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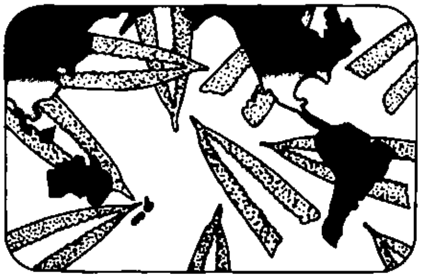

PALEOSCENE 15. Paleozoic Biostratigraphy

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INTRODUCTION AND BIOSTRATIGRAPHIC PRINCIPLES

Biostratigraphy is generally defined as the use of fossils in stratigraphic correlation (Holland, 1990), or the use of fossils as a stratigraphic tool. Furthermore, "it is the study of the biostratigraphic features in rocks that laid the foundation for modern stratigraphy, and it is biostratigraphy that still provides the most reliable means of correlation between sedimentary successions around the world" (Lemon, 1990, p. 203). In other words, the ultimate goal of biostratigraphy is to determine the relative temporal relationships between fossiliferous rocks of one area and those of another.

The foundations for biostratigraphy are rooted in the classic, pioneering studies of such individuals as William Smith of the early 19th century and of Alcide d'Orbigny and Albert Oppel of the mid-19th century (see Hofmann, 1987), but it is to Oppel that we owe our modern perception of what is meant by a biostratigraphic zone (= biozone of the North American Stratigraphic Code, 1983). It is no coincidence that all of the above three workers made their fundamental discoveries in the richly fossiliferous Jurassic strata of western Europe. However, comparable studies of the Paleozoic were not far behind, and by the mid-1800s, the use of fossils in the correlation of Silurian and Devonian rocks of Britain and continental Europe had been demonstrated by such pioneers as Murchison (Rudwick, 1985). Later, and more significantly and specifically, Charles Lapworth in a seminal series of publications (1879-1880) clearly demonstrated the value of Ordovician and Silurian graptolites as regional biostratigraphic tools. Farther afield, parallel studies of Barrande (1850) and Perner (1894-1899) in Bohemia and James Hall in Quebec and New York State (1865) were no less significant, since these studies, of necessity, had no recourse but to rely entirely on the fossil content of the rocks to correlate them with the type sections of Great Britain. Many of these correlations, especially those of Hall, were remarkably accurate. In short, these geological giants fully demonstrated the value of fossils as geographically long-range correlation tools.

The fundamental unit of biostratigraphy is the biozone (in this paper the terms "zone" and "biozone" are used interchangeably), much as the species is the fundamental unit of taxonomy. In essence, the biozone is the operational biostratigraphic unit, and may be defined as a body of strata distinguished by a unique assemblage of species, a definition that developed from the time of Oppel (1856). The biozone is named after an important faunal element, the first appearance of which usually defines its base. For example, the base of the Silurian is now universally recognized to be at the base of the *Parakidograptus acuminatus* Zone (Cocks, 1988); similarly, the base of the Devonian is defined at the base of *Monograptus uniformis uniformis* Zone (Martinsson, 1977), marked by the first appearance of the subspecies.

It is generally assumed that the first appearance of that species may approximate a time line, or one that is as close as possible in the geological sense (see Murphy (1977) for a general discussion; and Finney and Bergström (1986) for the detailed discussion of the *Nemagraptus gracilis* Biozone). Independent tests for this are, however, difficult to come by, although magnetostratigraphy may ultimately provide such a check because of the short durations of magnetic reversals (Johnson and Nigrini, 1985, p. 538).

In setting up any biostratigraphic zonation, two requirements are paramount: accurate and carefully control-

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led stratigraphic sampling of a number of sections, and sound taxonomy. These points, though obvious, need to be emphasized.

In some cases, multigroup biostratigraphy leads to a much-refined zonation. This has proven to be the case for Mesozoic biostratigraphy where the integration of the biostratigraphic schemes of different organismal groups (*e.g.*, bivalves, brachiopods, ammonites, foraminifera) has resulted in a separate set of unique zones which are much more refined than those derived from any individual group (Kauffman, 1970; Surlyk and Birkelund, 1977). This approach has seldom been attempted in the Paleozoic, but is, however, one which needs to be pursued with more vigor.

The quantitative or numerical approach to biostratigraphy has only occasionally been applied to Paleozoic biostratigraphy. Graphic Correlation, as developed by Shaw (1964), shows considerable potential for refined biostratigraphic zonation and correlation, and to express time equivalence between stratigraphic sections. The technique is based on interpretation of graphic plots of first- and last-occurrences of taxa. Edwards (1984), using simulated data, demonstrated that the method is sound.

Sweet (1984), for example, used graphic-correlation to establish a stratigraphic standard for the Middle and Upper Ordovician of the eastern North American Midcontinent Realm. Sweet's composite stratigraphic section representing about 37 million years is divisible into 80 Standard Time Units (STU) based on conodont ranges, an average of about 462,500 years per zone. These 80 STUs, by comparison, correspond to four zones and subzones of the North Atlantic Realm.

Finally, it is clear that biofacies analysis is an integral part of biostratigraphy (see also Ludvigsen *et al.*, 1986; Ludvigsen, 1989). The utility of various zonal nomenclatures and the limits to regional and inter-regional correlation can be fully understood only in an environmental and ecological context, and it is for that reason that the influence of biofacies patterns is emphasized in this paper.

PALEOZOIC BIOSTRATIGRAPHY

The Paleozoic world was profoundly different from the present one. It differed not only in the obvious faunal and floral differences, but also in continental and oceanographic configurations, all of which changed throughout the era. The Paleozoic world also differed strikingly in the presence of vast epicontinental seas, some with broad cratonic shelves. For more than the first half of the era, anoxic basins (often equated with dark, organic and pyrite-rich "graptolitic shales") were prevalent and widespread along continental margins. The North American paleocontinent (Laurentia) which lay within tropical and subtropical zones was, for example, covered by huge, north-south trending (relative to the current continental configuration) seas, the bottoms of which were often anoxic and excluded benthic faunas. Carbonate environments prevailed on the cratons and along the basin margins. The carbonates hosted richly diverse shelly faunas, including corals, brachiopods, stromatoporoids, bryozoans, echinoderms, conodont animals, and trilobites. During the Carboniferous and Permian, large, calcareous foraminfers and rich terrestrial floras were added to the overall biota. Basinal and slope faunas were dominated by graptolites during the the Ordovician to Lower Devonian, ammonoids (Lower Devonian to end of Permian), to some extent by conodonts and trilobites and, locally, during the Silurian and Devonian, by dacryoconarid tentaculitids.

In addition to major changes in the paleogeography of the continents and oceans, the Paleozoic world underwent two major climatic cycles: the "greenhouse" condition of the Ordovician to Devonian (interrupted by a brief latest Ordovician southern hemisphere glacial event), followed by a general worldwide cooling during the "icehouse" event of the Carboniferous and Permian (Fischer, 1984). All of these had profound effects on the evolution and distributions of the world's biota and, therefore, their biostratigraphic potential (see discussions in Johnson, 1971; and Johnson and Sandberg, 1988).

One of the challenges facing a biostratigrapher is that of provinciality: the existence of two or more globally distributed biogeographic realms which were influenced to a great extent by global climates and continental configurations. During periods of high cosmopolitanism, comparable biotic communities occupying similar environments are widely distributed over the Earth. At such times, genera and species, zonal assemblages, and even entire zonal successions are highly similar over large areas of the world, permitting long-range, precise correlation. For example, Llandovery graptolites, most Silurian conodonts, and Upper Devonian conodonts and brachiopods, are very widespread and strikingly similar. Refined correlation at these times is attainable.

During times of high provinciality, endemism is high, and a community of one realm shares few, or no, elements in common with that of other realms. Inter-provincial correlation may, therefore, be difficult. For example, late Arenig and early Llanvirn graptolites, Emsian brachiopods, Middle to Late Cambrian trilobites, and Late Ordovician and Late Permian conodonts differ considerably from province to province. During the Emsian, for instance, at least three separate brachiopod provinces prevailed (Johnson and Boucot, 1973).

Fortunately, however, the biogeographic boundaries of one group do not always closely coincide to those of another organismal group and, as a result, inter-provincial correlation can, in most instances, be achieved directly or indirectly. For instance, during the late Pragian and early Emsian, when brachiopod (and coral) provinciality was at a maximum, inter-provincial correlation of the brachiopod faunas is achieved using graptolites and conodonts, when present in the same beds.

Biofacies differentiation offers perhaps the greatest challenge facing the biostratigrapher. Differences in organismal preferences for factors such as water temperature, depth and chemistry (*e.g.*, salinity), nutrients, food and substrate differences, can lead to the establishment of a series of biofacies along an environmental gradient. The well-known Silurian brachiopod biofacies ("communities") recognized by Ziegler (Ziegler *et al.*, 1968; see also Fürsich and Hurst, 1974 for a discussion of the underlying environmental factors) are a classic example of this type of distribution pattern.

High levels of biofacies differentiation limit the areal extent over which zones may be recognized, even within a single basin. In any biofacies-lithofacies grouping, the numerically dominant taxa offer the best basis for zonations, simply because they have the highest probability of discovery in stratigraphic sections. Consequently, zonations tend to be biofacies specific, so that several parallel zonal schemes will be needed to adequately characterize the biostratigraphy within each biogeographic province (see Ludvigsen *et al.*, 1986 for further discussion). At least a few species will be shared between adjacent biofacies, so that correlations between local zonations can be established. Ludvigsen *et al.* (1986) termed this approach "dual biostratigraphy" in order to emphasize that both the environmental and temporal distributions of faunas must be considered in a complete biostratigraphic analysis.

Correlations between biozonations established for different biofacies are attainable because some taxa range well outside their preferred habitat, albeit in generally lesser abundance. For example, species and subspecies of the brachiopod *Eocoelia*, one of the key elements of the *Eocoelia* community, are found sparingly in the deeper water *Pentamerus* and *Stricklandia* communities (Ziegler *et al.*, 1968), permitting correlation among the three adjacent communities. Furthermore, environmental ranges of one organismal group, whether pelagic or benthic, need not coincide with those of another and, in fact, may be markedly different. Rare occurrences of one group in biofacies dominated by another provide important aids to correlation: for example, graptolites and/or conodonts within two or more shallow-water brachiopod or coral-dominated biofacies.

Integration of data from several fossil groups provides the best basis for biostratigraphic correlation, and this approach is strongly advocated (see "A Correlation Puzzle").

For this paper, no attempt has been made to cover or survey all, or even most, Paleozoic organismal groups; rather, a few groups of different life habits and strategies are examined in more detail. Groups examined comprise graptolites, brachiopods, conodonts, palynomorphs and trilobites.

Graptolites, representative of Paleozoic plankton, have long been considered as near-ideal biostratigraphic tools, at least for basin and basin margin settings. Overall, species ranges are short and species diversity was high throughout most of their existence. Ordovician faunas, especially those of the Arenig and Llanvirn as well as those of the Llandovery, show particularly high diversity. During such times of high diversity, zonal assemblages may comprise as many as 20-30 species, whereas during times of low diversity, as for example, the mid-Wenlock, Pridoli and Lower Devonian, individual zones may contain no more than two or three species.

Brachiopods, representing sessile benthos, were abundantly diverse and widespread throughout most of the Paleozoic, and most of the principles of paleocommunity analysis derive from Paleozoic brachiopods. Most individual brachiopod species are relatively long-ranging, but because of their collective overall abundance and high diversity in sequences of strata, are very amenable to the so-called assemblage zone approach. Correlation at the stage level is generally readily attainable. Some taxa (genus or species group), however, underwent rapid evolution and are capable of fine time resolution.

Conodonts, which range through the Paleozoic, are representative of Paleozoic nektobenthic and pelagic organisms which underwent rapid evolution. They ranged over much wider lithotopes than occupied by purely benthic organisms and, at times, their biostratigraphic precision equals, or even surpasses that, of graptolites. During parts of the Ordovician and during the late Devonian (Frasnian and Famennian), for example, their precision is unrivalled.

Carboniferous and Permian palynomorphs include spores, pollen, acritarchs and scolecodonts. Most extensively studied are spores and pollen derived from land plants, and these form the basis of most late Paleozoic palynological zonations. Spores and pollen, being dispersed by wind and transported by water, may be present in a variety of continental and sedimentary facies, thus making them valuable for correlation across facies boundaries and in areas where other fossil groups may be affected by local phenomena, such as water temperature or salinity (Traverse, 1988).

Trilobites also underwent rapid evolutionary turnover, especially during the Cambrian, and provide the basis for finely divided zonations. They have been used widely and successfully for correlation of Lower Paleozoic sequences across a variety of lithofacies within individual faunal provinces. Global correlation is often hindered by high degrees of provincialism, although Cambrian agnostid trilobites, which tend to be more cosmopolitan in distribution, have shown promise for global correlation of at least deep shelf and basinal facies.

A number of other groups are equally capable of high-resolution biostratigraphy. They are not discussed in this paper, a fact related only to the expertise of the contributors. Nevertheless, for the interested reader, a number of important groups and relevant citation(s) are included as follows: Carboniferous and Permian large calcareous foraminifers: Mamet (1977), Douglass (1977); Devonian ammonoids as representative of Paleozoic ammonoids: House (1962) and Chlupač and Turek (1983); Chitinozoa: Grahn (1982); dacryoconarid tentaculitids (especially Devonian representatives): Lardeux (1969); and Devonian acritarchs: Playford (1977).

The various sections of this paper are written by the following: introduction and graptolites are by A.C. Lenz, brachiopods are by J. Jin, conodonts are by A.D. McCracken, palynomorphs are by J. Utting, and trilobites are by S.R. Westrop.

GRAPTOLITES

Biostratigraphy and Biogeography

Graptoloid graptolites ("true" graptolites) flourished from almost earliest Ordovician (Arenig) until approximately mid-Early Devonian (end of Pragian). Because of rapid evolution and widespread distribution, graptolites are, arguably, the finest interbasinal biostratigraphic tool for the Lower Paleozoic basinal and slope environments (see discussion of principles of graptolite biostratigraphy in Berry, 1977), although their use in shallow, platformal environments may be limited.

The monumental studies of Elles and Wood (1901-1918) clearly demonstrated the biostratigraphic potential of graptolites for basin and basin-margin facies, and firmly laid the groundwork for graptolite zones and zonation. During the last thirty years, sparked, in part, by exploration of more remote regions of the world (*e.g.*, northern and Arctic Canada, northern and northeastern regions of Russia and Siberia, Kazakhstan and China) and, in part, by the stimulus of international studies on geologic systems and systemic boundaries, a vast amount of new data have been amassed. These continuing studies demonstrate that in basinal environments at least, graptolites are excellent correlation tools, and permit increasingly precise zonation and correlation of graptolitic sequences. As an example, the northern Yukon zonal scheme of Jackson and Lenz (1962) comprised 23 Arenig to Pragian (Lower Devonian) biozones, whereas there are now 50 spanning this 100 million year interval (Lenz, 1982, 1988a, 1988b; Lenz and Chen, 1985b; Lenz and Jackson, 1986; Lenz and McCracken, 1982). Even greater temporal refinements have been attained in the Silurian of the British Isles, where 30 zones are recognized (Rickards, 1976) in the Llandovery through Ludlow, an interval of approximately only 20 million years.

The use of graptolites as globally effective biostratigraphic tools is highly dependent on their biogeographic distribution. Graptolite species and genera exhibit a broad degree of cyclicity in the extent of global distribution; that is, there was oscillation between periods of cosmopolitanism and provincialism (Fig. 1). During the periods of cosmopolitanism, global correlation is realized, whereas during times of endemism, correlation may not extend beyond the boundaries of the individual provinces.

The *Tetragraptus approximatus* Zone of the early Arenig, the *Nemagraptus gracilis* Zone beginning in the late Llandeilo, almost all of the Llandovery with the exception of the uppermost zone, the early Ludlow *Neodiversograptus nilssoni* Zone, and part of the Lower Devonian were, for example, times of cosmopolitanism distributions of many species and species assemblages. Long-distance correlation of great accuracy, in the order of one million years or less per zone, is possible during these times.

