CONTROLS INFLUENCING THE COMPOSITION AND DISTRIBUTION OF ORDOVICIAN GRAPTOLITE FAUNAL PROVINCES

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ABSTRACT. Available evidence—palaeomagnetic, tectonic, biological, and environmental—convincingly demonstrates that latitudinal variation in surface-water temperature exerted a *primary* control upon the compositional characteristics and broad distributional patterns portrayed by Ordovician epipelagic graptolite faunas. The emergence of latitudinal climatic belts and a consequent steepening of thermal gradients between the Ordovician palaeoequator and the palaeopoles, foreshadowing the late Ordovician continental glaciation, was accompanied by an increased definition of two graptolite provinces. These provinces, one (Pacific) characterized by stenothermal tropical forms and the other (Atlantic or European) by graptolites showing a preference for the cooler waters of the temperate zone, achieved their maximum expression in late early Ordovician (Llanvirn) time.

The reduced expression of provincialism in the late Ordovician reflects a reduction in the over-all areal distribution of graptolite faunas with the onset of glaciation. Late Ordovician graptolite faunas were confined to the tropical zone, where the general environmental uniformity (measured in terms of surface-water temperatures) increased the possibility of interchange and hence favoured the establishment of more uniform compositional characteristics.

Local compositional characteristics and distribution patterns may reflect the operation of *secondary* controls, such as ocean currents, geographical and genetic isolation, and physical barriers.

THE consensus of present-day opinion supports the view that the early Ordovician witnessed the progressive development of two major graptolite faunal provinces—Pacific and Atlantic (or European). Pacific province faunas include those of Australia, New Zealand, China, Middle Asia, Taimyr, Kazakhstan, Kirgizia, North America, South America (Argentina), western Ireland, south-west Scotland, and west-central Norway. Atlantic province faunas, on the other hand, are found in Wales, England, south and east Ireland, continental Europe (from the Mediterranean northwards to the Baltic and from the western seaboard eastwards to Bohemia), North Africa, and South America (Bolivia and Peru). While the dissimilarity of extreme developments of the two provinces is indisputable, mingling of faunas is seen, at times, in Taimyr, Kazakhstan, Kirgizia, China, South America, eastern North America, and western Australia. Further to this, it must be emphasized that the early Ordovician included many pandemic forms.

In the late Ordovician, graptolite faunas took on a more cosmopolitan aspect, at least at the generic level, and provincialism is correspondingly less obvious.

Within the major provinces, sub-provincial developments can be delineated at times throughout the Ordovician. Thus, within the Atlantic province, the Baltic region, north-west England and eastern Ireland, on the one hand, and south-east England and Wales, on the other, maintain a degree of distinctiveness in the Early Ordovician. In the late Ordovician, Riva (1969) has demonstrated dissimilarities between coeval faunas in north-east North America and Texas, and it is noteworthy that parallel differences occur also in the conodont faunas (Bergström 1973).

The distinctive characteristics of the Pacific and Atlantic graptolite faunal provinces

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have been documented elsewhere (Bulman 1971; Skevington 1973*a*). The purpose of this communication is to analyse and relatively assess those factors which could have been responsible for the provincialism.

PREVIOUS EXPLANATIONS OF PROVINCIALISM

A perusal of the literature reveals a veritable plethora of possible explanations for the provincialism displayed by Ordovician graptolite faunas. These encompass a broad range of biological, physical, environmental, and tectonic controls, invoked either separately or in combination.

Berry (1960) proposed a combination of ocean current dispersal and limitations imposed thereon by the presence of land barriers. Ross (1961) and Berry (1962) favoured a depth-control hypothesis, maintaining that the widely distributed forms were surface-living while those with restricted geographical ranges were confined to considerable depth or may even have been bottom-living. This proposal, though unacceptable to Bulman (1964), has been resurrected by Berry and Boucot (1972) to explain Silurian graptolite distribution.

Bulman (1964) explored the possibility of temperature control and Bouček (1972) attached primary significance to the distribution of Ordovician climatic belts in the development and maintenance of provinces. Both authors made use of the palaeomagnetic evidence presented by Irving (1964) for the location of the Ordovician palaeopoles and palaeoequator.

In a more recent appraisal, Bulman (1971) drew attention to biological factors—such as competition and tolerance—which could have had a bearing on graptolite distribution patterns.

Environmental influences were suggested by Skevington (1969) to explain compositional changes in Atlantic province graptolite faunas of Llanvirn age within the confines of the British Isles. McTavish and Legg (1972) also favoured environmental controls and, further, they attempted to reconcile the disparate views on early Ordovician inter-provincial correlation by advocating 'two parallel graptolite successions, one distinguished by species of *Didymograptus*, and the other by biserial scandent graptolites, which evolved in markedly different tectono-environmental settings' (p. 472). Environmental factors, combined with physical separation due to land barriers or ocean currents, were advocated again by Erdtmann (1972) to explain graptolite provincialism.

