

## Chapter 26

### Graptolite palaeobiogeography

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**Abstract:** Graptolite faunas exhibited strong biogeographical differentiation during the Early Palaeozoic, particularly in the Ordovician. Skevington recognized two major faunal provinces, the high to mid palaeolatitude 'Atlantic Province' and the low-palaeolatitude 'Pacific Province'. Subsequent workers have generally accepted this pattern of graptolite distribution, but the controls on this pattern have been the subject of considerable debate. Two competing models have emerged: a surface water temperature model and a depth stratification model. It is likely that some of the physical and chemical oceanic factors that vary with latitude may also vary in a similar way along an onshore to offshore transect. Hence, it may be that both depth and surface temperature play an important role in biogeographical differentiation. Biogeography also played a critical role in the evolutionary history of graptoloids. Important examples include the origination of axonophorans in deep, offshore environments from isograptid and pseudisograptid ancestors and their subsequent migration into shallow water regions; the replacement of the Diplograptina by Neograptina in the low palaeolatitudes during the Late Ordovician extinction event; and the origination of expansograptids in the 'Atlantic' Province as shallow water endemics followed by their worldwide dispersal into the oceanic biofacies.

The palaeogeographical distribution of graptoloid graptolites (hereafter referred to simply as graptolites) has received a considerable amount of attention in recent years. Graptolites comprise the first abundant, well-preserved fossil record of macrozooplankton in Earth history, and their distribution provides a critical deep-time perspective on faunal response to changing climatic and oceanographic conditions. Two fundamental questions can be asked about the biogeography of any group of organisms: what are their patterns of distribution and what are the factors that control those patterns (Morrone 2009)? Graptolite faunas, like those of nearly all marine and terrestrial organisms, increase in species richness from the poles towards the equator and also exhibited strong biogeographical differentiation during the Early Palaeozoic, and particularly during the Ordovician. Skevington (1973, 1974) recognized two major graptolite faunal provinces: the high to mid palaeolatitude 'Atlantic Province' and the low-palaeolatitude 'Pacific Province'. Subsequent workers have generally accepted the pattern of graptolite distribution outlined by Skevington, but the controls on this distribution have been the subject of considerable debate (e.g. Berry 1960, 1962, 1979; Berry & Boucot 1972; Bulman 1964; Skevington 1974; Cisne & Chandlee 1982; Cooper *et al.* 1991; Finney & Berry 1997).

#### Historical development of graptolite palaeoecological and palaeobiogeographical models

Early studies on graptolite biogeography were motivated primarily by difficulties in precisely correlating Lower and Middle Ordovician strata between the British Isles and North America (e.g. Berry 1967; Skevington 1968). Provinciality in species distributions was variously attributed to ecological control by ocean currents and land barriers (Berry 1960), latitudinal climatic belts (Bouček 1972), water depth (Ross 1961; Berry 1962; Berry & Boucot 1972; Cisne & Chandlee 1982), water temperature (Bulman 1964) and biotic factors such as competition (Bulman

1971). Two competing models that sought to explain the controls on graptolite species distribution emerged from these studies – a surface water temperature model and a depth stratification model.

Skevington (1973, 1974) plotted faunas on Ordovician palaeogeographical maps and identified two major faunal provinces, the cool-temperate 'Atlantic Province' and the palaeotropical 'Pacific Province'. He concluded that latitudinal variation in surface water temperature exerted a primary control on this graptolite distribution pattern and noted that the provincialism increased to a maximum in the Llanvirn (now part of the Darriwilian Age), which he used as evidence for strong latitudinal gradients in temperature during the Mid Ordovician (Skevington 1974). The terms 'Atlantic Province' and 'Pacific Province' are widely used in the graptolite literature, although they are somewhat simplistic as well as misleading to the non-specialist. Therefore, throughout this paper we will simply discuss faunas that occupy high, medium or low palaeolatitudes.

