971); U, basal Caradoc siltstones, Narberth, SW Wales (R. Addison, pers. comm.).

Realms		Provinces																			
		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
American	—	50	27	22	50	45	55	55	25	38	50	27	42	50	30	50	39	45	20	A	
	27	22	16	17	00	11	17	39	44	11	23	61	30	37	33	45	13	B		
European	---	27	07	27	11	07	47	00	27	40	33	50	40	53	36	33	C				
	----	26	32	44	28	29	32	06	09	36	18	30	31	23	27	00	D				
	-.-.-.-	68	89	67	12	16	19	10	26	21	20	12	16	27	13	E					
		78	67	37	21	31	15	35	26	40	31	22	54	27	F						
		89	22	11	22	11	22	33	11	11	00	11	11	G							
		12	11	12	17	22	22	10	12	11	18	07	H								
		50	06	33	50	25	50	31	25	36	40	I									
		12	23	61	38	70	75	43	54	20	J										
		12	19	44	10	06	06	18	20	K											
		35	11	40	06	17	09	67	L												
		31	60	56	35	64	40	M													
		20	56	43	36	13	N														
		20	20	20	40	P															
		44	45	07	Q																
		45	20	R																	
		18	S																		
		T																			

Realms

American { — American
 Circum - American

European { --- Baltic
 -.-.-.- Bohemian



European. A small fauna known from the Argentine (Rusconi 1956) as well as a collection including *Dalmanella*, *Glyptorthis*, *Onniella*, *Platystrophia*, and *Sowerbyella* from the Quebra da Cordero, Venezuela, could not be unequivocally assigned to either Realm.

The proportion of pandemic genera shared by both realms is greater than that of Early Caradocian time, and include *Anisopleurella*, *Anoptambonites*, *Bellimurina*, *Bilobia*, *Cremnorthis*, *Cyphomena*, *Cyrtonotella*, *Dalmanella*, *Dinorthis*, *Dolerorthis*, *Eoplectodonta*, *Glyptorthis*, *Hesperorthis*, *Howellites*, *Leptaena*, *Leptellina*, *Leptestia*, *Lingulella*, *Macrocoelia*, *Nicolella*, *Onniella*, *Opikina*, *Orbiculoidea*, *Orthambonites*, *Petrocrania*, *Philhedra*, *Plaesiomys*, *Platystrophia*, *Plectorthis*, *Ptychoglyptus*, *Rafinesquina*, *Reuschella*, *Rostricellula*, *Schizocrania*, *Schizotreta*, *Sericoidea*, *Skenidioides*, *Sowerbyella*, *Strophomena*, *Trematis*, *Triplesia*, and *Vellamo*.

MID-ASHGILLIAN FAUNAS

One hundred and forty-six genera have been recorded from successions in twenty regions corresponding, more or less, to the shelly zones straddling the Cautleyan–Rawtheyan boundary (Ingham and Wright 1970, p. 236). Analysis of these assemblages results in the identification of three clusters and one independent assemblage (text-fig. 8).

The largest cluster consists of twelve assemblages from Mid-Ashgillian exposures in Alaska, Baffin Island, Quebec, Maine, Ireland, Scotland, Wales, England, Estonia, and Kazakhstan and shows the true extent of the N. European Province of Williams (1969a, p. 135). The Province contained eighty endemic genera, of which *Anisopleurella*, *Bancroftina*, *Christiania*, *Diambonia*, *Dicoelosia*, *Dolerorthis*, *Kullervo*, *Leangella*, *Nicolella*, *Orthambonites*, *Plectatrypa*, *Ptychoglyptus*, *Sampo*, and *Schizoporella* have been recorded in four or more districts.