Particularly striking are the *Nemagraptus gracilis* Zone, and the many zones of the major portion of the Llandovery. The *N. gracilis* Zone exhibits a near-global distribution in basinal and basin-margin facies (Fig. 2b), contains many co-occurring species (Finney, 1984; Cooper and Lindholm, 1990), and

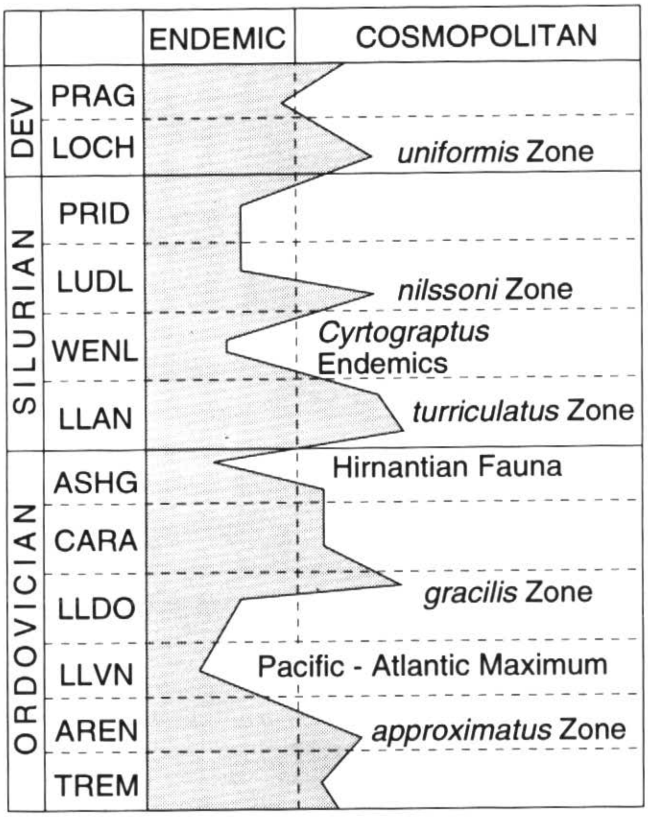


Figure 1 ***(above)*** *Chart showing alternation of periods of global endemism and cosmopolitanism in Ordovican to Early Devonian graptolites. Times of high endemism and cosmopolitanism are given specific labels, most of which are discussed in the text.*

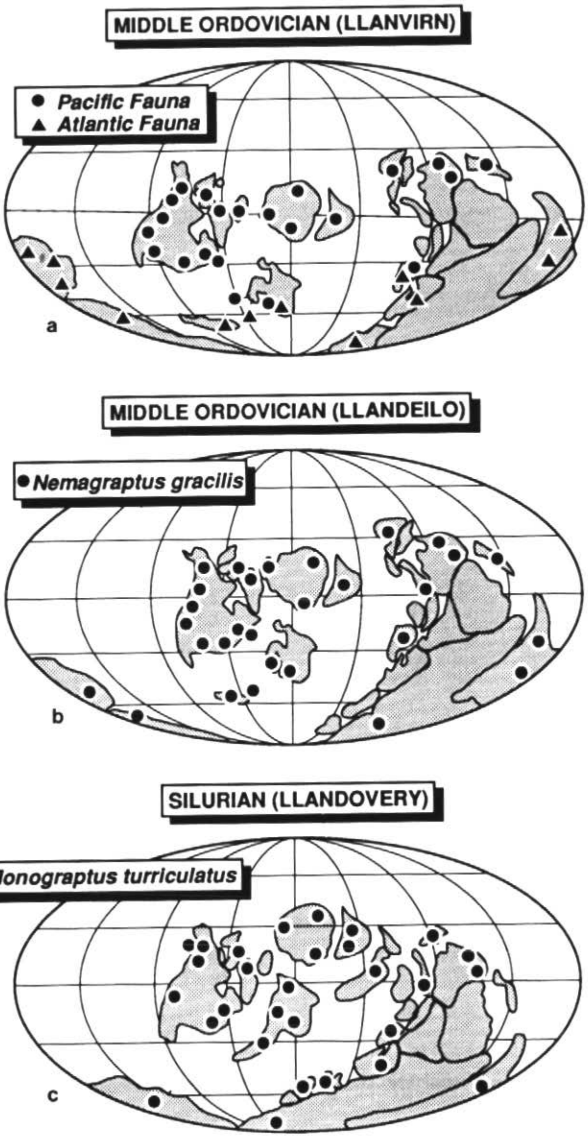


Figure 2 ***(right)*** (**a**) *Early Ordovician continental configurations showing the low-latitude distribution of the graptolites of the Pacific Faunal Province and mostly high-latitude position of the graptolites of the Atlantic Faunal Province. Continental configurations from Scotese and McKerrow (1991).* (**b**) *Early Middle Ordovician continental configurations showing the widespread distribution of* Nemagraptus gracilis. *Continental configurations from Scotese and McKerrow (1991).* (**c**) *Early Silurian continental configurations showing the high to low latitude distributions of* Monograptus turriculatus. *Continental configurations from Cocks and Scotese (1991).*

is a fine example of a widely applicable graptolite biozone. More striking are the sequences of faunas of all but the uppermost Llandovery, most of which are very widely distributed and precisely correlatable (see distribution of *Monograptus turriculatus*, Fig. 2c). A comparison of species, zonal sequences, and zonal assemblages shows them to be highly similar in regions as widely spread as northern Yukon (Lenz, 1982), Arctic Canada (Melchin, 1989), British Isles (Rickards, 1976), Siberia (Obut and Sennikov, 1977), Baltics region (Paskevicius, 1979), and China (Wang, 1987).

The late Pragian time is a particularly interesting one for the graptolites. At that time, just prior to their extinction, graptolite species-diversity was moderate, having increased dramatically from the impoverished underlying zones. They were distributed across many areas of the world (Cordilleran and Arctic North America, central Europe, north Africa, Australia, Thailand, southern China, Tibet (= Xizang), Timan, Kazakhstan and a number of localities in northeastern Siberia). In spite of increasing provincialism among benthic organisms (*e.g.*, brachiopods: Johnson, 1971; rugose corals: Oliver and Pedder, 1979), the value of these last graptolites as biostratigraphic tools is undiminished, a suggestion supported by their consistent association with particular species of conodonts (Klapper, 1977) and dacryoconarid tentaculitids (Lütke, 1979).

Graptolite endemism was high during the late Arenig to late Llanvirn, late Ashgill, and approximately the mid-Wenlock; moderately so during the late Ludlow and early Pridoli; and weak during the late Lochkovian and early Pragian. Most striking is the period of late Arenig to late Llanvirn (late Lancefieldian to late Darriwillian of the Australasian stage terminology: Fig. 3), during which time endemism was particularly pronounced. During that time, the graptolite world comprised two main and approximately equal-sized faunal provinces, the predominantly warm-water and carbonate-rich Pacific Province (Skevington, 1974, 1976; see also Scotese and McKerrow, 1991 for Ordovician continental configurations) and the mostly higher-latitude and cooler-water Atlantic Province (Fig. 2b). The faunas of the former are well known from, for example, Australasia (Cooper, 1979; Cas and Vandenberg, 1988), Canadian Cordillera (Lenz and Jackson, 1986; Lenz, 1988a), Newfoundland (Williams and Stevens, 1988), Texas (Berry, 1960), Great Basin (Ross and Berry, 1963), and northern Greenland (Bjerreskov, 1989), as well as from Siberia, Kazakhstan and south China. The various regions of the Pacific Province contain, overall, remarkably similar faunas and zonal assemblages, including distinctive elements as *Oncograptus* and *Cardiograptus*, and the various subspecies of the *Isograptus victoriae* group, a fact permitting highly precise intra-provincial correlations (Cooper and Lindholm, 1990).

	AUSTRALASIA	YUKON	S. BRIT. ISLES	
GISB	*gracilis*	*gracilis*	*gracilis*	LD
DAR	*euglyphus* *interstitus* *austrodentatus*	*teretiusculus* *decoratus* *tentaculatus*	*murchisoni* *artus* *hirundo*	LLVN
YAP	*crudus* *morsus* *upsilon*	*Oncograptus*	*gibberulus*	A R E N I G
CAS	*maximus* *victoriae* *lunatus*	*maximus* *lunatus*	*nitidus*	
CH	*protobifidus*	*protobifidus*		
BE	*fruticosus*	*fruticosus*	*deflexus*	
LA	*approximatus*	*approximatus*		

Figure 3 *Correlation chart comparing Australasian stages and zones of Australasia and Yukon (Pacific Faunal Province) with those of the classic southern British sequence (Atlantic Faunal Province). After Cooper and Lindholm (1990), Lenz and Chen (1985b), Lenz and Jackson (1986).* ***LA****, Lancefieldian;* ***BE****, Bendigonian;* ***CH****, Chewtonian;* ***CAS****, Castlemanian;* ***YAP****, Yapeenian;* ***DAR****, Darriwilian;* ***GISB****, Gisbornian;* ***LLVN****, Llanvirn;* ***LD****, Llandeilo.*

By comparison, graptolite faunas of the the Atlantic Province which are demonstrably shown to be coeval by associated conodont faunas (Bergström and Cooper, 1973; see also "A Correlation Puzzle" herein) and by rare occurrences of mixed faunas such as found in southern Sweden (Cooper and Lindholm, 1990), comprise the classic graptolite regions of southern Britain, most of western continental Europe, northern Africa, South America, and "central" China (Fig. 2a). These faunas are only moderately diverse and yield high abundances of robust "tuning fork" (*e.g.*, *Didymograptus (Didyomograptellus) murchisoni, D. (D.) artus*, and related species) and abundant extensiform-type of didymograptids.

Other times of endemism at a lesser level, include those of the late Ashgill, and the mid-Wenlock. Late Ashgill (*i.e.*, the Hirnantia-fauna interval) was a time of southern hemisphere glaciation (Beuf *et al.*, 1971), the results of which had a profound effect upon global faunas, including graptolites (see Sheehan, 1973, 1988 for a discussion of the overall faunal changes at that time; and Melchin and Mitchell, 1991, for a discussion of the graptolites). Endemism at the species level was moderately high, and correlation among various regions such as, for example, Arctic Canada, southern China, Australia, northeastern Siberia, and the British Isles, is impaired by the absence of widely distributed co-occurring species.

The Wenlock is marked by the almost universal occurrence of many species of the genus *Cyrtograptus* (Fig. 4). Some species of this genus were more or less cosmopolitan in their distribution during Early and Late Wenlock permitting good correlation at these times. During about mid-Wenlock, however, cyrtograptids briefly disappear from western Europe, but appear to have been continuously present and to have evolved local species in Arctic Canada and eastern Siberia (see Lenz and Melchin, 1989). Precise long-range correlation between the Arctic regions and, for example, western Europe, is difficult during this time interval.

Graptolite Biofacies and Lithofacies Controls

Graptolite occurrences are not, as once believed, independent of lithofacies, a fact that has become abundantly clear in recent years (Lenz and Chen, 1985a). Paleoecological analysis of graptolites is extremely difficult and the rocks containing their remains reveal little of their habitat or habitat preferences for two reasons. First, graptolites were pelagic and they could have been subjected to long-distance post-mortem transport. Second, and more importantly, "communities" would have been mixed during their post-mortem descent to the sea floor. It is well recognized that the highest diversity faunas occupied deep water "black shale" environments (Finney, 1984; Cooper, 1979; Ross and Berry, 1963; Lenz, 1982; Lenz and Jackson, 1986; Lenz and Chen, 1985a; Melchin, 1989, and especially Cooper *et al.*, 1991). However, even in these environments, diversity and compositional differences appear to more or less parallel those of the regional lithofacies. Finney (1984) demonstrated noteworthy differences between faunas occurring in deep water "black shale" facies and those in nearby and adjacent shallower calcareous shale facies.

Detailed studies of Silurian rocks and graptolites in the Baltic region (Paškevičius, 1979), perhaps the most intense and detailed regional ecostratigraphic study across a broad array of lithotopes to date, are illustrative. They show that maximum species diversity occurs in the faunas of basinal and basin-margin grey, greenish-grey and black shales, which also include many delicate species. In contrast, species found in the shallowest platformal carbonates comprise long-ranging and robust morphs such as *Monograptus priodon, Retiolites geinitzianus,* and large *Monoclimacis.*

The problem is further emphasized by a comparison of faunas of the classical North American Cincinnatian Series (Bergström and Mitchell, 1986; 1990) and the similar faunas of the St. Lawrence Valley (Riva, 1969, 1974) with those of either the basin or basin-margin faunas of the Appalachian Trough, or the continental margins of the North American Cordillera. The first faunas, termed "mid-continent" faunas, are of only moderate diversity and comprise mainly biserial forms (Mitchell and Bergström, 1991), whereas different biserial species and a rich population of *Dicellograptus, Dicranograptus* or *Leptograptus* are present in the basinal and/or continental margin settings. Correlation between these graptolite faunas is difficult (Bergström and Mitchell, 1986).

Relatively rare occurrences of Middle to Late Ordovician graptolite faunas of the North American shallow-water epicontinental carbonate sequences probably represented the extreme limits of graptolite tolerances. Hudson Bay (Jackson, 1973), northwestern Hudson Bay (Jackson, 1971), Akpatok Island (Cox, 1933; Workum *et al.*, 1976), Anticosti Island (Barrass, 1954), southern Baffin Island (Miller *et al.* 1954) and northeastern Ontario and adjacent Quebec (Foerste, 1924) have yielded well-preserved graptolite faunas, most of which are biserials of low species diversity. Correlation of these strata with other faunas in a similar cratonic setting, or with those in deeper-water lithofacies solely by means of their contained graptolites has not been achieved with satisfaction.

To account for the differences in graptolite litho- and biofacies, Berry and Boucot (1972) suggested that different species and morphotypes occupied different water depths; to these, Finney (1984) added a factor that he termed "water-mass specificity". Recently, Cooper *et al.* (1991), in a comprehensive study to account for Early Ordovician distributions, proposed that graptolites occupied a near-surface, oxygen-rich epipelagic zone, an intermediate depth, mesopelagic zone, and possibly a deep bathypelagic zone, the latter two being oxygen-poor, but diversity rich. They further recognized a somewhat ill-defined, low-diversity, inshore zone as a subdivision of the epipelagic zone.

In developing an actualistic model for the distribution of graptolites, Berry *et al.* (1987, and references therein) suggest that the oceanward projecting, below-surface, nitrate- and bacteria-rich tongues of waters on either side of the equator along the Pacific side of South America serve as good analogs for graptolite habitats, at least for those graptolites inhabiting moderate depths. Further, they suggest that with the long-term stability and equitable climates characteristic of most of the Ordovician

Figure 4 Cyrtograptus sakmaricus Koren, *from Arctic Canada. (Hypotype GSC 57523). Species of this genus are the main paleobiological tools for the zonation of latest Llandovery to late Wenlock strata and are widely distributed throughout the world.*

and Silurian, the depth and geographic distribution of the nitrate-rich, oxygen-depleted waters would be much more pervasive than at present.

The Berry *et al.* (1987) and Cooper *et al.* (1991) models, however, do not fully account for the distribution of some graptolites, in particular those low-diversity faunas found in far-inshore positions on very broad, shallow, platformal areas such as referred to above. A slight modification and extension of these models is proposed herein (Fig. 5).

It is suggested that in regions with very broad and gently sloping carbonate-rich areas, such as on the North American craton, only a few hardy species could thrive in the these regions of probably greater physical stress. Representatives include robust biserials in the Ordovician, and *Monograptus priodon* types and large monoclimacids in the Silurian, (species groups A and B of Fig. 5). Faunas B-E (Fig. 5), from the more offshore, less turbulent, but oxygen-rich near-surface waters would correspond to typical epipelagic faunas of Cooper *et al.* (1991). Silurian representatives of this ecotope include *Monograptus priodon* and other robust similar morphotypes, large retiolitids such as *Retiolites geinitzianus*, and probably a few robust cyrtograptids. Faunas F-R comprise high-diversity, low-oxygen-tolerant (or -loving) species comparable to those of the mesopelagic zone. Further, however, nitrate-rich, oxygen-poor waters might not so consistently and pervasively extend onto the intermediate-depth shelf margin, permitting the division into moderate-depth faunas F-L, and the consistently deeper-water faunas I-R (Fig. 5). The subtle differences in Appalachian Ordovician faunas discussed by Finney (1984) and Silurian faunas from northern Yukon described by Lenz and Chen (1985a) could fall into these two categories.

In this scenario (Fig. 5), the graptolite fossil record would (or could) record, at least, three coeval assemblages: 1) the very distinctive, low-diversity, shallow-water, platformal faunas (species groups A and B), 2) a moderate-diversity fauna of the more offshore, but near-surface and the intermediate depth assemblages (species groups B-E plus F-L), and 3) a high diversity, offshore deep water assemblage: the near-surface plus the deep-water species (species groups B-E plus I-R). Thus, graptolites of assemblage 1 and those of the more offshore, near-surface, taxa B-E, are generalized and eurytopic, and of low biostratigraphic potential; those of assemblages 2 and 3, comprising both eurytopic (B-E) and stenotopic species (F-L and I-R), have excellent biostratigraphic potential because of the rapid evolution of the stenotopic taxa.

BRACHIOPODS

Brachiopods constitute one of the most abundant and diverse groups in the Paleozoic fossil record, and they occur in nearly the entire array of marine sedimentary facies, from clastic to carbonate and shallow shelf to basinal. Articulate brachiopods in the Cambrian formed only minor parts of the benthic communities and are, therefore, of little biostratigraphic value, but inarticulate brachiopods have been used successfully to establish zones in the Upper Cambrian (*e.g.*, Kurtz, 1971). In the Ordovician to Devonian, articulate brachiopods became one of the major components of marine shelly faunas and have been used widely for biostratigraphic studies. Many groups of brachiopods become extinct near the end of the Devonian, and some others, especially the spiny or bizarre-shaped productids and chonetids, flourished in the carbonate shelf and reef environments during Carboniferous and Permian times. In the following discussion, particular groups in the Silurian will be used to illustrate various aspects of Paleozoic brachiopod biostratigraphy.

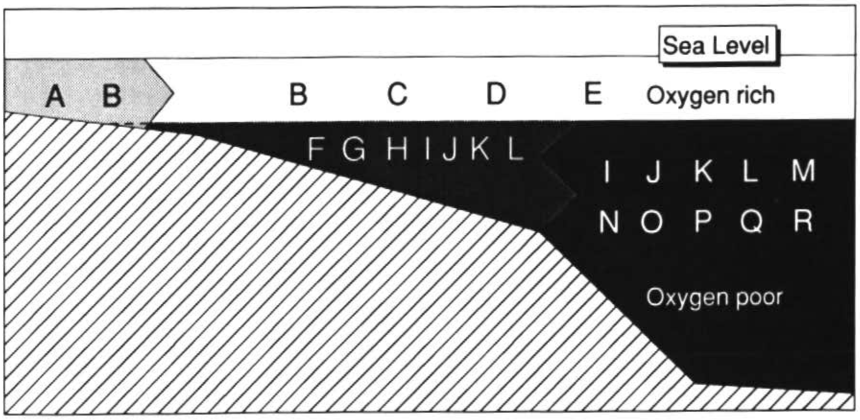


Figure 5 *Paleoecological interpretation of graptolite distributions. Species faunas A and B are of low diversity and mainly confined to broad, shallow, epicontinental, platformal areas; species faunas B to E are of low to intermediate diversity and are widespread, near-surface dwellers. Species faunas F to R are very widespread, deep water, and rapidly evolving faunas, with preferences for oxygen-poor, nitrate-rich waters. Potential fossil (seafloor) assemblages would comprise 1) species A and B on the shallow, platformal floor; 2) species B to E plus F to L on the intermediate depth, slope-margin floor; and 3) species B to E plus I to R on the deep water, basin- and basin- margin floors.*

Silurian Brachiopod Biostratigraphy

Brachiopods have been used in biostratigraphy most effectively in three ways:
1) unique associations or assemblages of numbers of taxa (including faunas, "communities") used as the bases for establishing biozones (the assemblage zone of the North American Stratigraphic Code, 1983),
2) short-lived but widespread individual species or genera serving as "index fossils" or as the bases for biozones,
3) rapid turnover and species replacement within a single genus or genus group in which the first appearance of each succeeding species forms the base of a biozone.

Assemblage Biozones

The importance of brachiopods in biostratigraphy lies in their overwhelming abundance and diversity, especially in Ordovician, Silurian and Devonian shallow-water carbonate sequences. Cooper's (1956) work on Middle and Late Ordovician brachiopods, for example, greatly improved the understanding of the Chazyan through Trentonian strata of North America, although later studies of conodonts have further refined the biostratigraphic correlation of these rocks.

Sophisticated delineation and correlation of brachiopod biozones have been applied successfully to some Devonian rocks. In central Nevada, for example, Johnson (1977, 1979) and coworkers (Johnson and Niebuhr, 1976; Johnson *et al.*, 1980) were able to recognize 30 faunal intervals, based on brachiopod zones and faunas (recently expanded into 46 brachiopod-dominated communities by Johnson (1990) based on numerical abundance data). These brachiopod biozones have been directly correlated with the conodont biozones of the same region. Some of the biozones attain a resolution equal to, if not higher than, the conodont biozones. Unfortunately, many of these biozones are largely endemic to Nevada and southeastern California and cannot be correlated precisely with coeval brachiopod faunas in other regions of North America, or elsewhere.