Cisne & Chandlee (1982) used a depth stratification model to explain the graptolite distribution patterns in the Late Ordovician Utica Shale outcrops of the Mohawk Valley of New York State (eastern USA). These strata were deposited along the western margin of the Taconic Foreland Basin in response to long-term, regional subsidence or tilting of the craton during the Taconic Orogeny (Jacobi 1981; Quinlan & Beaumont 1984; Etensohn 1991). Cisne & Chandlee (1982) believed that graptolite faunas were depth-stratified and migrated along with westward shift of the Utica black shale over time as the foreland developed during the early Late Ordovician. Hence, Ruedemann's (1912, 1947) classic zonal scheme actually represented an ecological as opposed to 'chronostratigraphical' zonation. Finney (1986), however, examined graptolite distribution across Laurentia, including these same Mohawk Valley faunas, and concluded that the pattern was best explained by lateral differentiation by water mass specificity and not depth stratification.

Cooper *et al.* (1991) provided a detailed description of the species compositions of different graptolite biofacies and proposed a comprehensive depth stratification model for the Early (now

Early and Mid Ordovician to explain the fossil distributions. Cooper *et al.* (1991) recognized a shallow epipelagic biotope that contained cosmopolitan species found in all biofacies, a deeper mesopelagic biotope (the 'Isograptid Biofacies') composed of species that occurred only in a deep-water biofacies, and an inshore biotope (the 'Didymograptid Biofacies') that contained shelf-restricted species and cosmopolitan epipelagic taxa. Within each of these three biotopes, 'Pacific Province', 'Atlantic Province' and pandemic species were also identified.

In this model the primary influences on graptolite distribution were water depth and onshore–offshore differentiation, with surface water temperature as a less important, secondary control. In a recent study on the Early and Mid Ordovician graptolite diversity and biogeography of South China, Zhang *et al.* (2010) also found water depth and distance from the palaeoshoreline to be the main controls on local and regional distributions. Both Skivington (1974) and Cooper *et al.* (1991) primarily discussed the provincialism of the Pan-Sinograptid and the Pan-Reclinata, which includes the isograptids, didymograptids and tetragraptids (Maletz *et al.* 2009; Maletz 2010), and noted that biserial taxa (now Axonophora) tended to contain cosmopolitan taxa. Cooper *et al.*'s (1991) recognition that habitat preference was a species-level character trait accompanied the assignment of individual species (as opposed to genera) to biogeographical provinces, and represented a major step forward in our understanding of graptolite distribution.

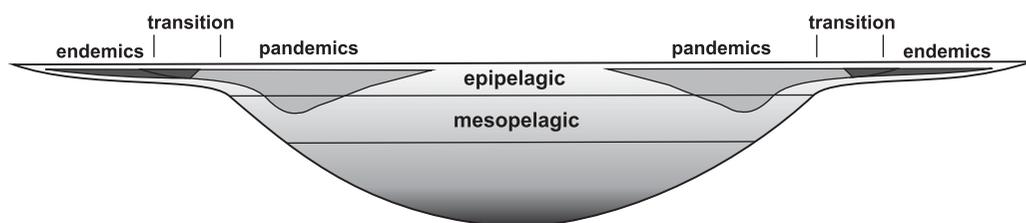
Goldman *et al.* (1995) applied the Cooper *et al.* (1991) model to Late Ordovician biserial taxa, and were able to recognize three distinct Late Ordovician diplograptid biotopes. These included a cosmopolitan epipelagic biotope that includes the species *Orthograptus quadrimucronatus*, *Rectograptus amplexicaulis*, *Amplexograptus latus*, *Diplacanthograptus spiniferus*, *Dicranograptus nicholsoni* and *Orthoretiolites hami*; a cosmopolitan mesopelagic biotope that contained most dicellograptids and dicranograptids, *Climacograptus nevadensis*, *C. tubuliferus*, *Orthograptus calcarius* and *A. fastigata*; and a cratonic endemic biotope for eastern Laurentia that included the species *Geniculograptus typicalis*, *Geniculograptus pygmaeus* and *Amplexograptus manitoulinensis*.