The other clusters are much more compact. The second and third groups indicate geographical disjunction in a reduced American Province. One cluster, the Mid-American Province, consists of assemblages from Texas, Missouri, and Idaho with *Diceromyonia* and *Onniella* as the only widespread constituents of the four endemic genera known. The third cluster identifies a N. American Province because it includes assemblages from the Great Slave Lake area, Devon Island, Anticosti, Ohio, and Kentucky. *Craniops* and *Mendacella* are the only endemic genera recorded. Finally,

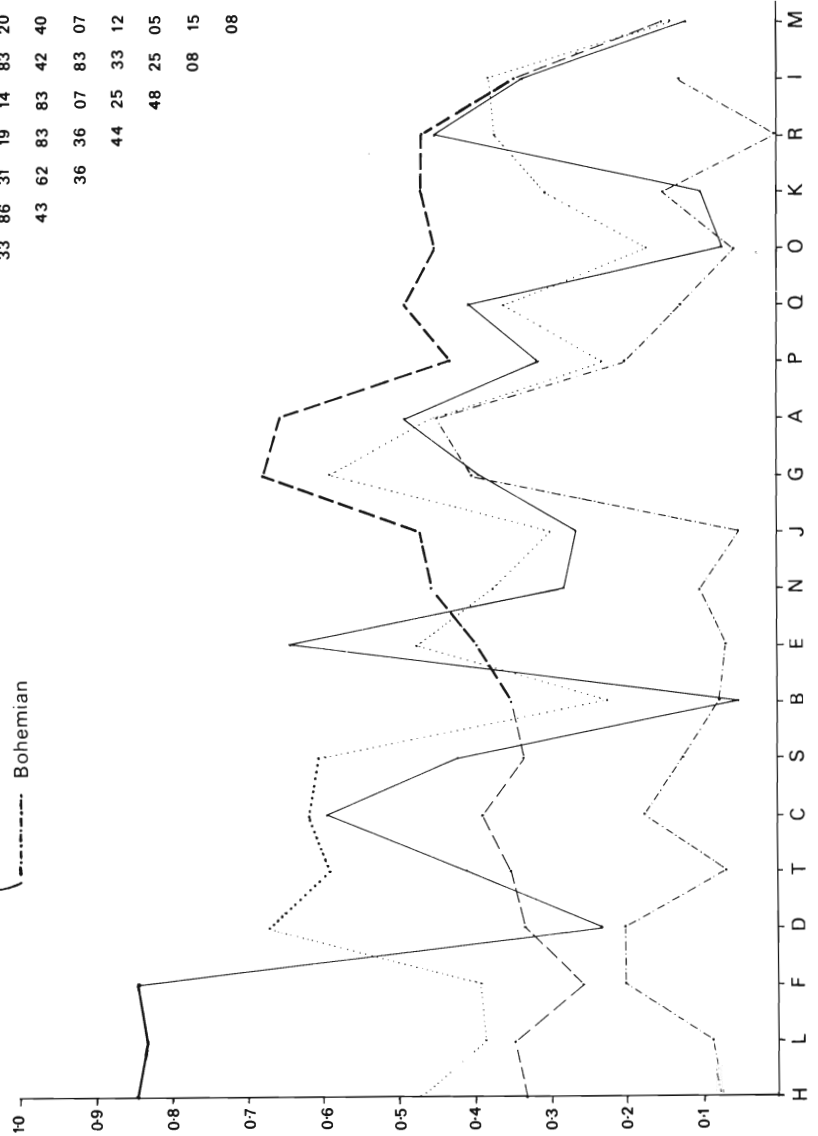
TEXT-FIG. 7. Coefficients of association between nineteen later Caradocian brachiopod assemblages, and graphs showing the degree of association between faunas included in each defined province (indicated by a thickening of the correlation line) and all other faunas. A, Bardahessiagh beds, N. Ireland (W. I. Mitchell, pers. comm.); B, Ashland Formation, Maine (Neuman 1968); C, Uqua Formation, Carnic Alps (Vai 1971); D, Keila Limestones (D11), E. Baltic (Rõõmusoks 1970); E, Lebanon Formation, Alabama–Tennessee (Cooper 1956); F, Rockland Formation, NW. New York, S. Ontario, and the Ottawa Valley (Cooper 1956); G, Witten Formation, Virginia (Cooper 1956); H, McGregor Formation, Minnesota (Cooper 1956); I, Longvillian Stage, Shropshire (Dean 1958); J, Gell-grin Calcareous Series, N. Wales (Williams 1963); K, Nal'chanskaya State, NE. U.S.S.R. (Rozman *et al.* 1970); L, Chlustina beds, Czechoslovakia (Havlíček and Vaněk 1966); M, Whittery beds, W. Shropshire (Williams MS.); N, Tormitchell conglomerate, SW Scotland (Williams 1962); P, Ur. Caradocian mudstones with ash pellets, Portugal (W. I. Mitchell, pers. comm.); Q, Kullberg Limestone, Sweden (A. D. Wright MS.); R, Naungkangyi beds, Shan States (Reed 1906, 1915, 1936); S, Caradocian beds, Chorhoti Pass, Central Himalayas (Reed 1912); T, Ur. Ktaoua Group, Morocco (Havlíček 1971).