Index Taxa

Study of the *Virgiana* faunas has greatly helped to refine correlation of the lower Llandovery (Rhuddanian) carbonate rocks of North America (Berry and Boucot, 1970). Most species of *Virgiana* are characterized by relatively large, coarsely ribbed, posteriorly rounded and umbonally much-thickened shells (Fig. 6a, b), which commonly occur in rocks indicating shallow and turbulent water conditions, associated with such sedimentary structures as channelling, scour and fill, cross-stratification, and common coquinas of broken *Virgiana*

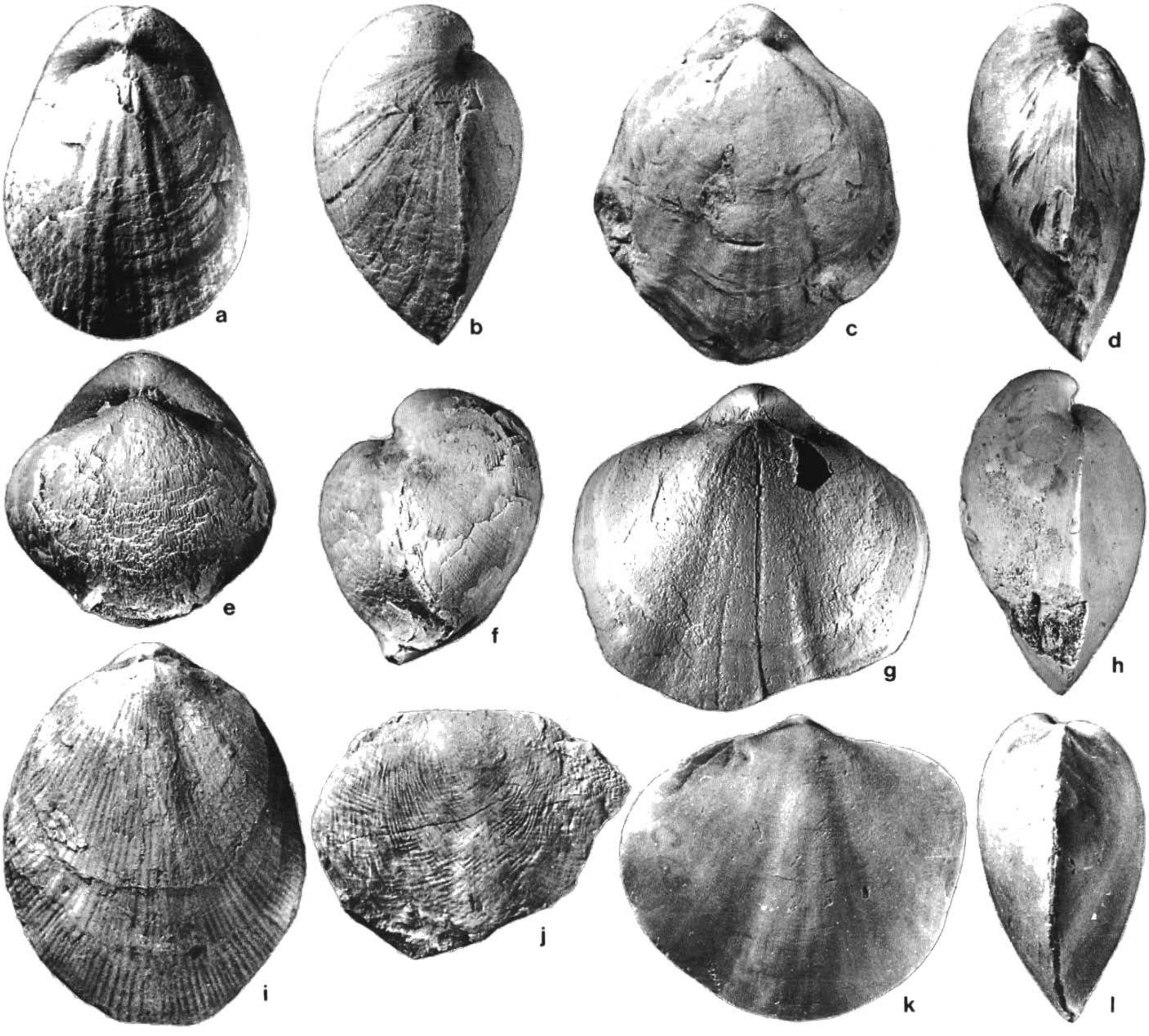


Figure 6 *Characteristic pentamerid brachiopods of Early Silurian age.* (**a, b**) Virgiana barrandei *(Billings, 1857), lectotype GSC 2372b, Becscie Formation, Anticosti Island, Quebec, 1.2×.* (**c, d**) Pentamerus oblongus *(J. de C. Sowerby, 1839), hypotype GSC 59165, upper Jupiter Formation, Anticosti Island, 1.2×.* (**e, f**) Clorinda tumidula *(Billings, 1866), hypotype GSC 95508, lower Attiwapiskat Formation, Ekwan River, Hudson Bay Lowlands, 3×.* (**g, h**) Pentameroides septentrionalis *(Whiteaves, 1904), type GSC 95499, Attiwapiskat Formation, Attiwapiskat River, Hudson Bay Lowlands, 1.5×.* (**i**) Costistricklandia gaspeensis *(Billings, 1859), lectotype GSC 3047a, Gaspésie, Quebec, 0.68×.* (**j**) Kulumbella biconvexa *Nikiforova, in Nikforova and Andreeva, (1961), hypotype GSC 59174, upper Gun River Formation, Anticosti Island, 1.43×.* (**k, l**) Stricklandia lens intermedia *Williams, 1951, hypotype GSC 59176, lowermost Jupiter Formation, Anticosti Island, 1.4×.*

shells (Sheehan, 1980a; Copper, 1981; Jin and Caldwell, 1991).

With the ending of the latest Ordovician glaciation in the southern hemisphere (for recent summary, see Sheehan, 1988) and the beginning of the Early Silurian transgression, the shallow-water (intertidal to upper subtidal) *Virgiana* communities evolved abruptly, dispersed widely in North America and Siberia, and disappeared by latest Rhuddanian-earliest Aeronian time. As a result, various species of *Virgiana* have served as excellent biostratigraphic tools.

Intercontinental correlation can be shown by the co-occurrence of *Virgiana barrandei* from both Anticosti Island and the Siberian platform, where the *Virgiana*-bearing beds from both regions are correlated with the late Rhuddanian *Coronograptus cyphus* Zone (Copper and Long, 1989; Lopushinskaya, 1976, respectively). During the Late Ordovician and Early Silurian, both North America and Siberia were stable carbonate platforms covered by shallow epicontiental seas. Destruction and closure of the Iapetus Ocean in the late Silurian time probably pulled North America and Siberia, as well as northern Europe (Baltica), close together (Pickering *et al.*, 1988). With the onset of marine transgression after the terminal Ordovician glaciation, the *Virgiana* faunas probably followed the shallow-water environment and spread onto both continents.

A similarly short-lived but widespread genus is the middle Llandovery stricklandiid *Kulumbella* (Fig. 6j) originally described from Siberia (Nikiforova and Andreeva, 1961; Lopushinskaya, 1976). The genus, found in abundance in only the upper Gun River Formation (lower Aeronian) of Anticosti Island (Jin and Caldwell, 1991), also occurs in rocks of the same age in Estonia (Rubel, 1970), Greenland (Hurst and Sheehan, 1982), and South China (Rong and Yang, 1981).

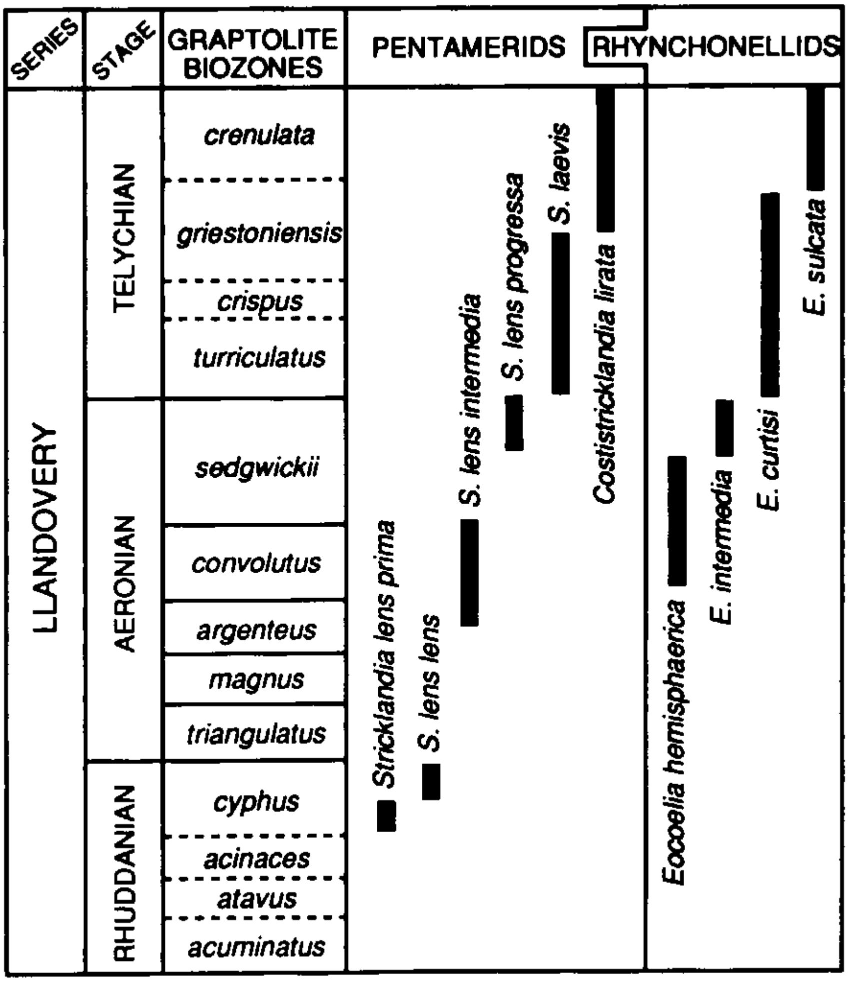


Figure 7 *Correlation of standard graptolite biozones with brachiopod biozones in the Llandovery type area, Llandovery, Wales. (Modified after Cocks* et al.*, 1984).*

Rapid Turnover and Species Replacement in a Single Genus

Although brachiopods generally show slow rates of evolution, some genera are known to have speciated rapidly and spread widely and, therefore, can be used as the basis for establishing biozones. In Llandovery time, the large-shelled pentamerids, *Pentamerus* and *Stricklandia* (Fig. 6c, d, k, j) and the small-shelled rhynchonellid, *Eocoelia*, flourished in shallow shelf environments and epicontinental seas of North America, Siberia-Kazakhstan, northern Europe, and South China. Average duration of species in these stocks is unusually short, approaching that of contemporaneous graptolite species. As shown in Figure 7, the five species or subspecies of *Stricklandia* in the Llandovery Series had an average span of 2 m.y., and the four species of *Eocoelia* in the late Aeronian and Telychian probably had an even shorter one. These short-ranged successions have proven to be valuable tools for regional, and even global, correlations.

Careful study of brachiopod morphological and speciation trends has lead to important biostratigraphic implications. In the type area for the Llandovery Series, Wales, rapid evolution in two generic groups, *Stricklandia-Costistricklandia* and *Eocoelia*, have been used as bases for biozones supplementary to the standard graptolite zones (Cocks *et al.*, 1984). Speciation trends in *Stricklandia* to *Costistricklandia* were first examined by Williams (1951), who identified a number of stratigraphically related directional trends including, 1) increase in the strength of the shell costae, 2) reduction of the outer brachial plates, and 3) enlargement of the cardinalia (see also Rubel, 1977). A quantitative biometric re-evaluation of the *Stricklandia* stock by Baarli (1986) has confirmed the validity of the *Stricklandia-Costistricklandia* trends, although one of the trends (enlargement of cardinalia) was regarded by Baarli as ecologically controlled. In the Llandovery type area, the two earliest subspecies of the lineage, *Stricklandia lens prima* and *S. lens lens*, are known to be associated with the graptolite *Coronograptus cyphys* Zone (Fig. 7), *S. lens intermedia* and *S. lens progressa* with the *Monograptus convolutus* and *M.*

sedgwicki zones, *S. laevis* with *M. turriculatus* through *M. griestoniensis* zones, and *Costistricklandia lirata* with the *M. griestoniensis* through *M. centrifugus* zones (Cocks *et al.*, 1984). The integration of data between graptolite and brachiopod biozones serves as a crucial tool for correlating of rocks of basinal facies with those of shelf and platform facies, where graptolites are rare or absent. In graptolite-poor carbonate sequences of North America, *Stricklandia* and *Costistricklandia* are common in the Anticosti (Fig. 8: see also Jin, 1984; Copper and Long, 1989) and American mid-continental basins (Johnson, 1979), and along the western marginal platforms. Species- and subspecies-level identification enables reliable correlation of the stricklandiid-bearing beds with those in the Llandovery type area and, ultimately, with the standard graptolite biozones.

The *Eocoelia* succession presents yet another example of the successful application of brachiopod evolution to biostratigraphy. The genus is believed to have lived in shallow-water habitats, probably in the upper subtidal zone (Ziegler, 1965; Boucot, 1975). By examining mainly the collections from British Isles, Ziegler (1966) recognized four successive and short-ranged species, *E. hemisphaerica-E. intermedia-E. curtisi-E. sulcata*, characterized by progressive reduction of shell costae and gradual strengthening of the articulatory mechanism from late Aeronian to earliest Wenlock time. Various species of *Eocoelia* are widely distributed in northern Europe (for example, Britain and Norway), eastern North America (Anticosti Island, Quebec and Nova Scotia; see Ma, 1984), and Siberia (Tunguska region; refer to Nikiforova and Andreeva, 1961). Ma's (1984) detailed study of *Eocoelia* not only confirms the species succession as recognized in Britain, but also recognizes other intermediate forms, in the Jupiter Formation (late Aeronian-early Telychian) of Anticosti Island. In the British Llandovery type area, the specific ranges of *Eocoelia* have been correlated to the standard graptolite zones (Cocks *et al.*, 1984). Indirectly, therefore, correlation of the *Eocoelia* succession from eastern North America with that of Britain is of chronostratigraphic significance.

In North America, dating and correlation of the upper Llandovery carbonate rocks have relied heavily upon the replacement of *Pentamerus oblongus* by *Pentameroides suberectus*. This replacement has been well recorded in the upper Jupiter Formation of Anticosti Island (Jin, 1984), the upper Fossil Hill Formation of Manitoulin Island, Ontario, and the Hopkinson Dolomite of eastern Iowa (Johnson, 1979). Despite the long species duration of *P. oblongus* and *P. suberectus* compared to that of the species of *Stricklandia* and *Eocoelia*, they have been used widely to correlate Lower Silurian rocks because of their unusual abundance and cosmopolitan distribution.

Endemic taxa generally have very limited biostratigraphic value except for local correlations. Recently, however, Jin *et al.* (1990) reported a rapid turnover in the rhynchonellid brachiopod *Fenestrirostra* from the Merrimack and lower Gun River formations (late Rhuddanian) of Anticosti Island. Three successive species, *F. primaeva*, *F. glacialis*, and *F. pyrrha*, show a directed trend of reduction in the strength of shell costae and hinge structures, which may have been adaptive responses to low-energy marine conditions. The evolutionary modifications were unusually rapid for brachiopods, estimated to have been accomplished in less than 1 m.y., with an average species duration of 0.3-0.4 m.y. (Fig. 8). Biostratigraphic application of the fast-evolving *Fenestrirotra* succession, however, is confined to the Anticosti Basin, because the stock has not, as yet, been found in any other regions.

Although there is still some debate as to whether some of the morphological changes recognized in brachiopods are the result of evolution or of ecological control, some genera or species of brachiopods seem more susceptible to

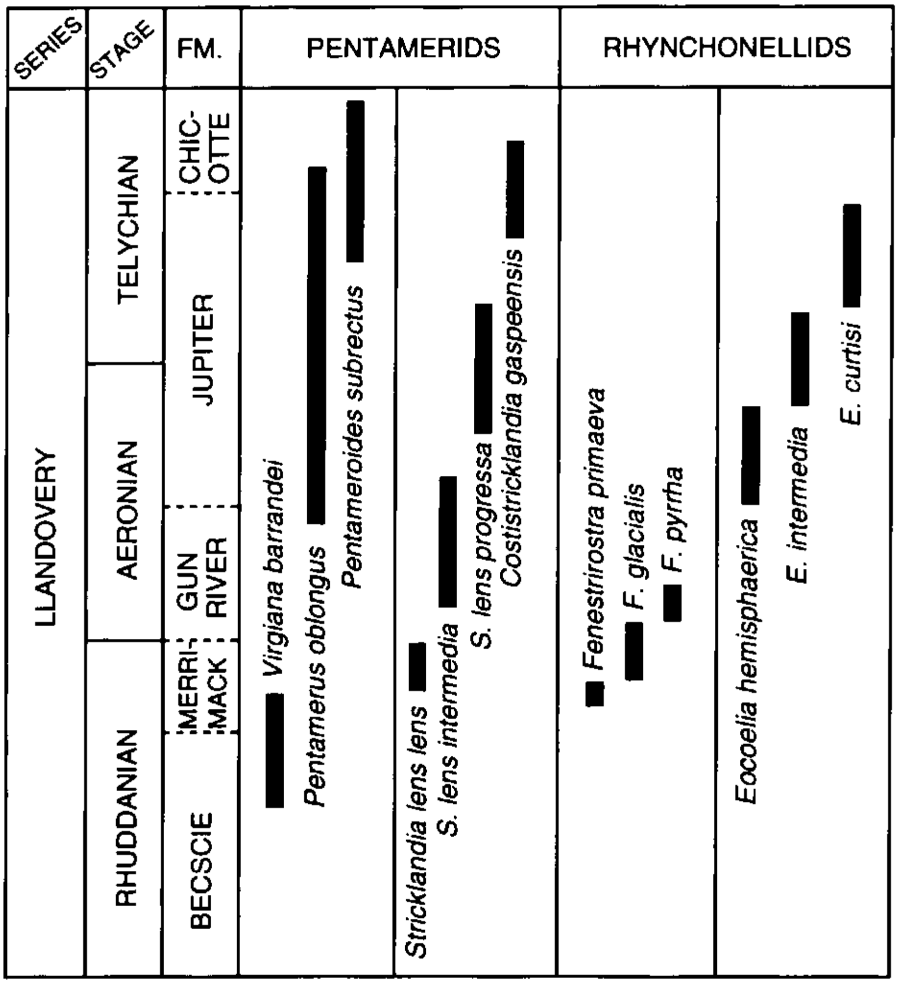


Figure 8 *Occurrences of a succession of four brachiopod species in the Llandovery Series of Anticosti Island, Quebec. (Data from Jin, 1984; Ma, 1984; Copper and Long, 1989; and Jin* et al.*, 1990).*

morphological modification by environmental factors than others. Most species of Early Silurian *Eocoelia, Pentamerus,* and *Stricklandia* stocks, for example, show little ecologically induced variation and can be found virtually unchanged from platform carbonate facies in North America to siliciclastic facies in Wales and the Welsh borderland. On the other hand, the Late Silurian genus *Atrypoidea,* as documented from Arctic Canada by Jones and Narbonne (1984), shows great morphological plasticity controlled by environmental factors. Three morphologically gradational species, *A. phoca, A. foxi,* and *A. bioherma,* have been interpreted to occupy respectively, the low intertidal, shallow intertidal and biohermal zones. Fluctuations in sea level and bathymetry resulted in horizontal shifts and, consequently, an apparent vertical succession of species of *Atrypoidea*. Obviously, these apparent biostratigraphic zones based on successions of environmentally controlled species are analagous to a diachronous rock unit and, thus, much less reliable than biozones based on environmentally more independent species.