In addition to the discussions about the controls of biogeographical distribution, new ideas on the specific habitat of graptolites were also being proposed. Berry *et al.* (1987) and Berry & Wilde (1990) noted that graptolites could be considered ancient analogues of modern zooplankton such as copepods and euphausiids, and proposed that planktic graptolites inhabited a denitrified low oxygen zone in Early Palaeozoic oceans where the abundant availability of nitrogen compounds provided a rich source of nutrients. In modern oceans, this oxygen-poor, nutrient-rich layer tends to be most extensively developed beneath highly productive low-latitude surface waters, but it can also form in upwelling regions at higher latitudes where organic productivity is high. Berry & Wilde (1990) also suggested that the denitrified low-oxygen zone was more widespread in the stratified Early Palaeozoic oceans than it is in today's ventilated oceans, providing an extensive habitat for graptolites, and that graptolite evolutionary trends were linked to depth migration of this layer over time.

Based on the graptolite distribution patterns found in the Ordovician Vinini Formation of Nevada (western USA), Finney & Berry (1997) proposed that the main graptolite biotope was restricted to a narrow region just oceanward of the shelf-slope break where upwelling occurred. They noted that, in several intervals in the Vinini Formation, substantial thicknesses of black shale interpreted to be deposited in a deep ocean basin and considered classic graptolite biofacies contained almost no graptolites. Building on Berry *et al.* (1987) and Berry & Wilde's (1990) habitat model, and using the distribution of zooplankton in the modern eastern Pacific Ocean as an analogue for Early Palaeozoic graptolite distributions, Finney & Berry (1997) suggested that the nutrient-poor open oceans were essentially devoid of graptolites and that inner shelf waters were only occasionally inhabited by a few opportunistic species. Depth stratification and lateral differentiation of faunas did occur, but only within the narrow outer shelf to proximal slope environment. It should be noted that the open ocean as a desert model of Finney & Berry (1997) does not adequately explain the rich graptolite successions that occur in places that have been interpreted as representing open ocean environments such as the Southern Uplands of Scotland (Zalasiewicz *et al.* 1995) and Peel River in the Canadian Cordillera (Lenz & Chen 1985). Egenhoff & Maletz (2007) noted that the majority of the species that Cooper *et al.* (1991) and Cooper (1999) referred to as their mesopelagic biofacies are instead part of an epipelagic biofacies, thus supporting the ideas of Finney & Berry (1997). Figure 26.1, which depicts a cross-section through a hypothetical Palaeozoic ocean, illustrates our favoured model of graptolite palaeoecology.

Most recently, Vandenbroucke *et al.* (2009) returned to a surface water temperature model to explain graptolite distribution. They used the hierarchical clustering method TWINSPAN and constrained seriation analysis to test for ecological structure in presence/absence data of graptolites occurring in the lower Sandbian *Nemagraptus gracilis* Biozone. Vandenbroucke *et al.* (2009) defined two main clusters of graptolite species that may represent the inhabitants of cosmopolitan mesopelagic and epipelagic biotopes. Within these main groupings constrained seriation produced higher-order clusters defined by palaeolatitudinal position. Their analyses suggested that these latitudinally distinct graptolite biotopes displayed a sharp equator-to-pole gradient, which in turn was evidence for a similarly pronounced gradient in sea surface temperature. On the other hand, Cooper & Sadler (2010) provided quantitative evidence based on study of species longevity and extinction risk, suggesting that different graptolite taxa that co-occur within deep-water assemblages inhabited separate, depth-stratified biotopes. In addition, Mitchell *et al.* (2008) provided evidence for a mixed biofacies at fairly high latitude.