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
54	47	50	73	38	58	50	56	61	65	58	45	62	72	84	72	84	72	61	44	40
23	20	00	08	46	08	31	38	31	00	08	61	23	31	38	31	31	38	31	15	B
60	60	47	65	64	44	35	29	67	18	35	12	29	47	41	65	60	C			
30	20	60	30	30	20	40	20	20	40	20	40	20	30	30	30	70	D			
53	67	64	33	27	75	07	40	53	47	53	47	E								
33	86	31	19	14	83	20	24	05	24	29	29	43	47	F						
43	62	83	83	42	40	67	83	76	64	58	52	60	G							
36	36	07	83	07	21	07	29	43	57	50	43	H								
44	25	33	12	50	19	19	56	37	37	40	I									
48	25	05	35	50	35	39	56	30	33	J										
08	15	39	67	39	48	43	26	27	K											
08	25	08	42	50	50	33	L													
10	05	20	12	00	12	07	M													
33	25	42	46	33	40	N														
39	50	33	17	20	O															
32	52	20	13	P																
44	28	40	Q																	
30	47	R																		
47	S																			

Realms

Provinces

- Mid American
- N. American
- - - N. European
- . - . Bohemian



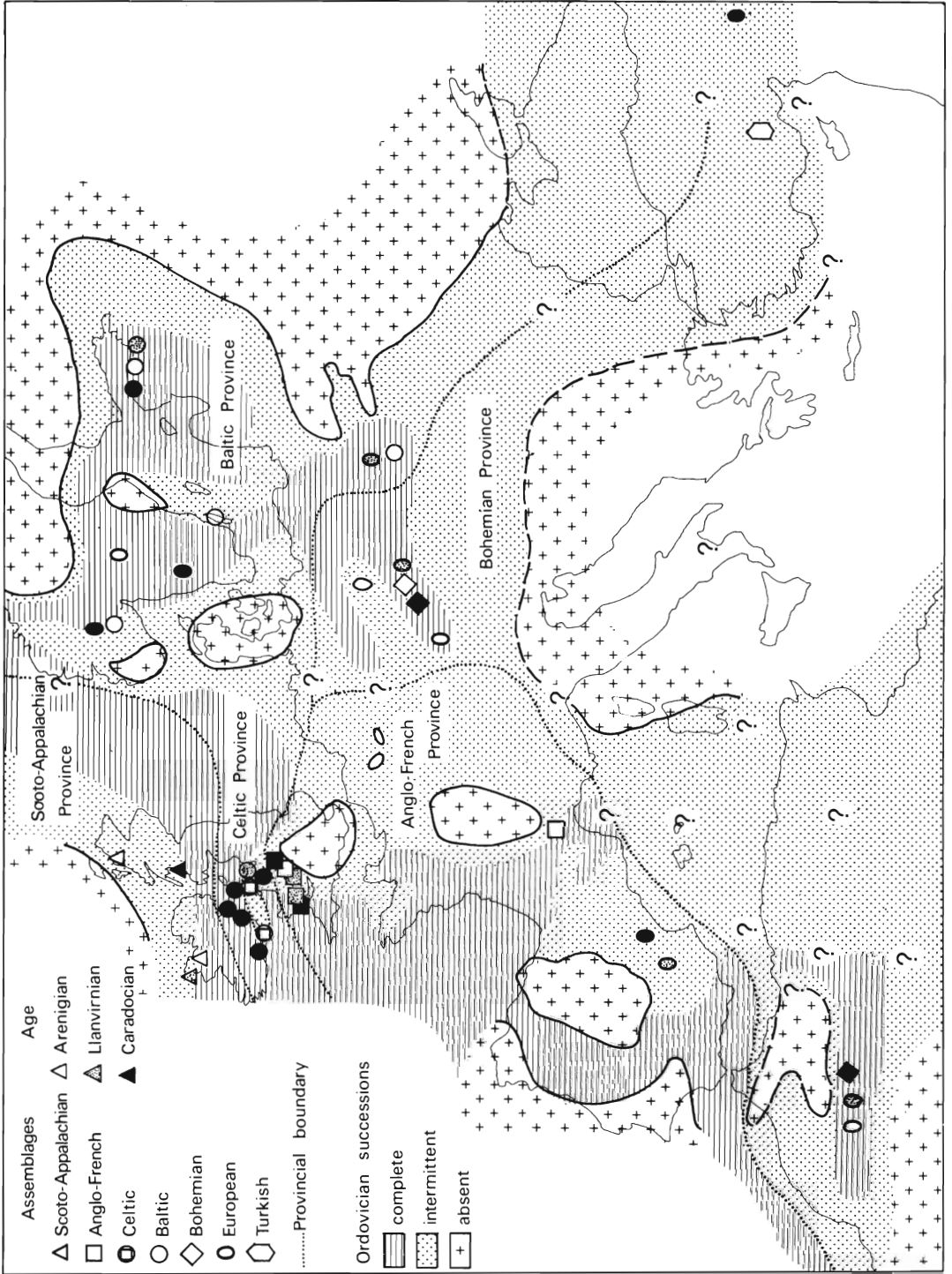
the Bohemian assemblage with a relatively high proportion of endemic genera (*Comatopoma*, *Dedzetina*, *Foliomena*, and *Kozlowskites*), did not combine with any other group, although it is interesting to note that the small Ashgillian fauna from Morocco shows that close connections were maintained between the two regions from Later Caradocian time.