THE PRIMARY CONTROL

In the writer's opinion, a sufficiently comprehensive body of information—palaeomagnetic, tectonic, biological, and environmental—is now available to merit a reappraisal of this issue. The evidence, it is believed, convincingly demonstrates that latitudinal variation in surface-water temperature exerted a primary control upon the compositional characteristics and broad distributional patterns portrayed by Ordovician epipelagic graptolite faunas.

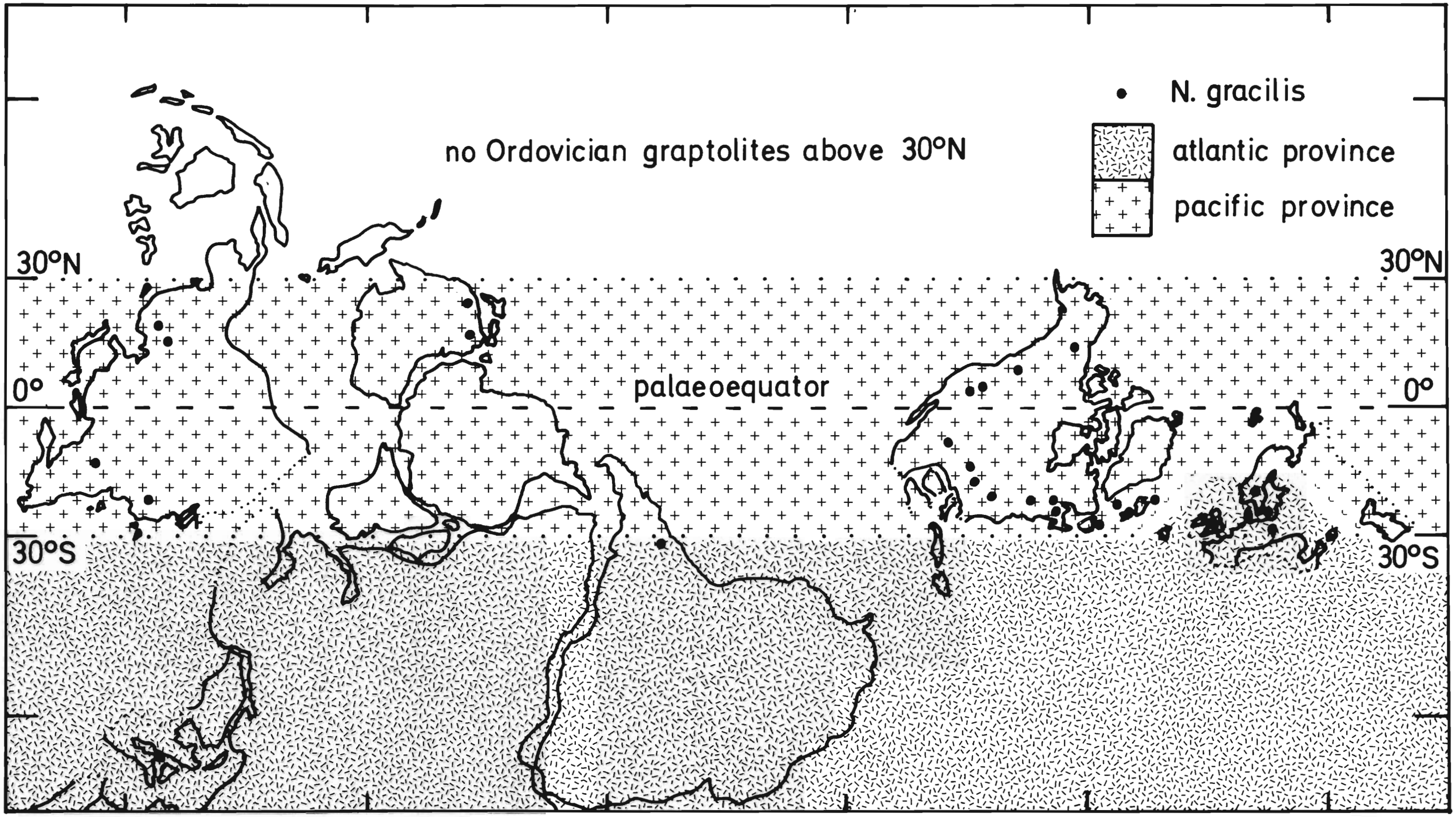
Recent palaeomagnetic data (Smith *et al.* 1973), supported by evidence of a late Ordovician glacial episode (Beuf *et al.* 1971; Harland 1972), establishes the position of the Ordovician South Pole in what is now north-west Africa. This location differs significantly from that proposed by Irving (1964), who, in terms of present-day geography, positioned the southern palaeopole in the South Atlantic. The revised (north-west African) site requires a concomitant shift in the location of the Ordovician palaeoequator, and, on current evidence, this is interpreted to run from southern California to the west of Hudson's Bay, thence north of Greenland and across north-east Asia towards western Australia (see Smith *et al.* 1973, text-figs. 13, 21A, 21B).