It is clear from the preceding review that no consensus on the depth stratification v. surface temperature control on graptolite distribution yet exists. We think, however, that it is very likely that some of the physical and chemical oceanic factors that vary with latitude may vary in a similar way along an onshore–offshore transect. These may include temperature, oxygenation, nutrient cycling, changes in phytoplankton communities or some



**Fig. 26.1.** Model of graptolite palaeoecology showing a cross section through a hypothetical Palaeozoic ocean (adapted from Egenhoff & Maletz 2007). The model incorporates both depth and onshore–offshore position as controlling factors on graptolite distribution.

combination of these factors. Thus, the answer to the controversy probably lies somewhere in the middle – both depth stratification and surface temperature play an important role in biogeographical differentiation (see also Cooper *et al.* 2012).

### Graptolite biogeography revisited

Recent work on graptolite biogeography suggests that several new ideas need to be incorporated into the seminal models of Skevington (1973, 1974), and Cooper *et al.* (1991). First, as noted above, we think that a synthesis of the depth stratification and surface temperature distribution control models that is based more directly on how the physical and chemical character of ocean water changes with latitude, depth and distance from shore is required to explain graptolite biogeographical patterns. This is clearly beyond the scope of this paper although we provide an example below that we think illustrates such a synthesis. Second, recent studies have demonstrated the existence of species that are endemic not just to a particular province but to an individual palaeocontinent or depositional basin. For example, Goldman *et al.* (1995) described several Late Ordovician species (*Geniculograptus typicalis*, *G. pygmaeus* and *Amplexograptus manitoulinensis*) that are endemic to Laurentia. Furthermore, these taxa appear to be completely restricted to the northern Appalachian Basin and a portion of the North American Midcontinent. Similarly, Chen *et al.* (2005) have noted that several Late Ordovician biserial taxa such as *Neodiplograptus charis*, *Sudburigraptus angustifolius* and species of *Tangyagraptus* have only been recorded from the Yangtze Platform in South China. Hence, although graptoloids were pelagic organisms, some were apparently endemic to individual depositional basins or perhaps to persistent but isolated oceanic circulation cells.

A third modification of existing models is the recognition that the biserial Axonophora also exhibit provinciality. Although Skevington (1974) and Cooper *et al.* (1991) focused mainly on the Pan-Sinograptia and the Pan-Reclinata, they also noted that the Axonophora tended to be cosmopolitan taxa. It is now clear not only that biserial graptolites exhibit provinciality, but that biogeography also played an important role in the evolution of the Axonophora (Zhang & Chen 2007, 2008; Maletz 2010).

Finally, there have been relatively few studies that explore the geographical origin of graptolite sub-clades (in both a regional and an environmental sense) and their subsequent migration and expansion. We will discuss several examples that examine the geographical origin of graptolite sub-clades and their subsequent migration and expansion in a later section of this paper. Perhaps most importantly, recent studies on graptolite evolution have utilized parsimony-based techniques to produce phylogenetic trees that can be used in biogeographical analysis (e.g. Mitchell *et al.* 2007a; Maletz *et al.* 2009; Melchin *et al.* 2011).

### Ordovician graptolite biogeography

#### *Tremadocian*

Although the origin of planktic graptolites has traditionally been linked with the base of the Tremadocian and has been considered indicative of this important chronostratigraphical level (see Erdtmann 1982, 1988; Cooper 1999, among others), it is the First Appearance Datum (FAD) of the conodont species *Iapetognathus fluctivagus* that correlates the base of the Tremadocian Stage (Cooper *et al.* 2001). Planktic graptolites first appeared slightly above the base of the Ordovician and quickly became one of the major groups of planktic organisms in the Early Palaeozoic oceans. They originated from a benthic ancestor in the Palaeozoic shelf regions, presumably from a form similar to the genus

*Dictyonema*, but the details are difficult to ascertain owing to the poor and incomplete fossil record of these earlier benthic forms. Rigby (1997) suggested the origination of the planktic lifestyle through paedomorphosis in an organism with a planktic larval stage, a view that is supported by a recent phylogenetic analysis that shows the extant pterobranch *Rhabdopleura* nested among the Graptolithina (Mitchell *et al.* 2013).