A second-order cluster analysis of the partially pandemic genera in the three clusters and one assemblage reflecting Mid-Ashgillian brachiopod distribution, is superfluous. The coefficients of association between the N. European Province on the one hand and the Bohemian, N. and Mid-American Provinces on the other, are 1.00, 0.94, and 0.91 respectively; and, although those between the American and Bohemian provinces are low, they do not detract from the essential homogeneity of the fauna, because with the exception of *Megamyonia* and *Opikina*, the following pandemic genera invariably occur in the N. European Province: *Aegiria*, *Austinella*, *Catazyga*, *Chonetoidea*, *Conotreta*, *Cyclospira*, *Dalmanella*, *Dayia*, *Eoplectodonta*, *Eostropheodonta*, *Fardenia*, *Glyptorthis*, *Gunnarella*, *Hebertella*, *Hesperorthis*, *Holtedahlina*, *Howellites*, *Hypsiptycha*, *Lepidocyclus*, *Leptaena*, *Leptestiina*, *Leptobolus*, *Lingulella*, *Oxoplecia*, *Parastrophinella*, *Paterula*, *Petrocrania*, *Plaesiomys*, *Platystrophia*, *Ptychopleurella*, *Rafinesquina*, *Retrorsirostra*, *Rhynchotrema*, *Rynchotreta*, *Rostricellula*, *Schizocrania*, *Schizotreta*, *Skenidioides*, *Sowerbyella*, *Strophomena*, *Trematis*, *Triplexia*, and *Zygospira*. Effectively, all groups now constitute a single realm equivalent in pandemic content to the N. European Province.