Paleocommunities and Paleoecology

Due to their sedentary mode of life, brachiopods constitute one of the fossil groups that is ideal for paleoecological studies. For the Ordovician, Silurian and Devonian periods, numerous brachiopod biofacies have been recognized and reconstructed to indicate various biofacies or substrate conditions (*The Ecology of Fossils* edited by McKerrow (1978) provides an excellent summary). One of the best examples is the reconstruction of Silurian brachiopod biofacies (= "communities" of Ziegler *et al.*, 1968; "benthic assemblages" of Boucot, 1975), which show both vertical succession and lateral replacement in shelf environments (Ziegler, 1965; Cocks and McKerrow, 1978; Johnson and Campbell, 1980; Sheehan, 1980b). In Llandovery time, an array of *Lingula, Eocoelia, Pentamerus, Stricklandia,* and *Clorinda* assemblages spread from intertidal, subtidal, to marginal zones, and merged into the basinal graptolite facies (Fig. 9; for a recent summary, see Pickerill and Brenchley, 1991). Although there is some extent of mixing of characteristic taxa among these benthic assemblages, each assemblage can be recognized by quantitative analysis of species composition (Ziegler *et al.*, 1968). In general, the *Eocoelia, Pentamerus* and *Stricklandia* assemblages are confined to the inner to mid-shelf facies and rarely occur in either the intertidal or basinal facies. By the Wenlock and Ludlow times, the shallow-water habitat of *Eocoelia* was taken over by the *Salopina* assemblage, the deeper-water habitats of *Pentamerus* and *Stricklandia* assemblages were occupied by the *Sphaerirhynchia* and *Isorthis* assemblages, and the marginal *Clorinda* assemblage gave way to the *Dicoelosia* and *Visbyella* assemblages. Because many brachiopod communities could successfully establish themselves in both carbonate and siliciclastic environments, study of these brachiopod associations can provide crucial information for inter-basinal analysis and paleobiogeographic reconstructions.

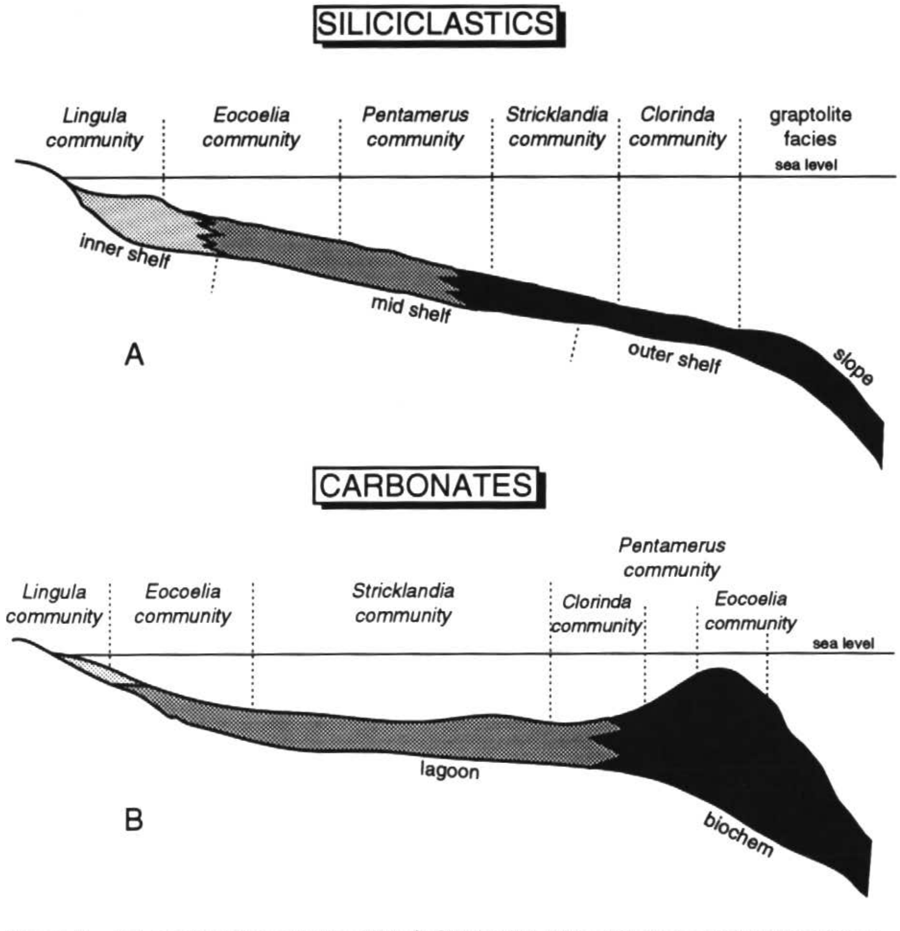


Figure 9 *Schematic representation of Early Silurian brachiopod biofacies distribution:* (**A**) *on a siliciclastic shelf with a relatively uniform gradient, the assemblages are depth-related and arranged in zones parallel to shoreline, perhaps with some extent of overlapping and mixing.* (**B**) *a carbonate platform with bioherms providing irregular substrate conditions; local water-energy level becomes more important than water depth in controlling the community distribution.*

Studies on Lower Silurian brachiopod biostratigraphy and recognition of water-depth related brachiopod biofacies (Boucot, 1975, p. 50) have inspired a series of attempts to reconstruct changes in sea level (McKerrow, 1979; Johnson and Campbell, 1980; Johnson *et al.*, 1981; Johnson *et al.*, 1985). For example, by tabulating the occurrences of the *Pentamerus, Stricklandia, Clorinda* and other assemblages, Johnson and co-workers were able to recognize four minor transgression-regression cycles in the carbonate stratigraphic sequences in Iowa, New York, Michigan, Anticosti Island, and other regions of eastern North America.

In translating stratigraphic occurrences of the depth-related assemblages into sea-level curves, however, caution is needed to take into consideration facies changes. Ziegler's original model of "community" zonations was proposed on the basis of brachiopod occurrences in an essentially clastic setting, where a sediment ramp with a fairly uniform gradient from intertidal zone to shelf margin is assumed to have existed. In comparison, North America, being in a low paleolatitude in Silurian time, was dominated by a carbonate environment with shallow inland basins and marginal platforms dotted with coral-algal-stromatoporoid reefs and bioherms. Like modern carbonate platforms, the Early Silurian carbonate seas must have had a much greater degree of heterogeneity (with minimal gradient) in their substrate topography than in a clastic environment and, consequently, distribution of biofacies would have been complicated by a combination of water-depth, water-energy, and other factors. In the clastic environment, an assemblage (for example, *Stricklandia* or *Clorinda*) occupied a relatively deep-water zone probably because it preferred quiet substrate conditions. In a carbonate environment, both high- and low-energy conditions can exist adjacent to each other within a biohermal complex and the "deep water" community can be found in the the generally shallow biohermal setting (Fig. 9). This is shown clearly by the brachiopods in the biohermal rocks of the Attiwapiskat Formation in the Hudson Bay Lowlands, where both *Pentameroides* (*Pentamerus* community of Ziegler, 1965 = Benthic Assemblage 3 of Boucot, 1975), and *Clorinda* (= Benthic Assemblage 5) occur in great numbers and in the same beds (Jin and Caldwell, 1991). The most feasible interpretation is that, within a single biohermal complex, the large thick-shelled *Pentameroides* lived in relatively turbulent-water niches and the small-sized *Clorinda* preferred quiet, protected ones.

CONODONTS

Conodonts are the phosphatic mouth parts of small, eel-like chordates that lived from Cambrian through Triassic times (Aldridge, 1987). The term "conodont" covers three groups (each arguably of phylum rank; Sweet, 1988), each differing in their histology (Bengtson, 1983): protoconodonts, paraconodonts and euconodonts ("true conodonts"). Conodonts are invaluable tools for Paleozoic and lower Mesozoic biostratigraphy because of their rapid evolution, abundance and widespread distribution in marine rocks of a variety of lithologies. These durable microfossils are most easily isolated from carbonate rock by acid digestion and, thus, most of the data are from carbonate platform or shelf environments. Species distribution suggests that many conodonts were pelagic while others were nektobenthic (*cf.* Sweet and Bergström, 1984; Sweet, 1988; Pohler and Barnes, 1990).

Lower and Middle Paleozoic Conodont Provincialism and Biostratigraphy

Conodont biostratigraphic schemes reflect changes not only in the evolution of the conodont animal, but also in their paleoecology, which is influenced by continental configurations (Fåhræus, 1976). Charpentier (1984) presented quantitative analyses of distribution records to show similarities between conodont faunas; these analyses involved data from the entire stratigraphic range of the conodonts. Periods of strong provinciality which occurred in the Ordovician, Early Devonian, and Permian, alternated with times of endemism and it seems likely that climatic temperature was the principal regulator of conodont distribution. The following discussion on biostratigraphy during the Cambrian to Devonian relies heavily on Charpentier's data.

Cambrian

Provincialism began, after the appearance of euconodonts, in two broad realms: a warm-water realm of shallow seas at low to mid-paleolatitudes, and a cold-water realm comprising high latitudes and more open oceans, as well as deep-water marginal seas of low-latitude continents (Miller, 1984). Euconodont faunas displaced proto- and paraconodont faunas and dominated the Warm Faunal Realm by latest Cambrian time, while the latter continued to dominate the Cold Faunal Realm through the earliest Ordovician (Dubinina (1991) has recognized a third, "Transitional Realm" in Upper Cambrian and Lower Ordovician). Two biostratigraphic schemes reflect these provincial differences in Late Cambrian and earliest Ordovician (Miller, 1984).

Ordovician

The two conodont realms which began during the latest Cambrian-earliest Ordovician (*cf.* Charpentier, 1984; Ethington and Repetski, 1984) continued through to the glacial period at the end of the Ordovician (Pohler and Barnes, 1990). These (Fig. 10a) are the North American Midcontinent and North Atlantic realms representing the warm-water, low-latitude, and the cold-water, high-latitude faunas, respectively (*cf.* Bergström, 1971, 1973; Sweet and Bergström, 1974, 1984). Faunas of the North American Midcontinent Realm are associated with lithic and paleomagnetic data, suggesting that the strata accumulated within a latitudinal belt less than 30° from the paleoequator (Sweet and Bergström, 1984). By the time of the Late Ordovician *Oulodus velicuspis* Zone, two warm-water provinces (and six biofacies) and three cold-water provinces (three biofacies) are recognizable (Sweet and Bergström, 1984; Pohler and Barnes, 1990). The biofacies generally reflect water depth and temperature, or depth-related environmental factors.

The Late Ordovician biofacies are named for the taxon or taxa that numerically dominate the faunas. For example, in the North American Midcontinent Realm, species of *Plectodina* comprise 30-40% of the faunas in environments that were apparently more shallow than those comprising the contemporaneous *Phragmodus* Biofacies. These biofacies are found in both the Red River Province (a belt between 15°N and 16°S paleolatitude) and the Ohio Valley Province (south of 16°S paleolatitude). Species of *Phragmodus* and *Plectodina* are found in both provinces of this realm, and in biofacies of the North Atlantic Realm. It is this "sharing" of taxa between biofacies, and between provinces, that allows correlation of strata beyond the local scale.

The degree of provincialism in the Ordovician has led to the development of two parallel biostratigraphic schemes. The biostratigraphic succession in the Middle to Late Ordovician provides an example of how two regional schemes are integrated. Major contributions to the scheme for North America include Ethington and Clark (1981), Sweet *et al.* (1971), and Sweet (1984). The scheme used in Europe was developed by Lindström (1971) and Bergström (1971) and now comprises about 24 zones and subzones for strata of the North Atlantic Realm (Löfgren, 1978; Ross *et al.*, 1982; Bergström, 1983).

The biostratigraphic succession in the Middle and Late Ordovician provides examples of how two regional schemes are integrated. Sweet and

Bergström (1984) were not able to directly recognize the *Oulodus velicuspis* Zone outside North America because of the lack of the key species elsewhere. However, the recognition that the boundary between the *Amorphognathus superbus* and *A. ordovicicus* zones of the North Atlantic Realm corresponds to a level in the upper part of the North American *Oulodus velicuspis* Zone, permits indirect correlation between the two realms.

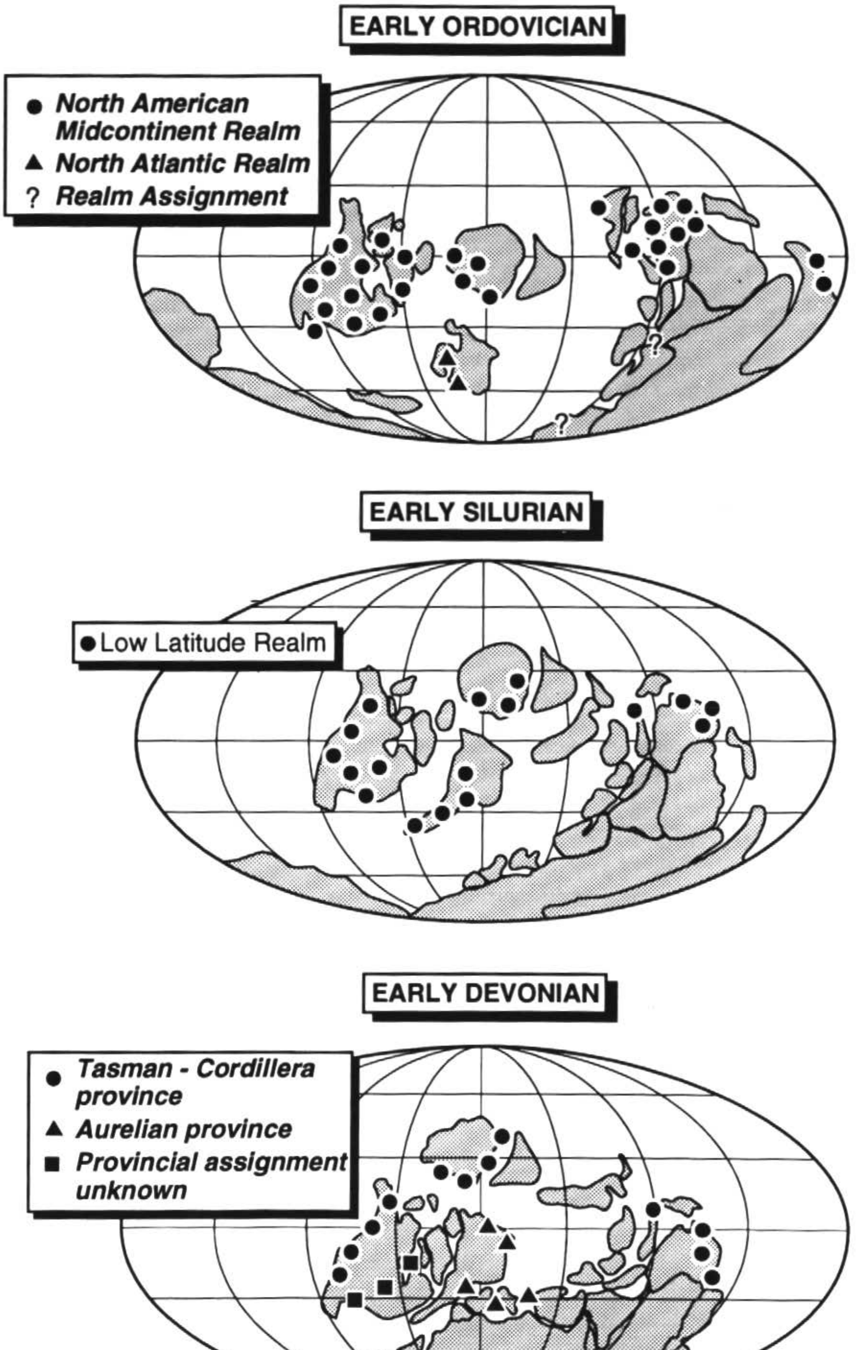


Figure 10 (**a**) *Early Ordovician (Arenig) conodont distribution. Paleogeographic reconstruction is from Scotese and McKerrow (1991), conodont data are from Charpentier (1984). Faunas of southern Gondwana are poorly known and cosmopolitan, hence realm assignment is unknown.* (**b**) *Early Silurian (Llandovery) conodont distribution. Paleogeographic reconstruction is from Cocks and Scotese (1991), conodont data are from Charpentier (1984).* (**c**) *Early Devonian (Lochkovian) conodont distribution. Paleogeographic reconstruction is from Cocks and Scotese (1991), conodont data are from Charpentier (1984). Faunas of eastern American Laurussia have low endemism and mainly cosmopolitan species, hence provincial assignment is unknown.*

The epicratonic areas of overlap in regional biostratigraphy are particularly interesting because not only do they allow integration of the two conodont schemes representing the warm- and cold-water realms, but they also provide the link between conodont and graptolite biostratigraphy. For example, Bergström (1978) reported on Middle and Upper Ordovician conodonts from the Marathon area of west Texas, and correlated between Pacific Province graptolite, North Atlantic Realm conodont, and Atlantic Province graptolite biozones (see "A Correlation Puzzle" herein, and Fig. 11).