The earliest planktic species belonging to the genera *Staurograptus* and *Rhabdinopora* are found commonly in continental slope deposits and, thus, Cooper (1999) interpreted them to have inhabited the deep-water biotope, from which they expanded into the shallow-water shelf environment and also into the deeper oceanic zone. Benthic graptolites are most common in shelf areas and occurrences in slope and basin environments are generally the result of transportation. As few benthic faunas are known to be preserved in their preferred environment (e.g. Erdtmann 1976), it is impossible to tell precisely where the earliest planktic forms of the genus *Rhabdinopora* originated.

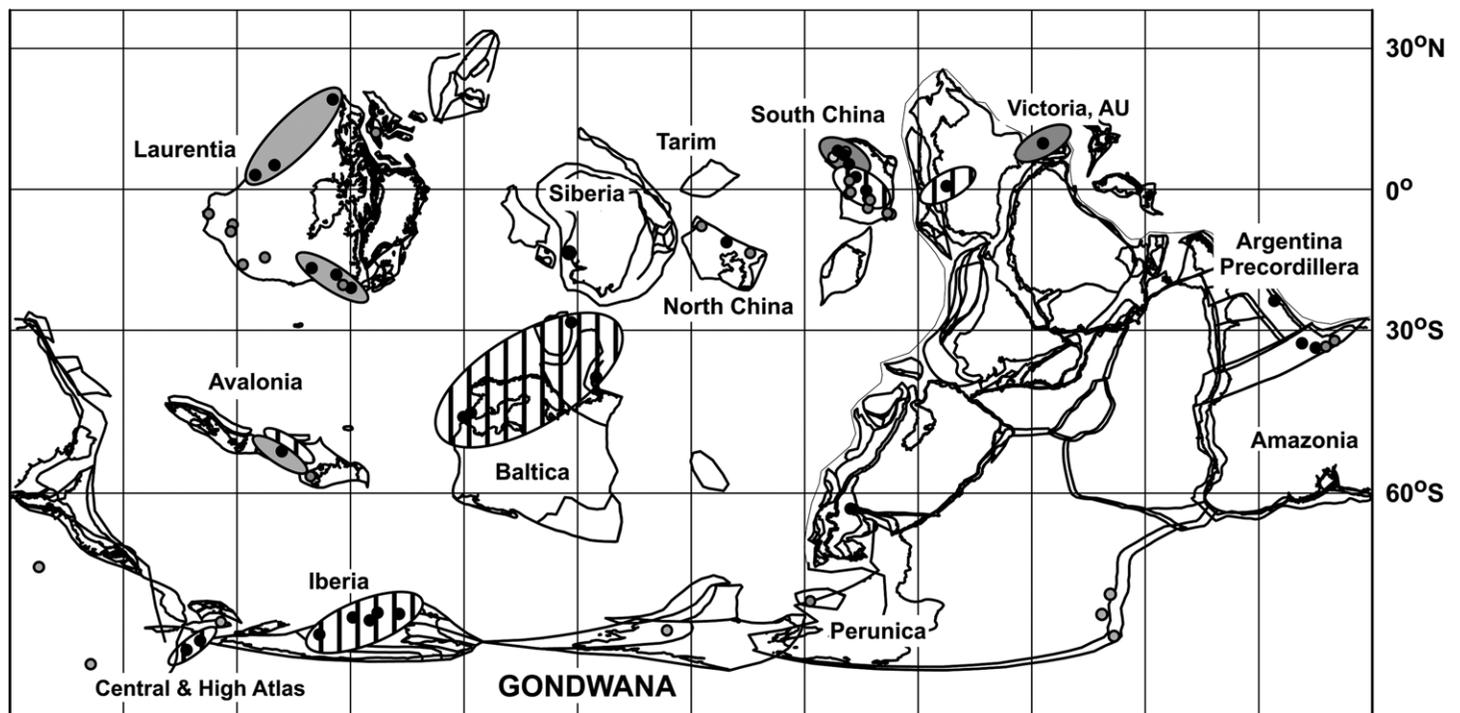
A biogeographical differentiation among the earliest planktic graptolites was not present in the early Tremadocian, and the graptolite biozones proposed by Cooper *et al.* (1998) and Cooper (1999) can be used on a worldwide scale. The faunas are of low diversity, but a slight depth differentiation of taxa can be recognized (Cooper 1999).