Bulman (1964) and Bouček (1972), in attempting to relate provincialism to latitudinal variation in surface-water temperature, encountered discrepancies between distribution patterns and palaeolatitudes based on Irving's (1964) data. If, however, the distributions of Atlantic and Pacific province faunas are superimposed upon the Cambrian/Lower Ordovician continental reconstruction maps prepared by Smith *et al.* (1973), the discrepancies are eliminated. Pacific province faunas straddle the palaeoequator, while Atlantic province faunas in general characterize latitudes higher than 30° S. (land areas positioned higher than 30° N. on the reconstruction maps have not yielded Ordovician graptolites). These facts strongly support the view that surface-water temperatures exerted a controlling influence on the areal extent of Atlantic and Pacific graptolite faunas. The Pacific province corresponds with the tropical zone (approximately 30° N. to 30° S. of the palaeoequator) and the Atlantic province with the southern temperate zone (see text-fig. 1).

Temperature is possibly the most important of all factors governing the distribution of epipelagic organisms at the present day and taxonomic diversity gradients are perhaps the most striking worldwide biogeographic patterns related to temperature. Species diversity, for most higher taxonomic categories, increases markedly from the poles towards the equator; conversely, though the number of species within a given taxon may be reduced in higher latitudes, the number of individuals within a given species may be very great.

These general features portrayed by present-day epipelagic faunas also characterize early Ordovician graptolite faunas, and particularly those of Llanvirn age. Generic diversity is greater in the tropical zone (Pacific province) and genera restricted thereto in the Llanvirn include *Brachiograptus*, *Cardiograptus*, *Paraglossograptus*, *Pseudobryograptus*, *Pseudotrigonograptus* and some of the more advanced Sinograptidae, such as *Allograptus*, *Sinograptus*, and *Holmograptus spinosus*. The temperate zone (Atlantic province) Llanvirn faunas are less diverse. Indeed, not a single genus is endemic to the Llanvirn Atlantic province, though certain species-group taxa—notably the pendent species of *Didymograptus*—are represented by an abundance of individuals.

Moreover, as one would expect, the taxonomic diversity gradient increases gradually towards the Ordovician palaeoequator and this feature is particularly well illustrated by the changing composition of Atlantic province Llanvirn faunas from south to north (i.e. in a palaeoequator-ward direction) within the confines of the British Isles. In the typical development of the Llanvirn Series, in South Wales, the dominance of pendent species of *Didymograptus* is well known from the descriptions given by Hicks (1875), Hopkinson and Lapworth (1875), Elles (1904), and Cox (1915). Atlantic province Llanvirn graptolite faunas are also well represented in the eastern Lake District (Skevington 1970; Wadge *et al.* 1972) and Cross Fell (Shotton



TEXT-FIG. 1. Distribution of early Ordovician (essentially late Arenig and Llanvirn) graptolite faunal provinces, together with recorded occurrences of *Nemagraptus gracilis*. (Continental reconstruction based on text-fig. 13, Map 8—'Cambrian/Lower Ordovician'—of Smith, Briden and Drewry (1973); Mercator projection.)

1935) areas of England and in eastern Ireland. In these more northerly occurrences, a slight, but none the less significant, increase in taxonomic diversity is evident and additional elements present, which are either rare or absent in South Wales, include *Phyllograptus*, *Aulograptus cucullus*, and *Nicholsonograptus fasciculatus* in the *bifidus* Zone, and probably *Pterograptus* in the *murchisoni* Zone.

It is noteworthy that, in general terms, present-day surface-water isotherms bear an approximate parallelism to lines of latitude, though, in detail, ocean-water circulation patterns disrupt this simple relationship. It is a truism, however, that stenothermal species—those tolerant of a narrow temperature range—do adopt an essentially latitudinal distribution pattern. Furthermore, as argued convincingly by Ewing and Donn (1956), the establishment of polar ice-caps will be accompanied by a steepening of latitudinal surface-water temperature gradients between equatorial and polar regions and there will be a concomitant increased definition of climatic zones; the absence of polar ice-caps, on the other hand, will result in a weak and uniform latitudinal temperature gradient.

It seems reasonable to assume that the late Ordovician glacial episode would have been preceded by a progressive steepening of thermal gradients from the palaeoequator towards the palaeopoles and that this would have been accompanied by the establishment of increasingly well-marked latitudinal climatic zones. In turn, the areal distributions of stenothermal epipelagic faunas would have been progressively restricted. At the opening of the Ordovician period, some 50–60 m.y. prior to the late Ordovician continental glaciation, the difference in average surface-water temperatures between low and high latitudes is likely to have been relatively slight. The accumulation of polar ice, culminating in the glacial episode, would have been reflected in a lowering of surface-water temperatures in higher latitudes and a consequent steepening of thermal gradients between palaeoequatorial and palaeopolar regions.