CONCLUSIONS

Cluster analysis of Ordovician brachiopod assemblages, as represented by genera, indicates that their distribution and composition underwent profound changes during the period. In Arenigian and Llanvirnian times, the identification of five clusters drawn from approximately the same territories, and a variable number of unattached assemblages, showed that the fauna was fragmented into at least five provinces with fairly stable boundaries. By Ashgillian times, however, not only had provincial clusters been reduced to three, but their palaeogeographic distributions had also undergone great changes. More importantly, a reclustering of the partially pandemic residues of provinces and unattached assemblages suggested that Ordovician brachiopods remained segregated into two distinct realms until Ashgillian time when a cosmopolitan fauna began to emerge. The implications are far-reaching as is illustrated by consideration of the nature and distribution of brachiopod assemblages in Europe and adjacent territories in their modern setting (text-fig. 9).

TEXT-FIG. 8. Coefficients of association between twenty Mid-Ashgillian brachiopod assemblages, and graphs showing the degree of association between faunas included in each defined province (indicated by a thickening of the correlation line) and all other faunas. A, Killeen Bridge beds, N. Ireland (W. I. Mitchell, pers. comm.); B, Ordovician Limestones, E. Alaska (Ross and Dutro 1966); C, Me. Richmond Group, Ohio (Dalvé 1948); D, La Martre and Chedabucto Lake Formations, NW. Territories (Norris 1965); E, Silliman Fossil Mountain Formation, Baffin Island (Miller *et al.* 1954); F, Maquoketa Formation, Upper Mississippi Valley (Wang 1949); G, Portrane Limestone, Co. Dublin (Wright 1963, 1964); H, Aleman Formation, Texas (Howe 1965-1967); I, Lr. Ashgillian of Kazakhstan, U.S.S.R. (Nikitin and Apollonov 1968); J, Ashgillian sandstones, Maine (Neuman 1967, 1968); K, Mid-Ashgillian calcareous mudstones, N. England (Ingham 1966); L, Saturday Mountain Formation, Idaho (Ross 1959); M, Kralův Dvůr Shales, Czechoslovakia (Havlíček and Vaněk 1966); N, Whitehead Formation, Quebec (Cooper and Kindle 1936); O, Rhiwlas Limestone (Williams MS.); Whitehouse beds, SW. Scotland (A. D. Wright MS.); Q, Lr. Drummuck beds, SW. Scotland (Lamont 1935); R, Vormsi and Pirgu Limestones (F1b-c), E. Baltic (Oraspöld 1959, Rõõmusoks 1963, 1964); S, Vauréal Formation, Anticosti (Twenhofel 1928); T, Cornwallis Formation, Devon Island (Fortier *et al.* 1963).



TEXT-FIG. 9. A facies distribution map, based on the degree of completeness of Ordovician successions, of Europe and adjacent territories to show the inferred extent of tectonized provinces up to Early Caradocian times.