Rare, conodont-bearing carbonate beds occur in two forms in the graptolite-bearing fine-grained clastic strata of the basinal environment in the northern Canadian Cordillera. These represent either allochthonous debris flows, or autochthonous carbonate sedimentation. Typically, the Ordovician carbonates from basinal strata contain a mixture of conodont species from both warm- and cold-water faunas (*e.g.*, McCracken and Lenz, 1987), whereas conodonts from the purely carbonate facies are more characteristic of the warm water platformal facies up-slope (*e.g.*, Nowlan *et al.*, 1988).

Silurian

The end of the Late Ordovician glaciation, centered in southern Gondwana, was accompanied by a global shift toward a warmer and drier climate that lasted through the Devonian. In contrast to the Ordovician, one global scheme has generally been practicable, due, in part to changes in continental configurations and to collection biases. For example, Baltica, which was in high latitudes in the Ordovician, had drifted south by the Silurian to join Laurentia, Siberia and northern Gondwana in the low latitudes. In addition, as Sweet (1988) observed, most Silurian collections have been from between the present-day 40th parallels. Nevertheless, although independent biostratigraphic schemes for platformal sequences have been developed for strata in North America (*e.g.*, Rexroad and Nicoll, 1971) and in Wales (Aldridge, 1972), the biostratigraphic scheme developed by Walliser (1971) from strata in the Austrian Carnic Alps is generally still applicable for most known Silurian continental shelf faunas.

Work is now in progress to integrate the carbonate platform-based conodont biostratigraphic scheme for the Silurian with the graptolite biostratigraphic scheme of basinal environments. Although the latter is well documented (*e.g.*, Lenz and McCracken, 1989 for the northern Canadian Cordillera), earliest Silurian conodont faunas in the pelagic or offshore facies often cannot be correlated with the standard platform-based conodont zonation (*cf.* Cooper, 1980) because these conodont faunas lack the key short-ranged species. A parallel biostratigraphic scheme will eventually have to be established for the deeper-water facies. For this reason, Armstrong (1990) was forced to establish new earliest Silurian biostratigraphic units for the outer platform and slope facies in North Greenland. Two of his biozones promise to be useful in the basinal environments of northwestern Canada; a third early Llandovery basinal biozone was recently proposed by McCracken (1991).

Devonian

An apparent increase in provinciality occurred in the Early Devonian (*cf.* Baltica in Figs. 10b, 10c), one province being centered about a semi-restricted seaway (now Europe, Turkey), and the other on the margins of a larger oceanic basin (western American Laurussia, Siberia, Australian part of Gondwana). Both provinces were at low to mid-latitudes, but the former was likely warmer due to oceanic current patterns (Charpentier, 1984). A third, transitional fauna occurred in eastern American Laurussia. The subsequent increase in cosmopolitanism through the Middle and Late Devonian reflects the relative movement of Laurussia toward Gondwana.

As for the previous two periods, two biostratigraphic schemes have evolved for the Devonian (see Ziegler, 1971 for Europe, and Klapper *et al.*, 1971, for North America). The rapid evolution, short stratigraphic ranges and wide distribution, however, make Upper Devonian conodonts exceptionally useful for precise biostratigraphy (Fig. 12). The Upper Devonian conodont zonation of Germany has been refined such that the 14-20 million years is now represented by 32 conodont zones or subzones (*i.e.*, an average of approximately 437,500-625,000 years per unit), which represent pelagic or offshore environments. By comparison, nearshore environments are represented by only nine zones (or subzones) in the scheme of Sandberg and Dreesen (1984). In contrast to previously discussed biostratigraphic zonations, the Upper Devonian scheme (especially the offshore one) is built largely on the successive and steplike first appearances and replacements of short-ranged species and subspecies belonging to only a few genera, in particular the genus *Palmatolepis*. This scheme makes use of two distinct intervals of accelerated evolution in the polygnathid group of conodonts; the first beginning in latest Middle Devonian, the second in the mid-Late Devonian (Sweet and Bergström *in* Robison, 1981).

PALYNOMORPHS

During the Late Paleozoic, Pangaea was divided into a northern (Laurasia) and southern (Gondwana) continent. There were major influences on the flora due to glaciations in Gondwana and these had corresponding effects on climates and environments in Laurasia. As a result of all these factors there was extensive differentiation into regional floras (Chaloner and Meyen, 1973) and this differentiation has a significant bearing on palynological zones (Figs. 13, 14, 15).

Carboniferous and Permian microspores (male reproductive structures) vary in size, but generally range from 20-100 μm. The less common megaspores (female reproductive structures) are 200 μm or more, and some of the larger ones may be visible to the naked eye. The small size and abundance of palynomorphs are major advantages when dating very small pieces of rock from subsurface well cuttings or sidewall cores, hence the importance of palynology to the resource industry.

Pollen and spores may be found in a variety of rock types including grey shale, carbonaceous shale, coal, argillaceous carbonate, argillaceous anhydrite, and greenish glauconitic and fine-grained sandstone and siltstone. Some productive samples can yield up to tens of thousands of specimens per gram of rock. Normally unproductive

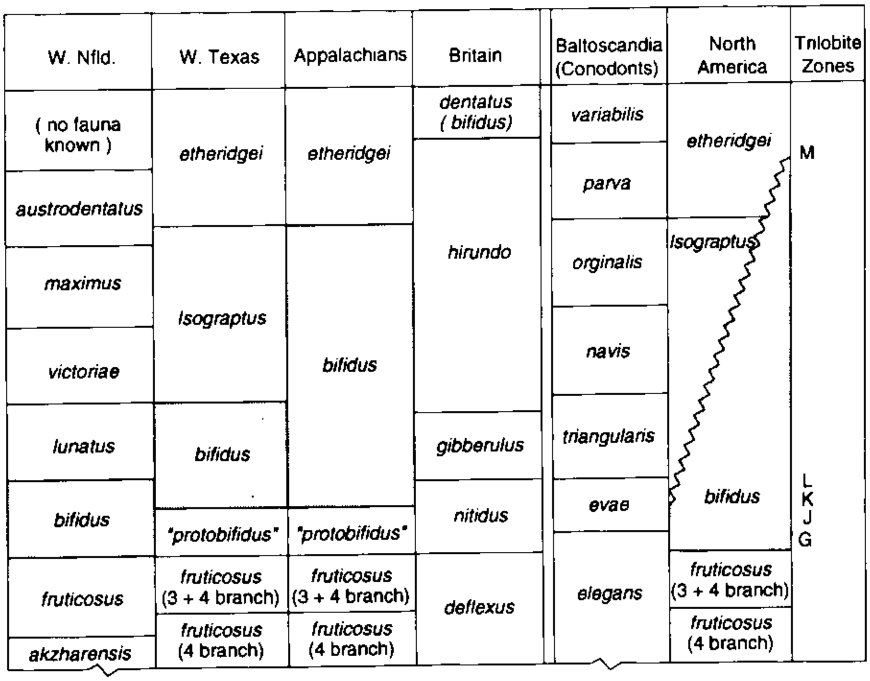


Figure 11 *Correlation of Early Ordovician* Didymograptus (Didymograptellus) bifidus *graptolite zone in North America and Europe using trilobites and conodonts. Data from Williams and Stevens, (1988) for western Newfoundland; Berry (1960), Finney (1982) for west Texas; Berry (1962, 1972) for Appalachians; Bergström and Cooper (1973) for Baltoscandic conodonts; Bergström and Cooper (1973), Williams and Stevens (1988) for Britain and North America; Ross (1951) for trilobite zones. Modified after Bergström and Cooper (1973).*

rock types include pale grey "clean" carbonate units, coarse clastics, and red-brown siltstone and sandstone speckled with greenish-grey in which the organic matter has been oxidized. In some facies, the generic and specific content of spore assemblages is much more diverse than in others, and this aspect is discussed further under paleoenvironments. Also, the total number of species may not accurately reflect the actual number of parent plant species. This is because the taxonomy of pollen and spores is based on morphological criteria, and the exact botanical affinities of many upper Paleozoic spore taxa below the level of family are unknown. In addition, a single sporangium may contain a considerable range of variations of mature grains (Schweitzer, 1986).

The quality of preservation (Fig. 16a) is important in making correct identifications and, thus, zonal determinations, and may also be an indicator of paleoenvironment and thermal maturity. The exines of pollen and spores from marine deep basinal black anoxic shales or continental lacustrine anoxic shales rich in pyrite, are often severely pitted by the growth of opaque sulphide minerals, making identification difficult or impossible (Figure 16b). The colour change of spores from yellow to black with increasing thermal maturity is a useful indicator of thermal history of a

		OFFSHORE BIOFACIES			NEARSHORE BIOFACIES		
SERIES /STAGE		CONODONT ZONE		DEFINED BY FIRST APPEARANCE OF :	CONODONT ZONE		DEFINED BY FIRST APPEARANCE OF :
UPPER DEVONIAN	FAMENNIAN	praesulcata	U	*Protognathodus kockeli*	*costatus*	U	NO FIRST APPEARANCE (Extinction of *"I." raymondi*)
			M				
			L	*Siphonodella praesulcata*			
		expansa	U	*Bispathodus ultimus*			
			M	*Bispathodus aculeatus*		M	*"I." costatus darbyensis*
			L	*Palmatolepis gracilis expansa*		L	*"I." costatus costatus* Morphotype 1
		postera	U	*Palmatolepis gracilis manca*			
			L	*Palmatolepis perlobata postera*			
		trachytera	U	*Pseudopolygnathus granulosus*			
			L	*Palmatolepis rugosa trachytera*			
		marginifera	Um	*Scaphigathus velifer velifer*			
			U	*Palmatolepis marginifera utahensis*	*cornutus*	U	*"Icriodus" chojnicensis*
			L	*Palmatolepis marginifera marginifera*			
		rhombidea	U				
			L	*Palmatolepis rhomboidea*		M	*Pelekysgnathus inclinatus*
		crepida	Um	*Palmatolepis glabra pectinata*			
			U	*Palmatolepis glabra prima*			
			M	*Palmatolepis termini*			
			L	*Palmatolepis crepida*			
		triangularis	U	*Palmatolepis minuta minuta*		L	*"Icriodus" cornutus*
			M	*Palmatolepis delicatula platys*			
	FRASNIAN		L	*Palmatolepis triangularis*	*planus*	M	*Icriodus alternatus alternatus*
		linguiformis		*Palmatolepis linguiformis*			
		rhenana	U	*Palmatolepis rhenana rhenana*			
			L	*Palmatolepis rhenana nasuta*		L	*Pelekysgnathus planus*
		jamieae		*Palmatolepis jamieae*			
		hassi	U	*Ancyrognathus triangularis*	*symmetricus*		*Icriodus symmetricus*
			L	*Palmatolepis hassi*			
		punctata		*Palmatolepis punctata*			
		transitans		*Palmatolepis transitans*			
		falsiovalis	U	*Mesotaxis asymmetrica*			
			L	*Mesotaxis falsiovalis*			
?	?						

Figure 12 *Correlation of Late Devonian conodont zonal schemes for offshore and nearshore biofacies. Note that many bases of the biozones and subzones are defined using short-ranged and rapidly evolving species of one genus. From Ziegler and Sandberg (1984), Sandberg and Dreesen (1984), Austin* et al. *(1985), Klapper and Johnson (1990). See Irwin and Orchard (1991) for other references.*

SYSTEM		STAGE		EASTERN CANADA SPORE ZONE	ZONE TYPE	FACIES	CLIMATE	AUTHOR
PERMIAN	UPPER	OCHOAN		No Data				
		GUADALUPIAN						
	LOWER	LEONARDIAN						
		WOLFCAMPIAN		*Vittatina*	CR	C	Arid	1,2,3
CARBONIFEROUS	UPPER	STEPHANIAN		*Potonieisporites*	A	C	Arid	1,2,3
		WESTPHALIAN	D	*Thymospora*	CR	C	Humid	1,2,3,4
			C	*Torispora* *Vestispora*				
			B	*Vestispora cancellata* *Lycospora*	ACME			
			A	*Reticulatisporites polygonalis*	A			
		NAMURIAN	C	No Data				
			B					
			A	*Potonieisporites elegans*	CR	C	Hot/Arid	1,2,3
	LOWER	VISEAN	V_3	*G. spinosa* - *Ib. magnificus* *S. acadiensis* - *K. triradiatus*	CR	M/C	Hot	3,6
			V_2	*L. noctuina* var. *noctuina* *K. stephanephorus*			Arid	
			V_1	No Data				
		TOURNAISIAN	II	*C. decorus* - *S. claviger*	A	C	Mod.	3,8,9
				S. pretiosus var. *pretiosus*	ACME			
				V. vallatus { *S. cabotii* *U. distinctus*-*U. abstrusus*	A		Humid	
			I	*E. rotatus* - *I. explanatus*				

STAGE		WESTERN AND NORTHERN CANADA SPORE ZONE	ZONE TYPE	FACIES	CLIMATE	AUTHOR
TATARIAN		No Data				
KAZANIAN		*Taeniaesporites* sp.	CR	M	Cool Arid	10
UFIMIAN		*A. plicatus* - *Jugasporites* sp.	CR	M/C	Warm Humid	10
KUNGURIAN		No Data				
ARTINSKIAN		*L. monstruosus* - *V. costabilis*	A	M	Hot Arid	10
SAKMARIAN		*V. striata* - *P. perfectus*	A	M	Hot Arid	10,11
ASSELIAN		*Potonieisporites* spp. - *Vittatina* sp.	A	M	Arid	10,11
GZHELIAN						
KASIMOVIAN		*Potonieisporites novicus* *Vittatina* sp.	CR	M	Arid	10,11
MOSCOVIAN		*Vittatina* sp. appears *Potonieisporites magnus* taeniate disaccates present	A	M	Arid	10,11 12,13
BASHKIRIAN						
SERPUKHOVIAN		*Potonieisporites elegans*	CR	M	Humid	11,12
VISEAN	V_3	*M. aurita* - *R. fracta*	A	M	Humid	11,12,13 14,15,16 17
	V_2	*Convolutispora* *Densospore*		C/M		
	V_1	No Data				
TOURNAISIAN	II	*Tripartites incisotrilobus* *Tumulispora rarituberculuta*	A	C/M	Humid	12
	I	No Data				

Figure 13 ***(facing page)*** *Spore zones of Carboniferous and Permian of eastern, and western and northern Canada.* G. spinosa = Grandispora spinosa; Ib. magnificus = Ibrahimispores magnificus; S. acadiensis = Schopfipollenites acadiensis; K. triradiatus = Knoxisporites triradiatus; L. noctuina *var.* noctuina = Lycospora noctuina *var.* noctuina; K. stephanephorus = Knoxisporites stephanephorus; C. decorus = Colatisporites decorus; S. claviger = Schopfites claviger; S. pretiosus *var.* pretiosus = Spelaeotriletes pretiosus *var.* pretiosus; V. vallatus = Vallatisporites vallatus; S. cabotii = Spelaeotriletes cabotii; E. rotatus = Emphanisporites rotatus; I. explanatus = Indotriradites explanatus; A. plicatus = Alisporites plicatus; L. monstruosus = Limitisporites monstruosus; V. costabilis = Vittatina costabilis; V. striata = Vittatina striata; P. perfectus = Protohaploxypinus perfectus; M. aurita = Murospora aurita; R. fracta = Rotaspora fracta. *Also shown is zone type (**CR**, Concurrent Range Zone; **A**, Assemblage Zone); facies (**C**, continental; **M**, marine); climate (arid); author = source of data (see numerals listed below): 1) Barss* et al., *1963; 2) Barss and Hacquebard, 1967; 3) Hacquebard, 1972; 4) Yeo* et al., *1988; 5) Neves and Belt, 1971; 6) Utting, 1987a; 7) Playford 1964; 8) Utting, 1987b; 9) Utting, Keppie* et al., *1989; 10) Utting, 1989; 11) Bamber* et al., *1989; 12) Utting, 1991; 13) Utting, 1985; 14) Utting, Jachowicz* et al., *1989; 15) Braman and Hills, 1977; 16) Staplin, 1960; 17) Hacquebard and Barss, 1957.*

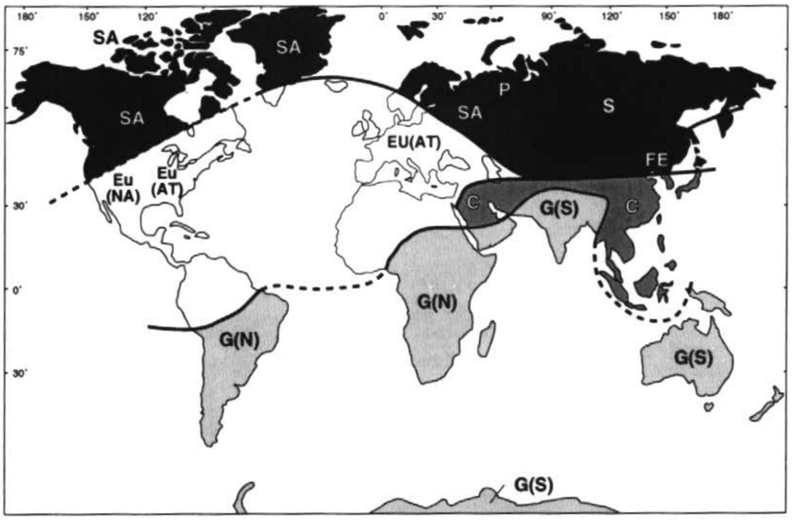


Figure 14 *Upper Paleozoic floral provinces based on macrofloral and microfloral data from Wagner (1962), Chaloner and Lacey (1973), Chaloner and Meyen (1973), Plumstead (1973), Kremp (1974), Meyen (1982, 1987), Chaloner and Creber (1988), and Utting and Piasecki (in press), Balme (pers. comm., 1992). **S**, Siberian; **P**, Pechoran; **SA**, Sub-Angara; **EU(AT)**, Euramerica (Atlantic); **EU(NA)**, Euramerica (North American); **C**, Cathaysia; **G(N)**, Gondwana (northern); **G(S)**, Gondwana (southern).*