A considerably more diverse graptolite fauna appeared in the upper Tremadocian, including a small radiation of biostratigraphically useful *Paradelograptus* species (Jackson & Lenz 1999, 2000, 2003). Egenhoff & Maletz (2007) referred the paradelograptids to a mesopelagic, pandemic biofacies based on their wide distribution, and general absence in shallow-water environments. Species of another common upper Tremadocian genus, *Kiaerograptus*, are mostly restricted to the shallow-water shelf of high-latitude regions, although the distribution of *Kiaerograptus supremus* appears to indicate a deep-water preference for this species. *Paradelograptus* species have been successfully used to subdivide the upper Tremadocian of the Yukon Territory, Canada (Jackson & Lenz 1999, 2000, 2003), but are not well known from most regions owing to their small size and propensity for being overlooked during sampling. However, they are uncommonly found in other localities and hence may represent cosmopolitan species that are not restricted biogeographically (Rushton *et al.* 1986; Erdtmann *et al.* 1987; Williams & Stevens 1988).

The genus *Bryograptus* is probably the oldest genus that can be used as an index for provinciality of Ordovician graptolite faunas. Recently, Maletz *et al.* (2010) revised the genus and documented its biogeographical restriction to the high palaeolatitudes. Another candidate for the indication of early graptolite faunal provinciality may be '*Kiaerograptus*' *supremus* Lindholm, a two-stiped dichograptid from the upper Tremadocian of Scandinavia and Bolivia (Lindholm 1991; Maletz & Egenhoff 2001). Maletz & Egenhoff (2001) did not detect a strong faunal provincialism in the late Tremadocian, but considered the genus *Psigraptus* to be biogeographically restricted in its distribution to the low palaeolatitudes. However, *Psigraptus* occurs in a relatively short biostratigraphical interval and its apparent absence elsewhere may be due to the appropriate stratigraphical levels not having been sampled.

#### *Floian*

Ordovician graptolite provincialism is probably best known and described from the late Floian to early Darriwilian (Early to Mid Ordovician) time interval (Fig. 26.2). Pendent didymograptids, which are now known to belong to a number of genera that are differentiated by their proximal end structures (Cooper & Fortey 1982; Gutiérrez-Marco 1986; Maletz 1994, 2010), are frequently used in the biostratigraphy of the interval. Misidentifications of these largely provincial faunal elements have often led to



**Fig. 26.2.** Early Mid (Dapingian, 470 Ma) Ordovician palaeocontinent reconstruction map showing graptolite localities and distribution of graptolite biofacies. Black dots are localities that have graptolite successions during the Dapingian; grey dots are in our locality list but have no Dapingian graptolites. Grey shaded ovals indicate oceanic (isograptid) biofacies and striped ovals indicate shelf (didymograptid) biofacies. Note that most low-palaeolatitude graptolite successions of Dapingian age belong to the offshore oceanic biofacies whereas middle- to high-palaeolatitude successions tend to contain shelf assemblages. Adapted from Cooper *et al.* (1991). The base map is from BugPlates (Torsvik 2009) and the localities are listed in the Appendix.

erroneous correlations, for example the correlation of the *Didymograptellus bifidus* Biozone (upper Floian) of North America with the Llanvirnian *Didymograptus artus* and *Didymograptus murchisoni* biozones (mid Darriwilian) of Scandinavia (see Berry 1960, 1967; Skevington 1963; Cooper & Fortey 1982; Maletz *et al.* 2005). These erroneous correlations in turn led to misunderstandings of biogeographical affinity.