The well-documented climatic history of the 60 m.y. period from the beginning of the Tertiary to the onset of the Pleistocene glaciation lends considerable support to the above proposals and the writer is deeply indebted to Professor B. M. Funnell (University of East Anglia) for the following authoritative statement: 'I think it fair to say, regarding the Tertiary, that the present climatic belts were reasonably well developed throughout that period and that one would need to go back as far as the Jurassic, or at least the earlier part of the Cretaceous, in order to find a climatic zonation which is qualitatively different to that at the present day. The Tertiary itself is characterized, even in the lower part, by the development of an Antarctic ice sheet and the circum-Antarctic climatic belts generated by it. The essential feature of Tertiary history is the intensification of the present climatic belts and the oscillating width which they display. The changes, which are quantitative rather than qualitative, were not entirely progressive but reflect an alternating pattern only cumulatively resulting in the more extreme conditions of the Pleistocene. In brief, it is entirely reasonable, and now well demonstrated, that the trend up to the Pleistocene glaciation certainly spanned many tens of millions of years from the Eocene onwards and, given that, essentially the present state of affairs has existed for most of the last ten million years.'

On the basis of such a climatic model, together with the belief that surface-water temperatures exerted a primary influence on the distribution of epipelagic graptolites, it is possible to offer an explanation for the compositional characteristics of Atlantic and Pacific faunas at various times during the Ordovician.

The opening of the Arenig is distinguished by the ubiquitous development of the *Tetragraptus approximatus* fauna. In the early and middle Arenig, *Phyllograptus* in association with pendent *Didymograptus*, and then *Isograptus*, enjoyed a similarly extensive (co-provincial) distribution. At the same time, multiramous Dichograptidae inhabited both provinces, as also did a variety of pauciramous forms other than those listed above, viz. *Azygograptus*, *Didymograptus* (extensiform and declined), and *Tetragraptus*. Recognition of Atlantic and Pacific provinces in the early and middle Arenig rests essentially on the restriction of certain multiramous genera to one province or the other. Most, if not all, such genera are not strict biological entities, however; rather, they are form-genera and their existence demonstrates only too well the long-held belief that many graptolite 'genera' are polyphyletic, and, as such, have little if any value in the delimitation of faunal provinces. In addition, three possibly valid genera—*Maeandrograptus*, *Kinnegraptus*, and *Oslograptus*—appear to be endemic to the Atlantic province in the early or middle Arenig. However, Bulman (1970) has questioned the validity of *Oslograptus*, while the geographical distribution of *Maeandrograptus* is dependent upon the interpretation of its generic characteristics. Thus, Bulman (1970) regards the genus as monotypic and so limits its distribution to that of the type species (southern Scandinavia), whereas Harris (1933) refers certain Australian species to the genus, thereby according it a co-provincial distribution. Indeed, only the diminutive *Kinnegraptus* has so far escaped without question, though Jackson (1969, and pers. comm.) records its presence in the Yukon and a four-stiped '*Kinnegraptus*' has been discovered recently in Kirgizia (Pacific province) by Dr. M. Zima (pers. comm.).

The evidence for clearly defined provincialism in the early and middle Arenig is thus slight indeed; rather, uniformity was the rule, and this is to be expected in view of the low thermal gradients postulated for that period of time.

This impression of uniformity persists into the late Arenig and, at the species level, is perhaps best illustrated by the ubiquitous *Pseudotrigonograptus ensiformis*; it is also expressed by the universal appearance of biserial scandent graptolites, particularly *Glyptograptus*, and the first Sinograptidae. On the other hand, there is clear evidence of incipient provincialism. Thus, late Arenig descendants of the pendent *Didymograptus* stock are confined to areas which, in the succeeding Llanvirn, are referable to a more clearly defined Atlantic province. Conversely, *Isograptus* flourishes and diversifies (leading to such extreme forms as *Oncograptus* and *Cardiograptus*) only within the confines of a developing Pacific province.

In the late Arenig, therefore, formerly widespread stocks suffer a restricted distribution, and this can be attributed to steepening thermal gradients and a consequent clearer demarcation of tropical and temperate zones. Stenothermal tendencies are portrayed by *Isograptus* and its derivatives and by the pendent forms of *Didymograptus*, with the former expressing a preference for the warmer waters of the tropical zone and the latter for the cooler waters of the temperate zone. At the same time, newly emergent stocks—such as the biserial graptolites (both dipleural and monopleural) and the sinograptids—were eurythermal and hence able to tolerate the range of temperatures experienced throughout the late Arenig tropical and temperate zones. Nevertheless, at least one dipleural biserial species, *Glyptograptus austrodentatus*, includes a number of readily detectable local populations or geographical races (Bulman 1963), and while genetic isolation may have been the principal factor involved in their development, it seems reasonable to assume that temperature variation played at least a contributory role.