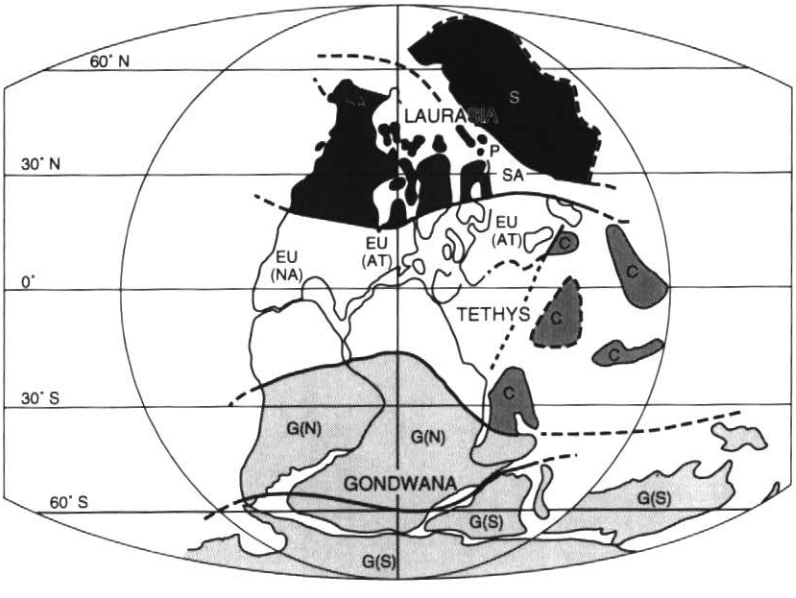


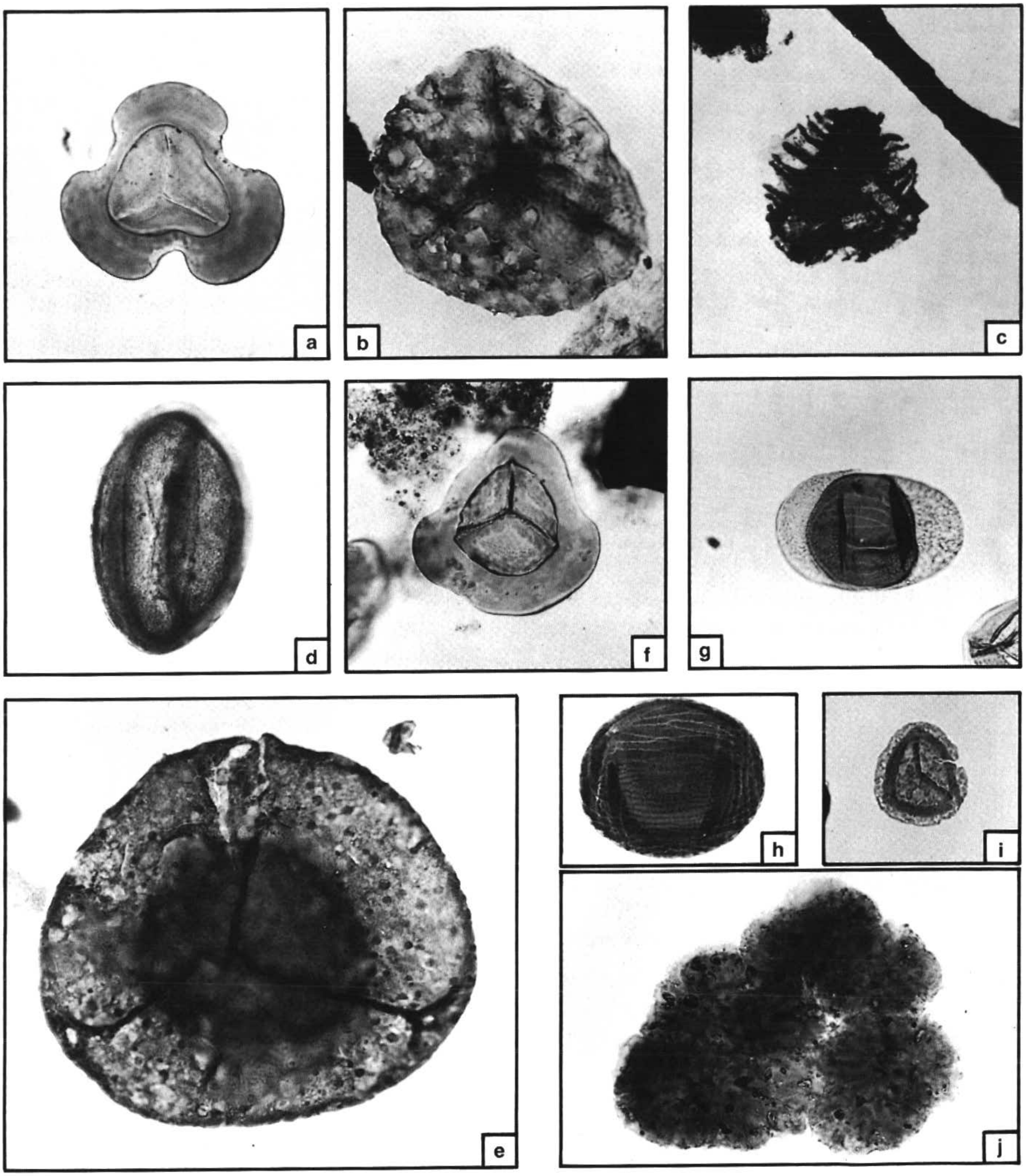
Figure 15 *Upper Paleozoic floral provinces, based on the data listed for Figure 14, plotted on paleogeographic reconstruction based on Lottes and Rowley (1990) and Nie* et al. *(1990). **S**, Siberian; **P**, Pechoran; **FE**, Far Eastern; **SA**, Sub-Angara; **EU(AT)**, Euramerica (Atlantic); **EU(NA)**, Euramerica (North American); **C**, Cathaysia; **G(N)**, Gondwana (northern); **G(S)**, Gondwana (southern).*

rock, and regional studies may assist in determining whether metamorphism is local (due to igneous intrusions), or regional. The Thermal Alteration Index (TAI) is also used to determine whether sufficient thermal alteration of the organic matter has taken place for the generation of oil and gas (*e.g.*, Utting and Hamblin, 1991). However, samples with a high TAI may contain spores that are so dark that it is impossible to identify them unless they have a prominent distinctive ornament, such as large distinctive spinose, baculate or verrucate elements, that extends beyond the spore margin. Viséan assemblages of the Kleybolte Peninsula of northern Ellesmere Island and Svartevaeg of northern Axel Heiberg of the Sverdrup Basin (Utting *et al.*, 1989) contain good examples of such thermally altered, but distinctive taxa (Fig. 16c).

Palynological Zones

Some spore zones in the Carboniferous and Permian of western and northern Canada are broader and less refined, whereas those in eastern Canada, where more detailed work has been carried out, are more precise and based on relatively few, short-ranged taxa (Fig. 13). First appearance of species, on which the base of a zone is established (Fig. 16d), and/or in some circumstances, the last appearance on which the top of a zone is established, can only be reliably determined by studying numerous sections and facies within a basin where sedimentation was approximately continuous. Species may disappear locally in a vertical succession due to environmental changes unfavourable for the growth of a particular plant species, only to reappear in younger rocks elsewhere, or even higher in the same section if a suitable environment is re-established on the land area. Even though an assemblage may contain 30-50 species, many of these may be long-ranging. The first appearance of taxa and the last appearance ("tops") are criteria given different emphasis by the palynologist depending on the type of work being carried out. The first appearance of a species is usually stressed for outcrop material, although "tops" may also be important. However, with subsurface well cuttings, "tops" are more important because down-hole contamination by caving can give false first stratigraphic appearances.

In addition to using unique associations of taxa to define zones, relative abundance of individual species in a part of the stratigraphic column (the acme zone of the Stratigraphic Code, 1983), is sometimes used in palynology. In spite of the fact that such a zone may be primarily of ecologic significance, it can be geographically widespread and significant within a basin, or regionally. For example, such a zone of possible



local significance occurs in the Lower Carboniferous (upper Tournaisian) of Atlantic Canada (Figs. 13, 16e), where, in the type section of the Cheverie Formation of the Horton Group, assemblages are dominated by *Spelaeotriletes pretiosus* (Playford) Neves and Belt var. *pretiosus* Utting (Playford, 1964; Utting *et al.*, 1989). Quantitative changes of genera and species in vertical sections can be of considerable importance to local correlations between beds. For example, quantitative data and coal petrology have been successfully used to correlate coal seams of the Upper Carboniferous of Atlantic Canada (Hacquebard and Donaldson, 1969; Yeo *et al.*, 1988; Hyde *et al.*, 1991).

Once a pollen and spore zonal scheme has been established, it is important that the age of the zones be established with regard to marine faunal groups. In some areas, for example, the Upper Carboniferous and Permian in Yukon and the Sverdrup Basin of the Canadian Arctic (Fig. 13), this has been achieved by studying palynological assemblages from sections dated by marine faunas of ammonoids, fusulinacean and non-fusulinacean foraminifers, conodonts, brachiopods and corals (Bamber *et al.* 1989; Utting, 1989). After the age has been established relative to the marine fauna, it is then subsequently possible to accurately date other non-marine rock sequences. In continental facies, the spore zones may be dated with respect to macro-plant fossils or vertebrates. For example, the age determination of the spore and pollen zones of the Upper Carboniferous of Atlantic Canada (Barss and Hacquebard, 1967; Hacquebard, 1972) were largely based on those established for the macroflora by Bell (1938, 1940, 1944, 1966), whereas the age of the Early Permian spore zone was determined from vertebrates described by Langston (1963) from Prince Edward Island.

No marine fauna are known from the Upper Carboniferous of Atlantic Canada, but the palynological assemblages have many features in common with those of western Europe, where a marine fauna of goniatites (Ramsbottom, 1981) and conodonts (Higgins and Austin, 1985) enables part of the sequence to be correlated. The fact that the generic and specific composition may be largely independent of facies enables correlations to be made across facies boundaries. An example of this is the late Viséan of Yukon (Bamber *et al.*, 1989; Utting, 1991) where marine shelf carbonate facies with shale intercalations, dated by brachiopods, foraminifers and goniatites, contain palynomorph assemblages similar to those of the lacustrine and fluviatile facies of the Sverdrup Basin of the Canadian Arctic Archipelago (Utting *et al.*, 1989). Assemblages from different facies may contain similar taxa qualitatively, but there may be significant differences in the relative quantitative proportions of genera and species. In some cases, it may not be clear to what extent these are related to slight age differences or due to the environment. For example, in the late Viséan of the northeastern part of the Sverdrup Basin, the dominantly fluviatile facies contains abundant cingulate genera (*i.e.*, stout forms with a thickened rim of exine at the equator), whereas to the southeast in the dominantly lacustrine facies, of probably similar age, the species composition shows greater diversity.

Provincialism

Three main macrofloral provinces have been established for the upper Paleozoic of the world (Angara, Euramerica/Cathaysia, and Gondwana; Fig. 15). These may be further subdivided into smaller units (Meyen, 1982, 1987). Western and northern Canada are part of the sub-province called Sub-Angara (Meyen, 1987) which includes eastern Greenland, Svalbard, the Pechora Basin and the Urals area of Russia. Eastern Canada is part of Euramerica which includes the eastern United States and western Europe (Fig. 14). The distinct provinces established by paleobotanists are clearly reflected in the palynological data. Sullivan (1965), van der Zwan (1981), and Clayton (1985)

Figure 16 ***(facing page)*** *Magnifications are all 500× unless otherwise stated; all specimens are Geological Survey of Canada (GSC) figured specimens.*

(a) *Well-preserved specimen of trilete spore* Murospora tripulvinata *Staplin from Lower Carboniferous (upper Viséan) lacustrine beds of Sverdrup Basin, Emma Fiord Formation, Grinnell Peninsula, Devon Island, Northwest Territories, GSC 92903.*

(b) *Poorly preserved trilete spore from Lower Carboniferous (Tournaisian) black, anoxic, lacustrine shales rich in pyrite, Newfoundland. Note cubic cavities showing impression of sulphide minerals. Crouse Harbour Formation, Conche, Great Northern Peninsula, Newfoundland, GSC 103389.*

(c) *Thermally altered (black) trilete spore* Diatomozonotriletes hughesii *Playford from Lower Carboniferous (upper Viséan) rocks of Sverdrup Basin. Note the distinctive equatorial ornament that enables identification to be made in spite of the high thermal maturity. Kleybolte Peninsula, Ellesmere Island, Northwest Territories, GSC 92943.*

(d) Schopfipollenites acadiensis *Utting from Lower Carboniferous (upper Viséan) rocks of Nova Scotia. An example of a distinctive species of monolete spore used to define the base of a concurrent range zone. Upper Windsor Group, Port Hood Island, Cape Breton, Nova Scotia, GSC 73822.*

(e) Spelaeotriletes pretiosus *(Playford) Neves and Belt var.* pretiosus *Utting that makes up 90% of the assemblage in an acme zone in the Lower Carboniferous of the Horton Group, Nova Scotia. Cheverie Formation, Nova Scotia, GSC 73799.*

(f) Murospora aurita *(Waltz) Playford from the Lower Carboniferous (upper Viséan) of Sverdrup Basin. Abundance of this species may indicate humid conditions. Emma Fiord Formation, Grinnell Peninsula, Devon Island, Northwest Terrritories, GSC 92900.*

(g) Protohaploxypinus perfectus *(Naumova) Samoilovich, from the Permian of western and northern Canada. This striate disaccate pollen has a wide stratigraphic range of several stages, but it is common in the Lower and Upper Permian. Trold Fiord Formation Grinnell Peninsula, Devon Island,Island, Northwest Territories, GSC 103390.*

(h) Vittatina striata *(Luber) Jansonius, from the Permian of western and northern Canada. A typical Permian species; however, abundance of this polyplicate pollen along with taeniate disaccate pollen may indicate an arid climate. Sabine Bay Formation, Melville Island, Northwest Territories, GSC 103391.*

(i) Lycospora *sp. from the Upper Carboniferous (Westphalian C) of Newfoundland. Abundance of this genus may indicate a forest vegetation in shallow more or less stagnant water in which decomposition was anerobic. Shears Seam, Barachois Group, southwestern Newfoundland, GSC 103392.*

(j) Botryococcus *sp. from the Lower Carboniferous (Tournaisian) of New Brunswick. Abundance of this freshwater alga may indicate good source rock potential for oil. Albert Formation, New Brunswick, GSC 76391 (750×).*

recognized regional differentiation of Lower Carboniferous palynomorph assemblages of western Europe and North America that can be related to the macroflora. Thus, not only does palynology provide useful information supporting the geographic distribution of floral provinces, but where no macrofloras are present, they may be the only evidence available (*e.g.*, the Upper Carboniferous and Permian of Yukon and the Sverdrup Basin). Identification and delineation of floral provinces provide useful data for plate reconstruction, although the differences in assemblages between floral provinces may make palynostratigraphic correlation more difficult. In general, correlation within the same floral province, but between areas that are now distant geographically due to subsequent migration of continents, is straightforward. For example, it is possible to correlate relatively precisely, Viséan assemblages of eastern Canada and those of western Europe, or Viséan material of western and northern Canada with those of Svalbard (Utting, 1987a; Utting, Jachowicz *et al.*, 1989). On the other hand, correlations between the different provinces of western and northern Canada, and eastern Canada are less precise. Regrettably, taxonomic treatment of upper Paleozoic pollen and spores has not been the same throughout the world, and this has hampered precise palynostratigraphic correlation. For example, the taxonomy used in Canada, the United States, and western Europe differs from that used in Russian literature. As a result, correlation with the stratotypes of Russia is made difficult, but not impossible (Utting and Piasecki, in press). The problem can be solved by closer communication and co-operative studies between workers.

Paleoclimate

The use of pollen and spores in determining paleoclimate for the upper Paleozoic is in its infancy, but has considerable potential. Many modern and fossil plant taxa are very sensitive to climatic change, and these changes will be reflected in the palynological record. It is important to know which taxa are climatically controlled when establishing a zonal scheme because the "first appearance" of climate-specific taxa may vary locally, and not represent the true first stratigraphic appearance. Based on the relationship between the composition of palynomorph assemblages, "climate sensitive" rocks, and phytogeographical distribution, as revealed by multivariate statistical analysis, van der Zwan (1981) and van der Zwan *et al.* (1985) proposed that for the Lower Carboniferous of North America and Europe, four climatic zones (dry, moderately humid, humid and very humid) could be recognized using key taxa. The relative frequency of certain species or genera are indicative of dry conditions, and others of humid conditions, while other species are neutral and not specific to any single climatic zone. Low diversity assemblages can be an indicator of aridity. For example, in Atlantic Canada (Fig. 13) middle to upper Viséan rocks consist of thick evaporites along with red-brown siltstone and carbonate, and spore assemblages are dominated by two species *Crassispora trychera* and *Rugospora minuta*, although some samples contain slightly more diverse assemblages reflecting periodic moderately humid intervals (van der Zwan *et al.*, 1985; and Utting, 1987a). Low diversity continues into the Namurian (Neves and Belt, 1971), but in the Westphalian (Fig. 13), there is increased diversification of assemblages in the coal measures (Hacquebard, *et al.*, 1960; Hacquebard, 1972; Hyde *et al.*, 1991), reflecting greater humidity. On the other hand, late Viséan rocks in western Canada (Braman and Hills, 1977; Staplin, 1960; Hacquebard and Barss, 1957; Barclay *et al.*, 1991), in Yukon (Bamber *et al.*, 1989; Utting 1991), and the Sverdrup Basin (Utting, Jachowicz *et al.*, 1989) contain diverse assemblages. They are similar to those of Svalbard (Playford, 1962, 1963) which, based on the abundance of *Densosporites* and *Murospora aurita* (Fig. 16f) in the middle Viséan, were subject to a very humid climate (van der Zwan, 1981; van der Zwan *et al.*, 1985). In the Lower Permian (Asselian-Sakmarian, Artinskian) of northern Canada (Fig. 13) dominance of taeniate disaccate (Fig. 16g) and polyplicate pollen (Fig. 16h) suggests an arid climate, and this conclusion is supported by the presence of evaporites at some horizons in the Sverdrup Basin. In overlying Ufimian (Roadian), diverse and abundant assemblages of trilete spores, taeniate and non-taeniate disaccate pollen and monosaccate pollen indicate increased humidity; these beds in places contain thin coal and carbonaceous shale intercalations (Utting, 1989).

Paleoenvironments and Biostratigraphy

Variations in the relative proportions of genera and species in assemblages may be used to determine local paleoenvironments within a zone or subzone, enabling local subdivisions and correlation similar to that discussed above for acme zones. For example, pioneer work carried out by Smith (1962) on the coal measures of Britain indicated that, on the basis of the abundance of certain taxa in coal seams, four different phases corresponding to distinct coal swamp environments could be recognized The Lycospore Phase (Fig. 16i) represents a forest vegetation in shallow, more or less stagnant water in which decomposition was anaerobic. A Transition Phase resulted from withdrawal of the ground water cover due to changes in sea level or elevation of bog surface due to accumulation of peat in a humid climate; the forest vegetation was replaced by a more diverse open vegetation with aerobic decomposition. A Densospore Phase occurred where there was high precipitation and humidity, and decomposition was aerobic, and an Incursion Phase records flooding of the environment, which had a catastrophic effect on vegetation, but which brought in material from other environments, producing diverse fossil assemblages. The general concept outlined by Smith (1962) has been applied successfully to coal measures in Atlantic Canada (Yeo *et al.*, 1988; Hyde *et al.*, 1991).