The Floian interval witnessed the emergence of a dramatic increase of both provincialism and endemism in graptolite faunas. Faunal endemism is best known from the high palaeolatitudes in the early Floian, but a considerable amount of endemism developed in the late Floian in low palaeolatitudes as well.

Egenhoff & Maletz (2007) discussed the faunal composition of the base of the Floian in the stratotype section at Diabasbrottet, Västergötland in detail and recognized both endemic and cosmopolitan faunal elements. The succession exhibits an endemic fauna of early two-stiped dichograptids included in the genus *Cymatograptus* that originated in the lower part of the *Tetragraptus phyllograptoides* Biozone (equivalent of the *Tetragraptus approximatus* Biozone; Maletz *et al.* 1996; Toro & Maletz 2008). *Tetragraptus phyllograptoides* from this interval represents the oldest endemic faunal element of the Tetragraptina. It is found only in Scandinavia (Baltica) and Gondwanan South America (Toro & Brussa 2003), both of which occupied high palaeolatitude regions during the Floian.

Another provincial genus is *Baltograptus*, now known from all high palaeolatitude regions in the world (Maletz 1994; Toro 1996; Toro & Maletz 2007). The genus, originally possessing a slightly declined two-stiped rhabdosome (*Baltograptus geometricus*: Törnquist 1901), evolved into a variety of rhabdosome shapes from sub-horizontal to declined, deflexed and pendent. It is especially common and diverse in the Upper Floian of Scandinavia (Maletz & Ahlberg 2011) and southwestern China (Mu *et al.* 1979).

Provinciality is strongly developed in the low palaeolatitudes from the mid Floian *Pendeograptus fruticosus* Biozone onwards,

as demonstrated by the occurrence of *Expansograptus nitidus* (Hall) and *Expansograptus pennatulus* (Hall) (Williams & Stevens 1988) exclusively in palaeotropical localities. In the Upper Floian (Chewtonian of the Australasian succession; VandenBerg & Cooper 1992), the apparent distinctiveness of low-palaeolatitude faunas increases with the origination of the pendent *Didymograptellus bifidus* (Hall) and *Yutagraptus mantuanus* Riva (Maletz 2010). Although *Didymograptellus bifidus* became extinct at the end of the Floian, *Yutagraptus mantuanus* (Riva 1994) and related forms survived into the early Darriwilian (identified as *Didymograptus bifidus* in Ross & Berry 1963; Finney & Ethington 1992; Riva 1994). The mid-continent North American species *Pseudophyllograptus archaios* (Braithwaite) from the *Didymograptellus bifidus* Biozone represents another unique faunal element of low palaeolatitudes (cf. Braithwaite 1976; Maletz *et al.* 2005).

#### Dapingian

The emergence and diversification of the isograptids (Harris 1933, Cooper 1973), a group of two-stiped reclined graptoloids, is the main characteristic of the Dapingian Age. The species are important as biostratigraphical index species for the cosmopolitan graptolite faunas and are used on a worldwide scale. Considerable endemism is seen in faunas of the high palaeolatitudes, in which members of the genus *Azygograptus* are found in monospecific, shallow-water assemblages (Zalasiewicz 1984; Beckly & Maletz 1991). *Azygograptus suecicus*, especially, has been used as a biostratigraphical index species in China (e.g. Mu *et al.* 1979; Zhang *et al.* 2007) as it is a common and easily recognizable species. *Expansograptus hirundo* appears to be another important endemic index species in the Dapingian (Mu *et al.* 1979; Zhang *et al.* 2007), but its exact stratigraphical range is uncertain. Maletz (2005) discussed the species and its stratigraphical range and suggested abandoning the *Expansograptus hirundo*

Biozone as it refers to an extremely long stratigraphical interval from the Lower Dapingian to the Lower Darriwilian. Very little is known about the endemic or relatively onshore graptolite faunas in the low palaeolatitudes as successions are generally carbonate-dominated and shelf graptolite faunas are rare or not preserved in the Dapingian. In stark contrast with high palaeolatitude assemblages, most low-palaeolatitude successions are dominated by diverse isograptid assemblages (e.g. Harris 1933; Williams & Stevens 1988). Figure 26.2 illustrates the dominance of shelf assemblages (Didymograptid biofacies) in high palaeolatitude regions and offshore assemblages (Isograptid biofacies) in low-palaeolatitude regions. Upper Dapingian graptolite faunas (upper Castlemainian to Yapeenian) have rarely been described from shelf regions.