The composition of Llanvirn faunas suggests a further steepening of latitudinal thermal gradients between the palaeoequator and the palaeopoles and a correspondingly more marked disparity between tropical and temperate zones. Thus the continued preference of *Isograptus* and its derivatives for the tropical zone and of pendent *Didymograptus* species for the temperate zone is clearly in evidence; indeed, it is the restricted geographical distribution of Llanvirn pendent *Didymograptus* species which gave origin to the bi-provincial concept. At the same time, *Phyllograptus*, *Pseudotrigonograptus*, and descendants of the late Arenig sinograptid stock, may be interpreted as stenothermal tropical, for they are essential constitutents of Pacific province faunas during the Llanvirn. The biserial scandent graptolites, on the other hand, remain eurythermal and hence are co-provincial in the Llanvirn, though their reduced representation in late Llanvirn faunas in southern England (Skevington 1973*b*) and northern Spain (Dr. M. Julivert pers. comm.) suggests that they were unable to tolerate the lower range of temperatures experienced in the temperate zone as the early Ordovician drew to a close.

On a worldwide scale it is important to recognize that no hard-and-fast line separates the two early Ordovician graptolite faunal provinces, even at the time of their maximum expression in the Llanvirn. This fact is implicit in the frequent reference to 'marginal areas', in which faunal elements considered diagnostic of one province occur in association with those distinctive for the other. Thus, Atlantic Llanvirn faunas are characterized essentially by the distribution of pendent species of *Didymograptus*; these forms are occasionally encountered, however, in Llanvirn faunas of Pacific type, as, for example, in north-west Argentina (Turner 1960; Harrington and Leanza 1957), western Australia (Skwarko 1967; Mr. D. Legg pers. comm.), Kazakhstan (Nikitin 1971), and China (Hsü 1934).

In regard to these pendent forms, it should be borne in mind that pre-Llanvirn representatives were co-provincial. They first appeared in mid Arenig time, in the *Didymograptus nitidus* Zone of the Atlantic province, and in the *D. protobifidus* Zone of the Pacific province. In the former province they proliferated and diversified and persisted through to the end of the Llanvirn, whereas in the Pacific province the species-group was short-lived and had effectively disappeared by the late Arenig. The occasional representatives in Pacific Llanvirn faunas are best interpreted as migrants from the Atlantic province.

The converse appears to be true in the case of *Isograptus* and the Sinograptidae, which may be regarded as essentially Pacific province graptolites. The appearance of *Isograptus*, in mid Arenig time, was synchronous in the two provinces, but it was only in the Pacific province that the genus assumed numerical importance and underwent extreme diversification, as exemplified by *Oncograptus* and *Cardiograptus*. In the Atlantic province the genus is scantily represented and *Oncograptus* and *Cardiograptus* are unknown; moreover, the rare representatives of *Isograptus* in Llanvirn

Atlantic faunas would appear to be Pacific migrants rather than direct descendants from the original Atlantic stock. Again, early sinograptids, such as *Holmograptus lentus*, were co-provincial, but later (Llanvirn) diversification within this family—as evidenced by *Holmograptus spinosus*, *Allograptus*, and *Sinograptus*—is a feature only of the Pacific province and such forms are not present in Atlantic Llanvirn faunas.

The biserial graptolites appeared simultaneously in the late Arenig in the two provinces (Skevington 1968). They did so gradually, however, during an interval spanning a number of graptolite zones. In both provinces, *Glyptograptus* is the earliest representative, though the relative appearance of other genera shows some variation. The degree of diversification, as evidenced by the several biserial form-genera, is comparable in the two provinces. Relative abundance, measured in terms of numbers of individuals, has not been assessed, however, and the only pointer on this score is a dearth of biserials in southernmost Atlantic province Llanvirn faunas in the British Isles and northern Spain.

The approximate parallelism of present-day surface-water isotherms to lines of latitude, coupled with the readily demonstrable relationship between the composition of early Ordovician graptolite faunas and the postulated palaeolatitudes, leads to the reasonable assumption that temperature variation was primarily responsible for the establishment and maintenance of the Atlantic and Pacific provinces. Moreover, the progressive development of the two provinces can be correlated with the gradual steepening of thermal gradients and the emergence of climatic belts which were essential precursors to the onset of the late Ordovician glacial episode.