Sedimentary environments may significantly affect spore assemblages. A good example is the "Neves effect" (Chaloner 1958; Chaloner and Muir, 1968, fig. 4; Traverse, 1988, fig. 17.15) in which saccate pollen (*Florinites*) of *Cordaites* trees is carried by both wind and water from upland areas into swamp and marine environments, whereas microspores of *Lepidodendron (Lycospora)* are produced in, and for the most part confined to, swamps. Thus, *Lycospora*, produced locally in coal swamps, overwhelms the few *Florinites* derived from elsewhere. In the non-marine, but non-swamp facies, there are more *Florinites*, but not proportionately as many as those occurring offshore. This phenomenon occurs in Upper Carboniferous coal measures of Atlantic Canada, although no representative of the marine offshore facies has yet been found.

Paleoenvironments can also be determined by assessing the relative proportions of different organic matter types, the quality of preservation of palynomorphs and organic matter, palynomorph composition, and the relative proportions of non-marine and marine palynomorphs (*e.g.*, acritarchs and scolecodonts). A number of classifications categorizing palynofacies exist; for example, Batten (1982) and Masran and Pocock (1981). In addition to determining environments, such data are of importance in assessing the hydrocarbon source rock potential. For example, the high proportion of the alga *Botryococcus* sp. (Fig. 16j) is the probable source of the oil of the Lower Carboniferous lacustrine/fluviatile Albert Formation of New Brunswick (Kalkreuth and Macauley, 1984; Utting, 1987b).

TRILOBITES

Trilobites, like other biostratigraphically important taxa, are characterized by high evolutionary turnover rates and, consequently, short stratigraphic ranges (Stanley, 1979; Foote, 1988) that enable fine subdivisions of strata to be made. As a typical example, the Upper Cambrian Sunwaptan Stage of southern Alberta has a duration of approximately five million years and has been divided into 11 trilobite zones and subzones (Westrop, 1986). Trilobites provide a primary basis for well-developed zonal schemes through much of the Cambrian and Lower Ordovician (see, for example, Fritz, 1972; Longacre, 1970; Stitt, 1977; Palmer, 1977; Palmer and Halley, 1979; Ross, 1951; Hintze, 1953; Ross, 1984; Fortey and Owens, 1987) and remain important in the remainder of the Ordovician and Silurian (Ludvigsen, 1979; Chatterton and Perry, 1983). In younger Paleozoic strata, trilobites are minor components of marine faunas and are of reduced biostratigraphic utility. Nonetheless, they have proved to be important for regional correlation in, for example, the Devonian of the Canadian Arctic (Ormiston, 1967). Trilobites also provide an excellent example of the influence of environmental and biogeographic factors, such as biofacies differentiation along environmental gradients or provincialism, on biostratigraphic analysis. These factors will be emphasized in the following section.

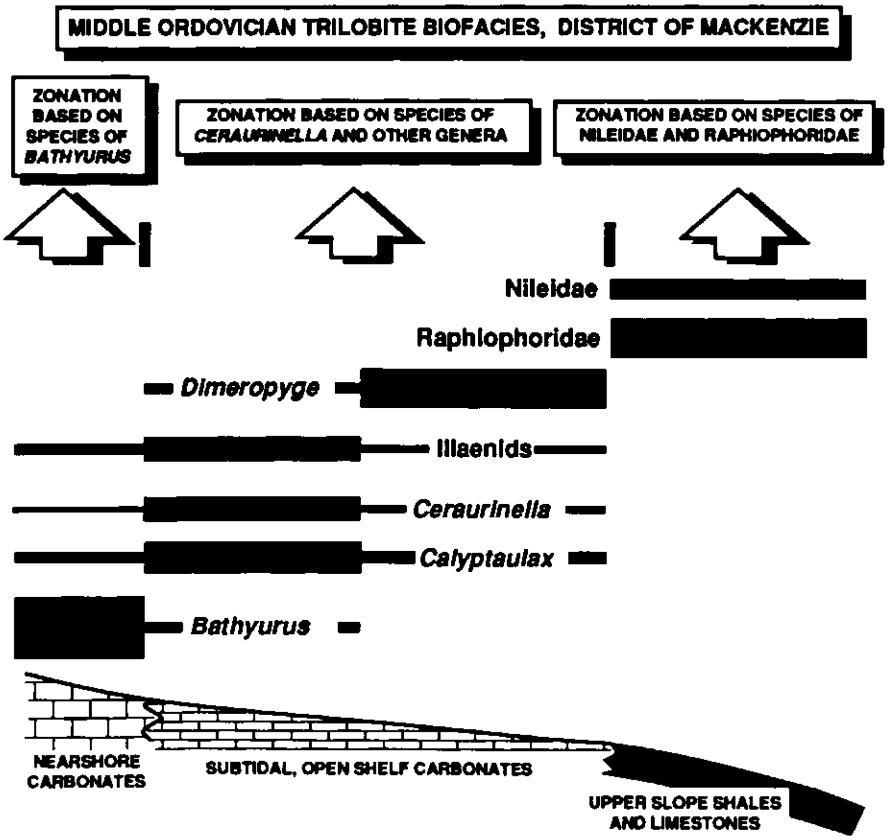


Figure 17 *Schematic transect across the Middle Ordovician shelf and upper slope, District of Mackenzie, showing abundances and distributions of selected trilobite taxa (based on data in Chatterton and Ludvigsen, 1976; Ludvigsen, 1978, 1979, 1980, 1981; Tremblay and Westrop, 1991). Thicknesses of spindles are proportional to relative abundance. In each of three major biofacies-lithofacies belts (nearshore carbonates; subtidal, open shelf carbonates; upper slope shales and limestones), zonations are based on species of different dominant taxa.*

Trilobite Biofacies and Their Biostratigraphic Implications

During the last 15 years, a variety of studies have shown that trilobites, like other benthic organisms, were segregated along environmental gradients into biofacies or "communities" (*e.g.*, Cambrian: Ludvigsen and Westrop, 1983; Westrop, 1986; Ordovician: Fortey, 1975; Ludvigsen, 1978; Tremblay and Westrop, 1991; Owen *et al.*, 1991; Silurian: Thomas, 1979; Mikulic and Watkins, 1981; Chlupač, 1987; Tetreault, in press; Devonian: Chlupač, 1983; Carboniferous: Brezinski, 1986). Biofacies are usually identified in terms of patterns of shifting abundance of taxa along the gradient: genera or higher taxa that are dominant in one biofacies are relatively rare or absent in other biofacies. In many cases, there is a strong relationship between lithofacies and biofacies distribution (*e.g.*, Ludvigsen and Westrop, 1983; Thomas, 1979), and biofacies are often arrayed along an apparent depth gradient (*e.g.*, Ludvigsen, 1978). Zones established in one biofacies may be difficult or even impossible to apply to other biofacies because key taxa are very rare or absent. In their "dual" approach, Ludvigsen *et al.* (1986), using trilobites as examples, argued strongly that zonal schemes must be established in the context of biofacies. This is well demonstrated in the ensuing discussion and examples.

Middle Ordovician trilobite faunas of the District of Mackenzie (Chatterton and Ludvigsen, 1976; Ludvigsen, 1978, 1980, 1981; Tremblay and Westrop, 1991) provide an excellent example of "dual biostratigraphy". Trilobite genera and families vary in abundance across the shelf, so that zonations in different facies must be based on different taxa (Fig. 17). For example, the genus *Bathyurus* is dominant in nearshore habitats, but is rare or absent in open shelf and upper slope settings. *Bathyurus* persisted through most of the Middle Ordovician, but, when examined in detail, the genus consists of a plexus of relatively short-ranging species (Fig. 18) which reflect a history of background extinction and speciation. The succession of species over time offers the basis for a zonal scheme for Middle Ordovician nearshore facies (Fig. 19; see also Tremblay and Westrop, 1991) that rivals those established for conodonts (*e.g.*, Sweet, 1984). In open shelf environments, at least two biofacies are present (Biofacies II and III of Ludvigsen, 1978), which share genera such as *Ceraurinella*, whose species have been used in zonal biostratigraphy (Figs. 17, 19; see also Ludvigsen, 1979). Relatively rare occurrences of some of the same species of *Ceraurinella* in nearshore carbonates (Fig. 17) enable correlations to be made between nearshore and open shelf zonations. In moving from shelf to slope environments, a sharp shift in facies from carbonates to shales is matched by an equally abrupt change in the composition of the trilobite faunas. Slope biofacies are completely different from coeval shelf biofacies, and zones must be based upon species of raphiophorid and nileid trilobites (Figs. 17, 19; Ludvigsen, 1980, 1981); approximate correlation between shelf and slope must rely upon other groups, such as conodonts (Ludvigsen, 1980, p. 97-98). The slope faunas are important however because, like other Cambrian and Ordovician deep cool-water biofacies (Fortey, 1975; Taylor, 1977; Ludvigsen, 1978), they include pandemic genera that occur outside of North America (*e.g.*, the raphiophorid *Cnemidopyge* is also known from Britain and Scandinavia; Ludvigsen, 1980) and that can be used in interprovincial correlation.

Well-developed biofacies also occur in parts of the Cambrian of North America, with similar biostratigraphic results. For example, in the late Sunwaptan (Late Cambrian) of North America, strong biofacies differentiation occurs both within and between shelf carbonate and siliciclastic facies (Fig. 20), so that at least six parallel zonations will be required for a complete biostratigraphy (Fig. 21). Correlation between different zonations is achieved through the use of a relatively small number of shared species. For example, species of *Euptychaspis* reach peak abundances in shallow, subtidal, "level-bottom" carbonates, but some also occur as very minor components of biofacies from shallow, subtidal reef mounds (Westrop, 1986), as well as from deep, subtidal to upper slope carbonates (Ludvigsen, 1982; Westrop, in press). Similarly, some species of *Stenopilus* occur in both shallow, subtidal, "level-bottom" carbonates and bank-edge carbonates and reef mounds (Ludvigsen *et al.*, 1989).

Times of reduced biofacies differentiation often correspond to major paleogeographic changes, such as sea level fluctuations, and/or intervals of mass extinction. For example, the early Sunwaptan of North America includes a trilobite extinction event (Westrop and Ludvigsen, 1987). In the aftermath of this extinction, low-diversity biofacies were spread widely over the North American shelf and their distributions cut sharply across lithofacies bound-

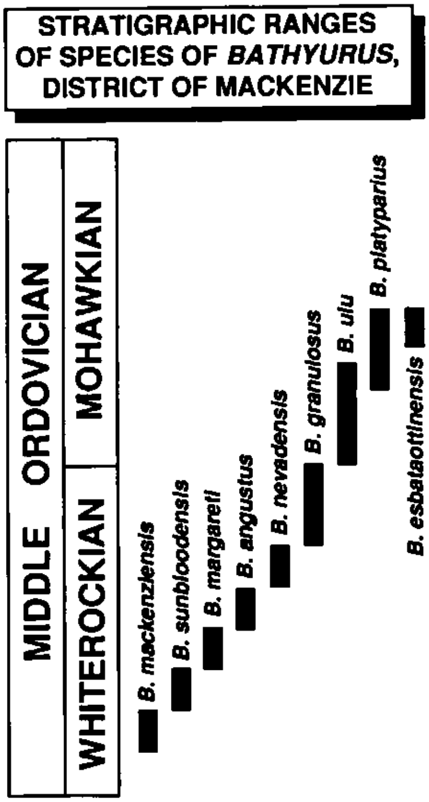


Figure 18 *Stratigraphic ranges of species of* Bathyurus, *Middle Ordovician, District of Mackenzie, which provide the basis for a zonation of nearshore biofacies and lithofacies (based on data in Ludvigsen, 1979 and Tremblay and Westrop, 1991).*

MIDDLE ORDOVICIAN TRILOBITE ZONES, DISTRICT OF MACKENZIE

		NEARSHORE BIOFACIES	OPEN SHELF BIOFACIES	UPPER SLOPE BIOFACIES
MOHAWKIAN	FRANKLINIAN	ZONATION NOT ESTABLISHED	*Ceraurinella necra* ?	?
	BLACKRIVERAN	*Gabriceraurus gabrielsi*	*Ceraurinella longispina*	*Cnemidopyge* Fauna
		Bathyurus ulu	?	
WHITEROCKIAN	"UPPER WHITEROCKIAN"	*Bathyurus granulosus*	*Ceraurinella nahanniensis*	
		Bathyurus nevadensis	ZONATION NOT ESTABLISHED	?
	"LOWER WHITEROCKIAN"	*B. margareti*		*Peraspis* Fauna
		B. sunbloodensis		
		B. mackenziensis		
		ZONATION NOT ESTABLISHED		?

Figure 19 *Zonal schemes for three major biofacies-lithofacies belts, Middle Ordovician, District of Mackenzie (Ludvigsen, 1979, 1980, 1981; Tremblay and Westrop, 1991). Dashed zonal boundaries reflect uncertainties in correlations between biofacies belts. Use of the Franklinian, instead of Trentonian, follows the recommendation of Sweet (1988).*

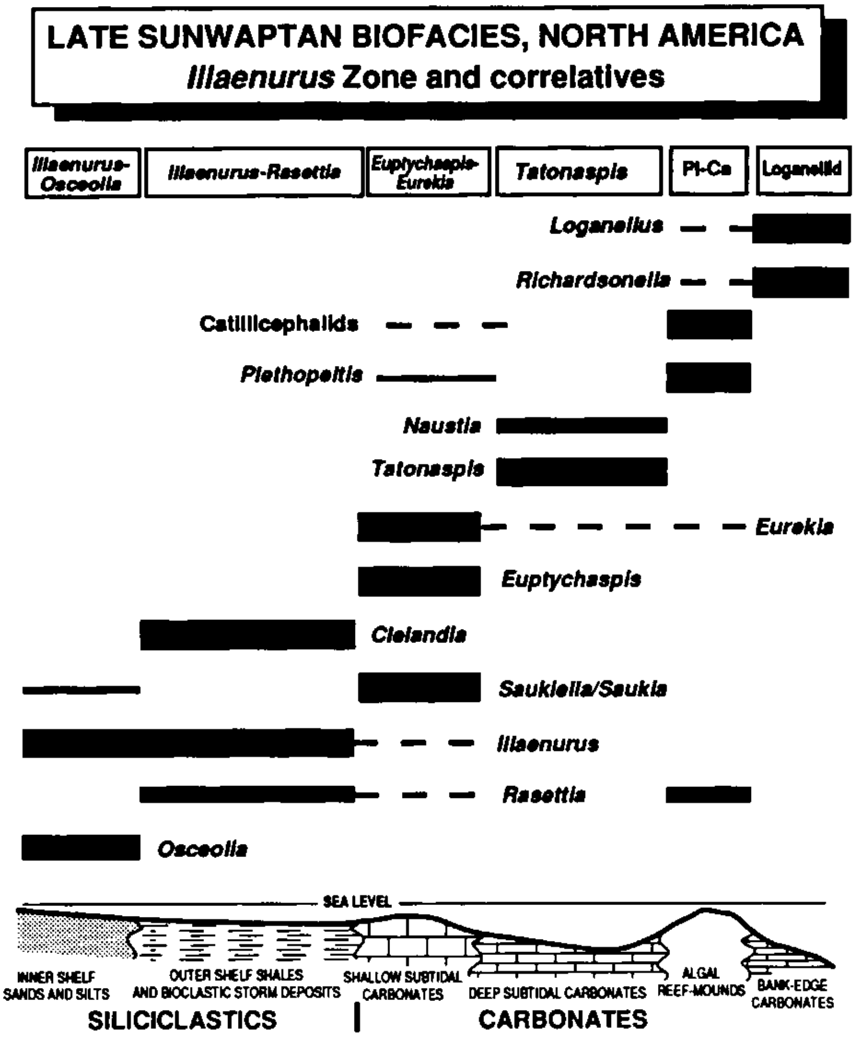


Figure 20 *Schematic transect across the late Sunwaptan (Late Cambrian) shelf of North America showing high levels of biofacies differentiation (modified from Westrop, 1990; data for deep shelf carbonates from Westrop (in press)). Spindles depict abundances and distributions of selected taxa; open rectangles at the top of the figure indicate biofacies ranges. Six major biofacies-lithofacies belts may be recognized and each will require a separate zonation based upon different taxa (Fig. 21). **Pl-Ca:** Plethopeltid-catillicephalid Biofacies.*

LATE SUNWAPTAN ZONES, NORTH AMERICA

INNER SHELF SANDS AND SILTS	OUTER SHELF SHALES AND BIOCLASTIC STORM DEPOSITS	SHALLOW SUBTIDAL "LEVEL-BOTTOM" CARBONATES		SHALLOW SUBTIDAL REEF MOUNDS		DEEP SUBTIDAL CARBONATES	BANK-EDGE CARBONATES AND REEF MOUNDS
SAUKIA	Zonation not established	SAUKIA	*Saukiella serotina*	SAUKIA	*Stenopilus glaber*	*Kathleenella subula*	*Keithia schucherti*
			Saukiella junia		*Proricephalus wilcoxensis*	*Naustia papillo*	
	ILLAENURUS		*Saukiella pyrene*		*Rasettia magna*		*Keithia subclavata*
		Saratogia					*Onchonotus richardsoni*

Figure 21 *Late Sunwaptan zonations for each of the six biofacies-lithofacies belts illustrated in Figure 20. Outer shelf shales and bioclastic storm deposits from Grant (1965) and Westrop (1986); inner shelf sands and silts from Raasch (1951); shallow, subtidal, "level-bottom" carbonate sequence is a composite from Longacre (1970) and Stitt (1977); shallow, subtidal, reef mounds sequence is a composite from Stitt (1977) and Westrop (1986); deep subtidal carbonates from Westrop (in press); bank-edge carbonates and reef mounds from Ludvigsen* et al. *(1989).*

aries (Fig. 22; see also Westrop, 1990). Key species of *Taenicephalus* and *Orygmaspis (Parabolinoides)* occur abundantly in several lithofacies, including inner shelf sands and silts, outer shelf shales and bioclastic storm deposits, and shallow subtidal carbonates, so that correlations can be readily made (see Westrop, 1986 for further discussion). Compared to the late Sunwaptan, the number of zonal schemes resulting is cut in half (Fig. 23).