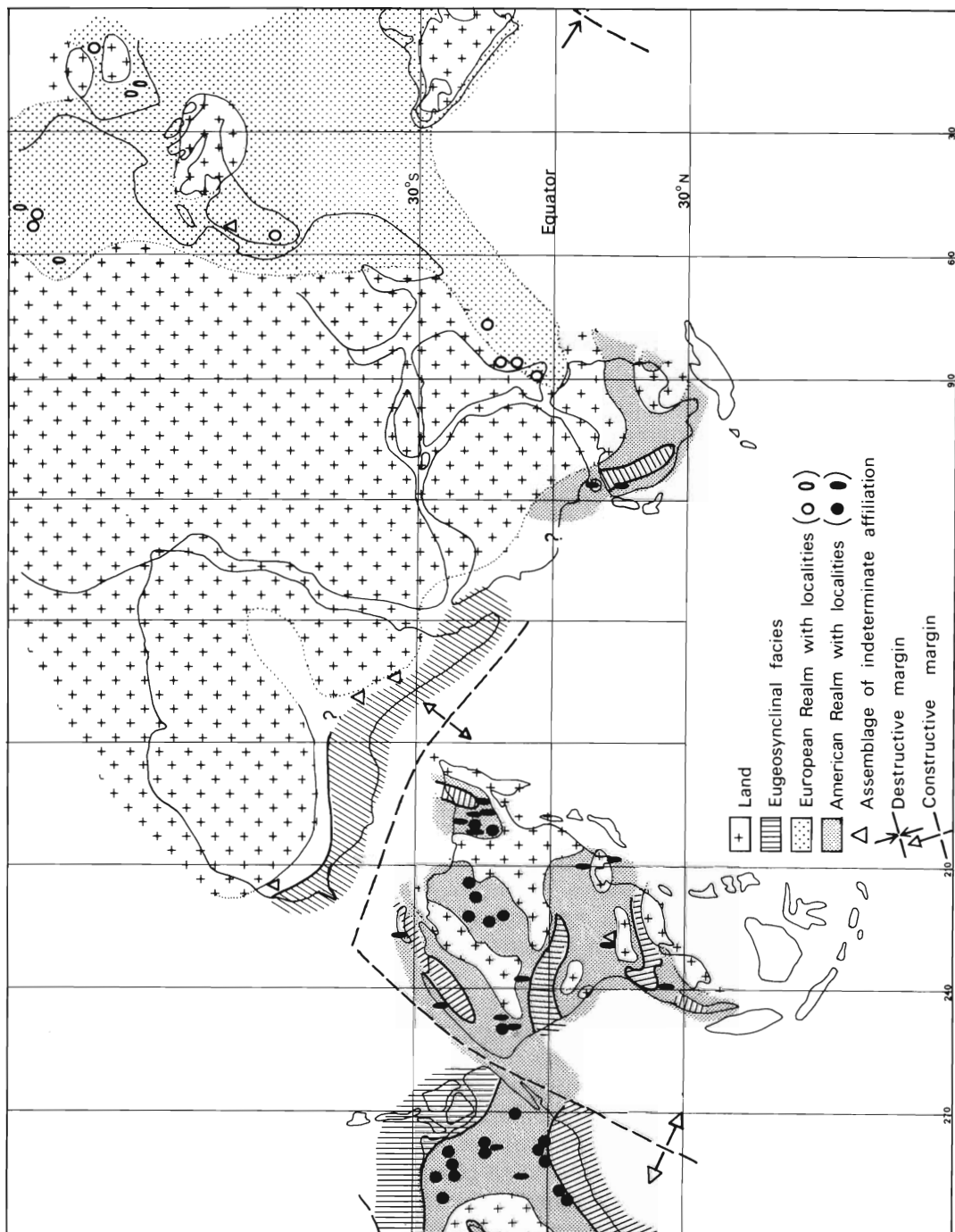
By Early Caradocian time, four persistent (and one transitory) provinces—Scoto-Appalachian, Baltic, Anglo-French, Bohemian (and Celtic) respectively—were identifiable. Each was affected by some exchange of taxa which may have been brought about by oceanic currents (Williams 1969*a*, p. 141); but each had a sufficiently endemic content to remain distinctive throughout much of the period. At present, the inter-provincial boundaries can be only approximately drawn over much of continental Europe, and there is no conclusive evidence why they should have persisted for so long. The Scoto-Appalachian and Baltic faunas tend to be associated with rocks with a higher carbonate content than the Anglo-French and Bohemian assemblages. Again, the relative richness and diversity of the first two faunas suggest that they flourished in warmer water than those of the Anglo-French and Bohemian provinces (Spjeldnaes 1961, p. 57; Havlíček and Vaněk 1966, p. 45; Williams 1969*a*, p. 146). Whatever the cause(s), the chief aspect of the distribution is that a second-order cluster analysis segregates the Scoto-Appalachian Province from a complex composed of the remaining provinces. Thus the boundary between these two palaeogeographic regions, which runs more or less north-east to south-west across the British Isles, is a break of fundamental importance.

Bearing in mind the persistence of the European and American realms, and the wealth of data by which each may be recognized, attention can now be given to their global distribution in pre-Ashgillian times. The results are encouraging even within the latitudinal constraints afforded by palaeomagnetism, because a pattern of distribution can be achieved which is too consistent to be dismissed as random (text-figs. 10, 11).