The sudden and virtually complete demise of the dichograptids and sinograptids at the close of the Llanvirn confers a uniformity on immediately post-Llanvirn graptolite faunas the world over which is maintained to the end of Ordovician times. The uniform generic composition of late Ordovician faunas is widely interpreted as indicative of an end to the provincialism which characterized the distribution of early Ordovician graptolites. In fact, however, there is evidence of provincial development at times during the late Ordovician, though the differences exist at the lowest taxonomic level—that of the species—and the provinces are correspondingly much less obvious. Indeed, in the light of Ekman's (1953) statement that endemic species have least value in provincial definition, the status of the late Ordovician provinces is seen to be exceedingly slight. Be that as it may, the continued existence of some degree of provincialism is apparent if an attempt is made to apply the standard British upper Ordovician graptolite zones, which were defined in southern Scotland, to graptolite-bearing sequences in Wales, while, further afield, Riva (1969) has drawn attention to differences in the composition of late Ordovician faunas between Texas and north-eastern North America.

In part, at least, the restricted diversification in rhabdosomal form, in comparison with the early Ordovician, is one factor contributing to the reduced expression of late Ordovician provincialism. Far greater importance, however, is attached to the lowering of surface-water temperatures in middle and high latitudes, which, it is believed, imposed a restriction on the over-all distribution of graptolite faunas in comparison with the early Ordovician. Thus, late Ordovician graptolites do not occur in North

Africa (Destombes 1971), though early Ordovician Atlantic province faunas have been reported therefrom, and are rare in north-west South America, an area which also supported rich Atlantic faunas in the early Ordovician. Maps prepared by Tamain (1971, figs. II–V), depicting the distribution of graptolites at various times during the Ordovician period in south-west Europe and north-west Africa, demonstrate the progressive withdrawal of faunas from the Ordovician southern polar region. Thus, Llanvirn graptolites occur in the Anti-Atlas, throughout the Iberian Peninsula, and in Brittany and Normandy (fig. II); *G. teretiusculus* Zone ('Llandeilo') forms are restricted to northern Spain and Brittany, while early Caradoc species are found only in Normandy (fig. III); and thereafter graptolites disappear from south-west Europe (figs. IV, V) (Tamain's late Caradoc map (fig. IV) indicates the presence of graptolites in the Anti-Atlas at that time; this is contrary to information given by Destombes (1971) and hence should be regarded with some doubt). The distribution of *Nemagraptus gracilis*—certainly the most distinctive and possibly the most widely distributed late Ordovician graptolite species—adds weight to the preceding observations. When occurrences of this species are plotted on the Smith *et al.* (1973) Cambrian/Lower Ordovician reconstruction maps, they are seen to fall within a zone bounded by the 30° N. and 30° S. palaeolatitude lines (text-fig. 1). In other words, the distributional limits of this species are the same as those which defined the extent of the Pacific province in the early Ordovician.

The foregoing evidence strongly suggests that in the late Ordovician *all* graptolite faunas, with rare exceptions, were confined to the tropical zone, where the general environmental uniformity (measured in terms of surface-water temperatures) was impressed upon the composition of the graptolite faunas. It is envisaged that the progressively steepening thermal gradients imparted a concomitant restriction upon the areal distribution of graptolites, such that, by the late Ordovician, the limits of temperature tolerance were located within a few tens of degrees on either side of the palaeoequator. This reduced geographical spread of graptolite faunas increased the possibility of interchange and hence favoured the establishment of more uniform compositional characteristics. With this progressive geographical limitation there occurred also a marked reduction in taxonomic diversity, such that latest Ordovician graptolite faunas include but a handful of species attributable only to some five or six genera (Berry and Boucot 1973), which can be regarded as a further expression of glacial influence.

SECONDARY CONTROLS

While the latitudinal temperature control hypothesis serves as an acceptable explanation of the general characteristics of Ordovician provincialism, it is appreciated that local patterns of distribution may reflect the operation of other factors—biological, physical, and environmental. Thus, it can be assumed that the Ordovician oceans supported circulation systems comparable, in broad outlines, with those in existence in oceans of the present, and this is all the more likely to have been the case as the temperature differential between the palaeoequator and the palaeopoles increased with the passage of time during the Ordovician period. In modern oceans the precise paths followed by ocean currents are influenced by the distribution and coastal configurations of the land masses. The outlines and relative longitudinal dispositions of Ordovician land areas are unknown, however, except in very general terms, and, at best, one can assume that, locally, warmer tropical waters were carried into higher latitudes and cooler, temperate waters found their way into lower latitudes. This is possibly sufficient to explain the occurrence of the occasional Llanvirn pendent *Didymograptus* in faunas which otherwise are distinctively Pacific in composition; conversely, the rare presence of *Isograptus* in Atlantic Llanvirn faunas may be attributable to the flowage of warm currents into the temperate zone.