Influence of Environmental and Biogeographic Factors on Global Correlation

In general, global correlation using trilobites is difficult because of strong provincialism (*e.g.*, Palmer, 1977; Shergold, 1988). As noted above, cool-water faunas tend to be pandemic, occurring in deep water at low latitudes and extending into shallow water at high latitudes (Taylor, 1977), and they enable comparisons to be made between faunal provinces. However, these often have to be made at the genus, or even family, level, so that correlations are relatively imprecise. In recent years, Cambrian agnostid trilobites have shown great promise for high-resolution, species-level correlation between successions on different continents (Robison, 1982, 1984; Rowell *et al.*, 1982; see also Palmer, 1962). Many species are widely distributed, occurring on several continents (Fig. 24), and several authors have suggested that this reflects a pelagic life-style (Robison, 1972; Jago, 1973; Müller and Wallossek, 1987; but see Fortey and Barnes (1977, p. 306) and Chatterton and Speyer (1990, p. 131) for alternative interpretations). Agnostids are minor components of Ordovician faunas, but pelagic telephinid trilobites such as *Carolinites* are equally widespread (Fig. 25; see also Fortey, 1985) and have a comparable biostratigraphic potential.

The advances in agnostid biostratigraphy have been a significant recent development in Cambrian global correlation and, in some parts (*e.g.*, mid-Cambrian), offer a level of resolution comparable to that provided by Ordovician and Silurian graptolites. However, it is important to realize that there remain strong facies controls on agnostid distribution that constrain their use. Work in the Great Basin of Nevada and Utah by Robison (1976) has shown that agnostids are confined largely to outer shelf shales and limestones (Fig. 26), presumably reflecting water mass-specific or depth-specific distributions similar to those inferred for some graptolites (*e.g.*, Finney, 1986; Cooper *et al.*, 1991; see also the graptolite section above). Consequently, accurate correlation between continents is restricted to a limited range of facies. Indeed, comparison of agnostid zones with polymerid (*i.e.*, non-agnostid) trilobite zones established for mid- to inner shelf carbonate and siliciclastic litho- and biofacies is difficult even within the Great Basin (see Robison, 1976, p. 106-107). Given these problems, it is likely that biostratigraphic nomenclatures, including suprazonal units (stages and series), will remain provincial in nature for the foreseeable future (Ludvigsen and Westrop, 1985; see also Palmer, 1977, p. 16; Ludvigsen *et al.*, 1986, p. 148).

A CORRELATION PUZZLE

The preceding has shown the need for correlation between geographic regions and between biostratigraphic schemes based on different fossil groups, and how dependent these schemes are on paleoecologic factors, both locally (*e.g.*, biofacies) and regionally (*e.g.*, provinces and realms). A final example is the Lower Ordovician didymograptid controversy. In brief, the *Didymograptus (Didymograptellus) bifidus* Zone of Early Ordovician in North America was interpreted by some workers as being either wholly or, at least partly, coeval to the zone of the same name in Britain, but by others as being much older.

The species *Didymograptus (Didymograptellus) bifidus* was established by Hall (1865) on material from Levis, Quebec, and was subsequently reported from a number of localities in North America and Europe. Berry (1962) studied Hall's fossil material and concluded that many specimens later assigned to this species had been incorrectly identified. Cooper and Fortey (1982) further explained the differences between the true *D. bifidus* and those misidentified from the Llanvirn of Britain by, for example, Elles and Wood (1901) (see Williams and Stevens (1988) for additional remarks on the species).

Trilobite-brachiopod faunas occurring in this part of the Lower Ordovician were markedly different between North America and Europe and, thus, of little use in resolving the *Didymograptus (Didymograptellus) bifidus* correlation conflict. But by using co-occurrences of graptolites, shelly fossils, and particularly, conodonts, Bergström and Cooper (1973) solved this interprovincial (and intercontinental) problem. Their evidence and solution to this argument are summarized here because it illustrates

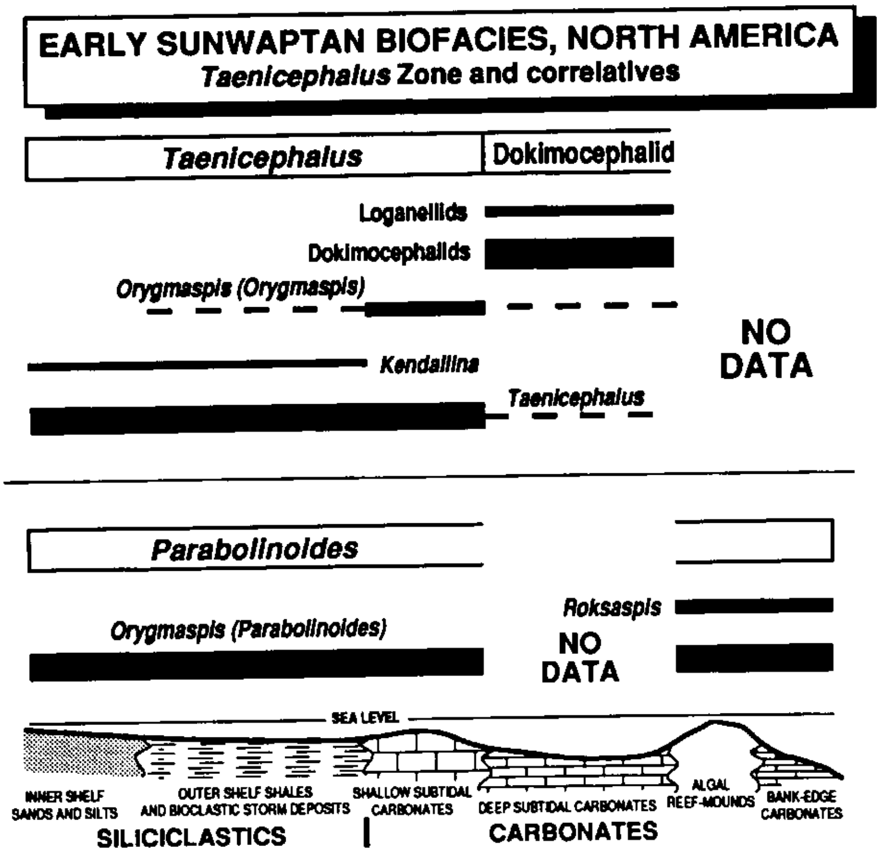


Figure 22 *Schematic transect across the Early Sunwaptan (Late Cambrian) shelf of North America showing low levels of biofacies differentiation (modified from Westrop, 1990). Spindles depict abundances and distributions of selected taxa; open rectangles at the top of the figure indicate biofacies ranges. In the* Parabolinoides *Subzone and correlatives (lower set of spindles), only a single biofacies has been identified in shelf environments. In the* Taenicephalus shumardi *Subzone and correlatives (upper set of spindles), at least two biofacies are present. Fewer sets of zones (Fig. 23) are required to characterize the biostratigraphy than in the Late Sunwaptan (Figs. 20, 21).*

EARLY SUNWAPTAN ZONES, NORTH AMERICA

	INNER SHELF SANDS AND SILTS	OUTER SHELF SHALES AND BIOCLASTIC STORM DEPOSITS	SHALLOW SUBTIDAL CARBONATES	DEEP SUBTIDAL CARBONATES	BANK-EDGE CARBONATES AND REEF MOUNDS
TAENICEPHALUS	*T. shumardi*	*T. shumardi*	*T. shumardi*	*Noelaspis* sp. nov.	*Roksaspis turbinella*
	Orygmaspis (Parabolinoides) contractus	*Orygmaspis (Parabolinoides) contractus*	*Orygmaspis (Parabolinoides) contractus*		
ELVINIA	*Irvingella major*	*Irvingella major*	*Irvingella major*	*Irvingella major*	

Figure 23 *Early Sunwaptan zones of North America, based in data in Westrop (1986),* Ludvigsen et al. *(1989) and Westrop (in press). Note that a single set of zones and subzones may be used in three different lithofacies (inner shelf sands and silts; outer shelf shales and bioclastic storm deposits; shallow, subtidal carbonates; cf. Fig. 21), reflecting low levels of biofacies differentiation (Fig. 22).*

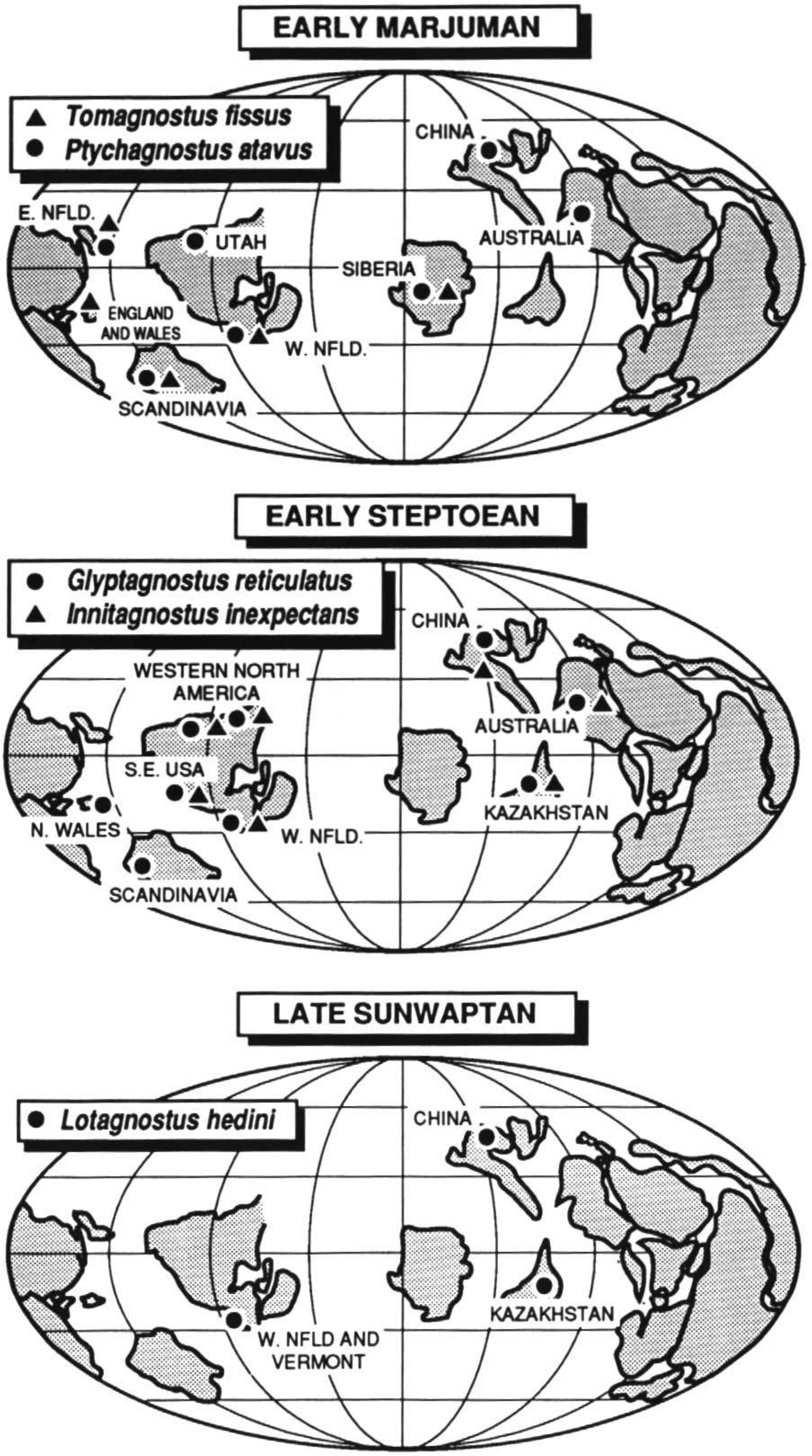


Figure 24 *Distributions of selected pandemic agnostid species plotted on Late Cambrian continental reconstruction (Scotese* et al., *1979). Early Marjuman is modified from Rowell* et al. *(1982); early Steptoean based on data in Palmer (1962), Shergold (1982) and unpublished data from the Cow Head Group of western Newfoundland; late Sunwaptan based on data in Ludvigsen* et al. *(1989).*

how and why biostratigraphic schemes are continually refined.

Some of the North American *Didymograptus (Didymograptellus) bifidus* faunas occurred with shelly fossils indicative of trilobite biozones L and M of Ross (1951) (Fig. 11), permitting a correlation between the graptolite and trilobite zones. Conodont collections from the *D. bifidus* Zone and zone M in Oklahoma probably correspond to the upper part of the *D. hirundo* to *D. "bifidus"* (=*D. artus*) zones of Britain (Bergström and Cooper, 1973), whereas conodonts from the true *D. bifidus* Zone in west Texas and western Newfoundland are older. Bergström and Cooper (1973) identified these conodonts as representing the *Prioniodus evae* conodont zone, which in Baltoscandia generally corresponds to the older British *D. nitidus* Zone rather than the younger *D. artus* (the correct name for the so-called *D. bifidus* of Britain) Zone. This possibly confusing correlation is clarified in Figure 11, which shows that strata in North America assigned to the true *D. bifidus* Zone range in age from the British *D. nitidus* to lower *Glyptograptus dentatus* (formerly *D. "bifidus"*) zones.

In a diplomatic solution to the *Didymograptus (Didymograptellus) bifidus* argument, Bergström and Cooper (1973) suggested that, depending on the locality, both interpretations are correct. Their conclusions were that the presence of *D. bifidus* through a range of strata may have been, in part, ecologically controlled, and that the *D. bifidus* Zone is of little use for precise local or regional correlation.

At first glance, pelagic organisms such as graptolites, and nektobenthics such as conodonts seem ideal for global biostratigraphic correlations, but the foregoing demonstrates that successful biostratigraphy, no matter what an organism's mode of life, must consider what influence paleoecologic factors can have on the stratigraphic (*i.e.*, temporal) and paleogeographic distribution of species. In spite of this complication, workable biostratigraphic schemes for a particular fossil group can be constructed, and used both globally and to improve correlations based on other groups.

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The illustrated fossils are in the type collections of invertebrate and plants fossils at the Geological Survey of Canada, Ottawa.

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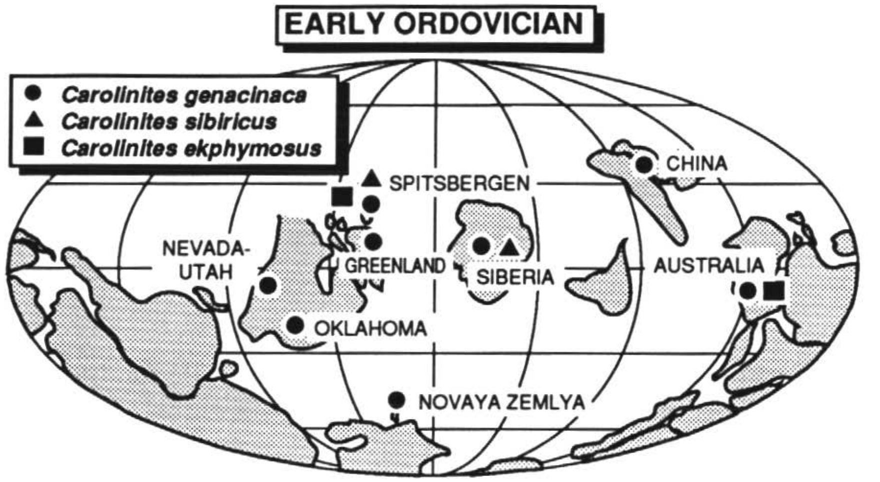

Figure 25 *Distributions of pandemic species of the telephinid trilobite* Carolinites *plotted on an Early Ordovician continental reconstruction (Scotese* et al., *1979). Modified from Fortey (1985) with additional data from Fortey (1980).*

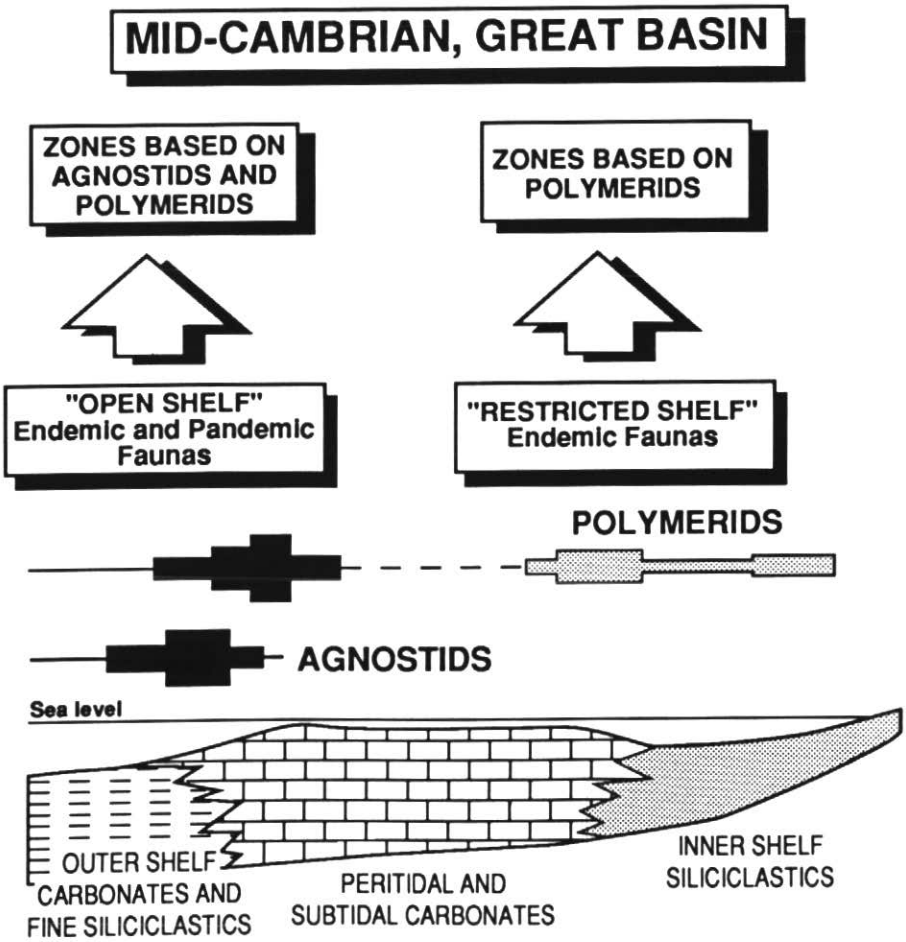

Figure 26 *Schematic transect across the mid-Cambrian shelf, Great Basin of Nevada and Utah (modified from Robison, 1976). Spindles show abundances and distributions of trilobite taxa. Differences in shading of spindles for polymerids in "open shelf" and "restricted shelf" biofacies reflect the fact that different genera dominate in these two settings (see Robison, 1976 for further discusssion). Pandemic agnostids, important for intercontinental correlation, are restricted to the outer edge of the carbonate belt and to outer shelf carbonates and fine siliciclastics ("open shelf" biofacies). Landward lithofacies are dominated by endemic polymerids ("restricted shelf" biofacies). Zonations in each of these biofacies belts are based on species of different taxa and correlation between them is often difficult.*

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