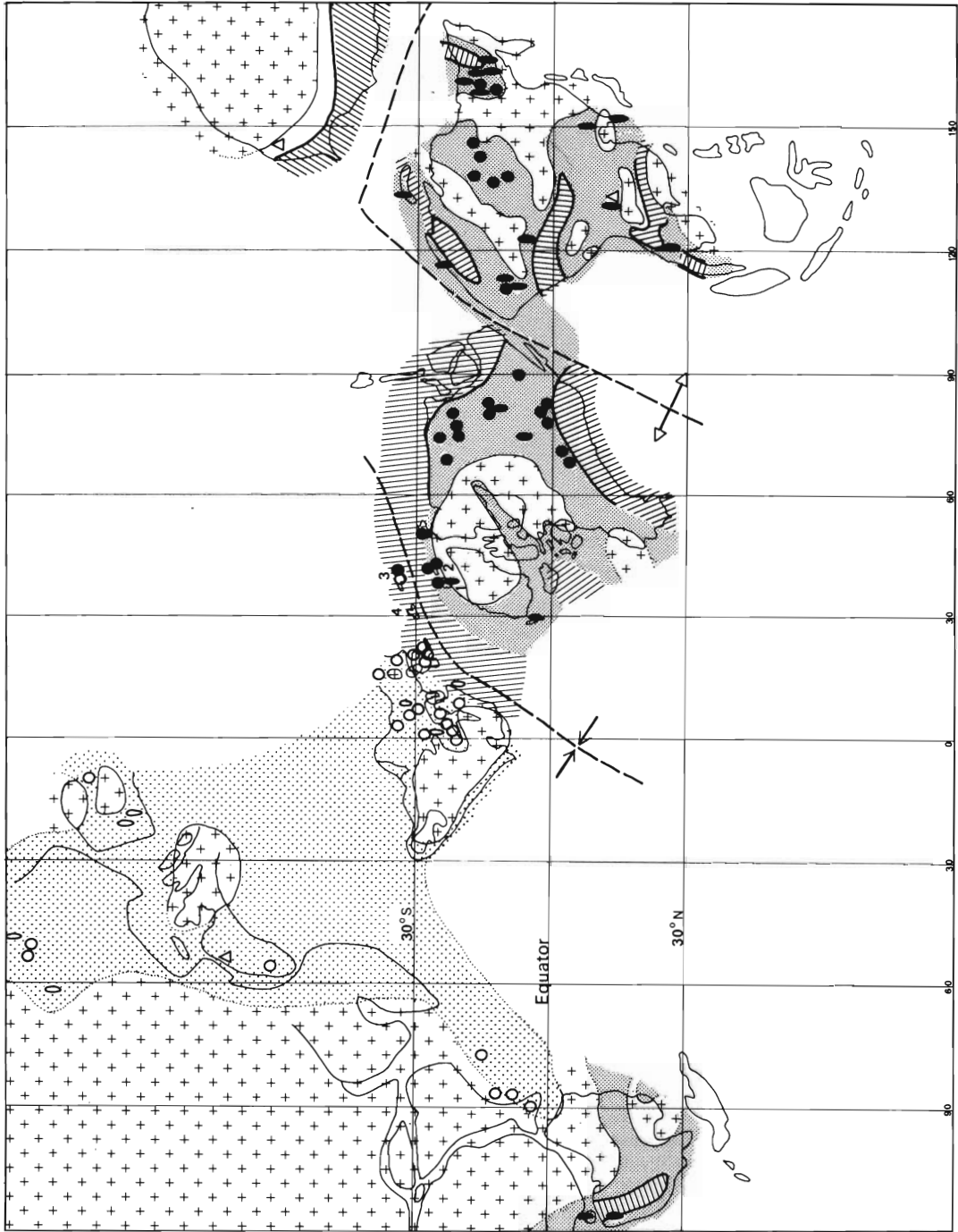
The standard faunas of the American Realm found in the miogeosynclinal and platform facies encircling the Canadian Shield also dominated Ordovician successions on the Siberian Shield and, as far as is known at present, extended along the western flanks of the Uralian Geosyncline, and appeared south of the Tsinglinshan-Seoul line in the Cathaysian Geosyncline as well as in the Tasman Geosyncline of Tasmania and New South Wales. Such a continuity could have been effected if the Siberian and Cathaysian Shields had been interpolated between the Canadian Shield and the western side of Gondwanaland in the manner shown in text-figs. 10 and 11. The connection between the Australian segment of Gondwanaland and the Siberian-Cathaysian Shields is the weakest link in this arrangement. But little is known of the Palaeozoic geosynclinal sediments of Antarctica (Smith and Hallam 1970, p. 4) and further work on the brachiopods of S. America and Australia should provide more evidence of the actual relationship.