It may be necessary to seek an alternative explanation to account for the early Ordovician Atlantic faunas of southern Scandinavia and the Baltic States. On the Smith *et al.* (1973) reconstruction maps these areas are positioned on or about the 20° S. palaeolatitude line and well within the tropical zone, though the early Ordovician faunas therefrom are temperate in character (text-fig. 1). It is possible that this tropical lobe of the Atlantic province was established and maintained by a cool current flowing from the temperate zone towards the palaeoequator; such a current, however, would have to have flowed unchanged and unchecked throughout the early Ordovician. As a corollary, it is worthy of note that this current would have flowed in the opposite direction to the South Equatorial Current invoked by Williams (1969) to explain aspects of Ordovician brachiopod provincialism in north-west Europe. A more likely explanation, achieving the same effect, would be to assume that in the early Ordovician the European continental mass was at least 10° further south than the position accorded to it on the Smith *et al.* (1973) maps, thereby placing southern Scandinavia and the Baltic States within the southern temperate zone. Acceptance of a proto-Atlantic Ocean (Wilson 1966) imposes no constraints on the extent of the separation of North America and Europe in the early Ordovician. A southward shift of Europe through 10° of latitude relative to North America would result in a greater separation of the two continents, and the areal extent of the proto-Atlantic Ocean would be enlarged accordingly, though not to an unacceptable degree when it is borne in mind that the early Ordovician witnessed the maximum development of the proto-Atlantic. Williams (1969) used the Bullard *et al.* (1965) Pangaea fit of the continents as a basis for his interpretation of Ordovician palaeogeography; in terms of this model, a southward displacement of Europe would involve a comparable shift in the position of North America and the consequent location of tropical (Pacific province) faunas in the temperate zone, which, in turn, would require further explanation. Thus, quite apart from any other consideration, the temperature control hypothesis invoked to interpret early Ordovician graptolite provincialism is best served by assuming the existence of a proto-Atlantic ocean of the same order of magnitude as the present North Atlantic.

Sub-provincial developments which arose at times during the late Ordovician are best attributed, perhaps, to physical barriers which imposed some degree of geographical (and genetic) isolation on a local scale, as, for example, between southern Scotland and Wales. In this case, the plate tectonic model proposed by Dewey (1969, 1971) for the evolution of the Caledonian orogen includes adequate provision for the emergence of physical barriers during the contraction phase of the proto-Atlantic Ocean—a phase which encompassed the late Ordovician. Thus, the establishment of tectonic features such as the Welsh Basin, the Irish Sea Horst, and, more particularly, volcanic island arcs, would have provided at least partial, if not complete, barriers between Wales and southern Scotland. At the same time it is worthy of note that the island arcs, while imposing a restriction on the free range of epipelagic graptolites, would have contributed to the uniformity of the late Ordovician benthos by providing an increased development of the shallow-water environment occupied by such organisms (see Williams 1969).

McTavish and Legg (1972) have suggested that the tectonic-sedimentary environment may well have influenced the composition of graptolite faunas in the early Ordovician and, indeed, the correspondence which exists in the British Isles between the tectonic zones of the Caledonian orogen (Dewey 1969) and the composition of Llanvirn graptolite faunas is superficially impressive. Thus, Pacific province faunas are confined to Zone A and Atlantic province faunas to Zones B and C. Moreover, in the Atlantic province, faunas characterized by a dominance of the pendent *Didymograptus* element are found in Zone C, whereas faunas richer in biserial graptolites occur within Zone B. This led Skevington (1969) to suggest that the pendent forms of *Didymograptus* were better suited to the shallow water, higher energy environment of the platform seas (Zone C), while the biserials flourished in the quieter surface waters of the proto-Atlantic Ocean (Zone B). A more rigorous quantitative assessment of Atlantic Llanvirn faunas from south to north in the British Isles reveals, however, that the compositional changes are gradually achieved and an abrupt change-over from a dominance of pendent *Didymograptus* to a dominance of biserials does not take place at the Zone C/Zone B interface.

Quantitative data on the relative abundance of pendent species of *Didymograptus* compared to other faunal elements are not available for the type developments of the *bifidus* and *murchisoni* Zones in South Wales. In recently recovered *murchisoni* Zone faunas from the sub-surface Llanvirn of southern England, however, pendent *Didymograptus* species (chiefly *D. artus*, *D. acutus*, and *D. murchisoni* s.l.) outnumber all other graptolites by a factor of twenty (Skevington 1973*b*; Dr. A. W. A. Rushton pers. comm.).

Further north and west in the British Isles, Atlantic province Llanvirn graptolite faunas are well represented in the eastern Lake District and Cross Fell areas of England and in eastern Ireland. In these occurrences, however, the Llanvirn faunas differ in two respects from those of South Wales and eastern England. Firstly, while pendent species of *Didymograptus* are normally present, they are markedly subordinate to other elements of the Llanvirn graptolite faunas; and secondly, a greater taxonomic diversity is evident in the composition of these more northerly faunas.

In the eastern Lake District, prolific *bifidus* and *murchisoni* Zone faunas have been obtained in recent years from aqueduct tunnels cut in lower Ordovician Skiddaw Slates (Skevington 1970; Wadge *et al.* 1972). The *bifidus* Zone fauna is comprised of more than 400 specimens belonging in 27 species; however, the pendent *Didymograptus* element in this fauna is represented by no more than 40 specimens attributable to 6 species. A *murchisoni* Zone fauna of comparable magnitude in terms of the number of specimens recovered has provided only 12 which are referable to the pendent *Didymograptus* species-group. Both the *bifidus* and *murchisoni* Zone faunas are dominated by biserial graptolites, particularly *Amplexograptus*, *Cryptograptus*, and *Glyptograptus*, and, to a lesser extent, *Climacograptus*, *Diplograptus*, and

Pseudoclimacograptus. Other elements, either rare or absent in South Wales, include *Phyllograptus*, *Aulograptus cucullus*, and *Nicholsonograptus fasciculatus* in the *bifidus* Zone, and a probable *Pterograptus* in the *murchisoni* Zone.

A *bifidus* Zone fauna from Cardrath, Co. Meath, Ireland, illustrates an extreme development of the compositional trends noted above. Thus, the pendent *Didymograptus* species-group is not represented and the fauna is comprised almost exclusively of biserial scandent graptolites and *Aulograptus cucullus* (Dr. M. Romano pers. comm.). At Bellewstown, Co. Meath, however, Harper and Rast (1964) have reported pendent forms of *Didymograptus* in a fauna which they attribute to the higher part of the *bifidus* Zone.

Graptolite-bearing strata of Llanvirn age are also well represented in North Wales, mid-way geographically between the English Lake District and South Wales. This intermediate location is reflected in the composition of the Llanvirn faunas. Thus an occurrence of the *bifidus* Zone at Nant Rhydau Gloewon in the Arenig district has yielded in excess of 550 specimens, of which 80% are biserial graptolites and 15% belong in the pendent *Didymograptus* group (Mr. M. Walters pers. comm.). Considerably smaller *bifidus* Zone collections from Tyddyn Bach Farm and Traeth Dulas, both on the island of Anglesey, show almost equal representation of pendent *Didymograptus* and biserial scandent forms. In the valley of the Afon Seiont, at Caernarvon, Elles (1904) has stated that pendent forms of *Didymograptus* (collectively referred to *D. bifidus*) are 'very common' in the *bifidus* Zone at Pont Seiont and in the left bank of the river; in the right bank, however, 'the *Didymograpti* are rarer and the Diplograptidae relatively more abundant' (op. cit., p. 203). She also reports that shales attributable to the *bifidus* Zone at Penarfynydd, on the Lleyn Peninsula, 'contain numerous and excellent specimens of *Didymograptus bifidus*' (op. cit., p. 204), while recent collecting in this area has yielded 178 specimens of graptolites, of which 67% are biserial scandent forms and 30% are attributable to the pendent *Didymograptus* species-group (Mr. M. Walters pers. comm.).

Thus, from south to north within the Atlantic province of the British Isles, a gradual reversal takes place in the relative status of the pendent *Didymograptus* and biserial elements of the Llanvirn graptolite faunas. These observations are more in accord with the belief that surface-water temperatures exerted a controlling influence on faunal composition and that any apparent correlation between composition and tectonic environment is nothing more than coincidental. This view is strengthened by the slight, but very significant, increase in taxonomic diversity evident in the northern compared to the southern Atlantic Llanvirn faunas, which can be attributed to closer proximity to the palaeoequator.

In the west of Ireland (Zone A), still further changes are found in the content of Llanvirn graptolite faunas, the most important being the total disappearance of pendent *Didymograptus* species and the presence of genera (and species) not seen elsewhere in the British Isles. These western Irish faunas are typically Pacific in aspect and can be compared with those of the Darriwil Series ('Middle Ordovician') of Victoria, Australia, the *Amplexograptus confertus* Zone of China, and the *Paraglossograptus etheridgei* Zone of North America. In terms of the Australian sequence, the presence of the MO2 and MO3 Zones has been established to date (Skevington and Archer 1971). Specimens are not abundant, but such distinctive Llanvirn age

Pacific province forms as *Brachiograptus etaformis*, *Holmograptus spinosus*, and *Pseudotrigonograptus ensiformis* have been recovered.

The abrupt change in the composition of Llanvirn faunas across the Zone A/Zone B interface is readily explained in terms of the plate tectonic interpretation of the Caledonian orogen proposed by Dewey (1969). In the Early Ordovician, the Pacific province faunas of Zone A were separated from those of Zone B by the major expanse of the proto-Atlantic Ocean. The present close juxtaposition of Pacific and Atlantic faunas in the northern parts of the British Isles reflects the subsequent contraction, or squeezing out, of the proto-Atlantic by lithosphere loss in a subduction zone located along the southern margin of Zone A. The tectono-sedimentary peculiarities of Zone A had no influence on the composition of early Ordovician graptolite faunas of that zone—those faunas derive their Pacific characteristics from the fact that, in the early Ordovician, they were located well within the tropical zone, in close proximity to the Ordovician palaeoequator.

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