Removal of the Siberian-Cathaysian Shields from a position immediately to the west of Gondwanaland also clarifies relationships there between the European Realm typified by faunas associated with the Baltic-Kisovograd Shield, the Mediterranean-African Shields, and the Indian subcontinent (including the Shan States). Other faunas, also known from the Iberian and African Shields, the Turkish area, and the Himalayas, unequivocally belong to the European Realm and confirm the geographic proximity of these areas during the Ordovician period.

It seems, therefore, that the individuality of the European and American Realms rested largely on the fact that the European faunas prevailed to the west of the Gondwanaland complex and the American faunas to the east. Yet there is an increasing

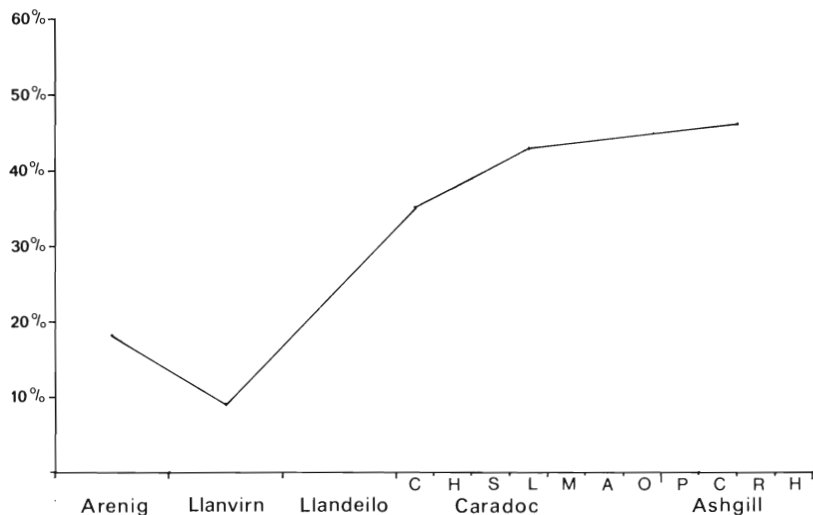


TEXT-FIG. 10. Distribution of the principal continental shields and associated Ordovician rocks in Mid-Caradocian times, according to the palaeogeographic distribution of brachiopod faunas. The circles represent assemblages used in cluster analysis, the ellipses assemblages classified according to realm after second-order cluster analysis. 1, Scotland; 2, Northern and western Ireland; 3, Eastern New England



TEXT-FIG. 11. Continuation of text-fig. 10.

admixture of the two faunas as expressed in the proportion of pandemic to endemic genera during the period (text-fig. 12). In this respect the boundary between the European and American Realms involving the British Isles, Newfoundland, and Maine is especially relevant. As a destructive margin between two continental plates (Dewey 1969, p. 127; Fitton and Hughes 1970, p. 226), it would have promoted an



TEXT-FIG. 12. The proportion of pandemic genera expressed as a percentage of endemic genera in the ninety assemblages of Ordovician brachiopods subjected to cluster analysis.

admixture of two independently derived faunas thereby heralding the ubiquity of many Silurian brachiopod stocks. The beginning of the faunal exchange, which followed the clash of continental plates, is, of course, fairly precisely dated as Mid-Caradocian. In contrast to this plate movement, one would expect a constructive margin to have existed between the Canadian and Siberian Shields and possibly between the latter and Gondwanaland, precursory to the rotation of the Siberian-Cathaysian plate into the position it occupied in Devonian times.

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