### Darriwilian

A dramatic change in the composition of graptolite faunas occurred during the Darriwilian, in both endemic and cosmopolitan faunas. Lower Darriwilian graptolite faunas are highly diverse, consisting largely of multiramous to pauciramous taxa, associated with early axonophorans. The diversity plunged considerably during the mid Darriwilian and only recovered slowly (Cooper *et al.* 2004). A distinct faunal provincialism is, however, discernable through most of the interval.

High palaeolatitude elements include the extremely common and characteristic pendent and deflexed didymograptids of the genera *Aulograptus* and *Corymbograptus* (e.g. Bouček 1973; Cooper *et al.* 2004), which are stratigraphically succeeded by the genus *Didymograptus* (Cooper & Fortey 1982; Maletz 1994, 1997a). These genera died out before the end of the Darriwilian without leaving any descendants. Several early axonophorans, including *Undulograptus formosus* (Mu & Lee 1958) and *Oelandograptus oelandicus* (Bulman 1963), have also been identified as possibly endemic to the Atlantic Faunal Province. The first recorded species of *Normalograptus* appear in Baltoscandia in the mid Darriwilian.

The upper Darriwilian interval is dominated by various biserials, of which some appear to be endemic to the high palaeolatitudes (see Maletz *et al.* 2011), but the faunas are generally not known well enough for detailed statements. Only easily recognizable forms like *Gymnograptus linnarssoni* (Moberg 1896), *Pseudamplexograptus distichus* (Eichwald 1840), and the genus *Proclimacograptus* (Maletz 1997a) can be recognized as endemic to the high palaeolatitudes (Maletz 1997a).

In the lower Darriwilian the low-palaeolatitude successions include a number of endemic faunal elements such as the genus *Paraglossograptus* and the very common axonophoran *Archiclimacograptus decoratus* (Maletz & Mitchell 1995). Generally, however, graptolite biodiversity decreases considerably owing to the extinction of most multiramous to pauciramous forms, and provinciality is more difficult to observe owing to the monotonous composition of mid to upper Darriwilian graptolite faunas, which consist largely of various archiclimacograptids and early orthograptids. The global appearance of the horizontal and reclined biserial taxa, *Dicellograptus*, *Dicranograptus* and *Nemagraptus*, in the upper Darriwilian also adds to the more cosmopolitan aspect of late Mid and early Late Ordovician faunas.

### Sandbian

The base of the Sandbian Stage and thus of the Upper Ordovician Series is correlated by the first appearance of *Nemagraptus gracilis*. The Sandbian comprises the *N. gracilis* and *Climacograptus bicornis* graptolite biozones, and represents a time of reduced provinciality (Finney & Bergström 1986). A proliferation of the Diplograptina (primarily species of *Diplograptus*,

*Dicranograptus*, and *Climacograptus*) occurred during the Sandbian as the primitive members of the Pan-Reclinata waned in diversity and the derived biserials became the dominant faunal elements on all continents. Diverse assemblages of *Archiclimacograptus*, *Climacograptus*, *Orthograptus*, *Hustedograptus*, *Dicellograptus* and *Dicranograptus* occur in nearly all tropical to high-latitude regions around the world (see Vandenbroucke *et al.* 2009 and references therein). The global appearance of *N. gracilis*, followed by *Climacograptus bicornis* and *Orthograptus calcareatus* species group members, and a profusion of large *Dicranograptidae* species makes the Sandbian Stage one of the easiest to correlate across the globe.

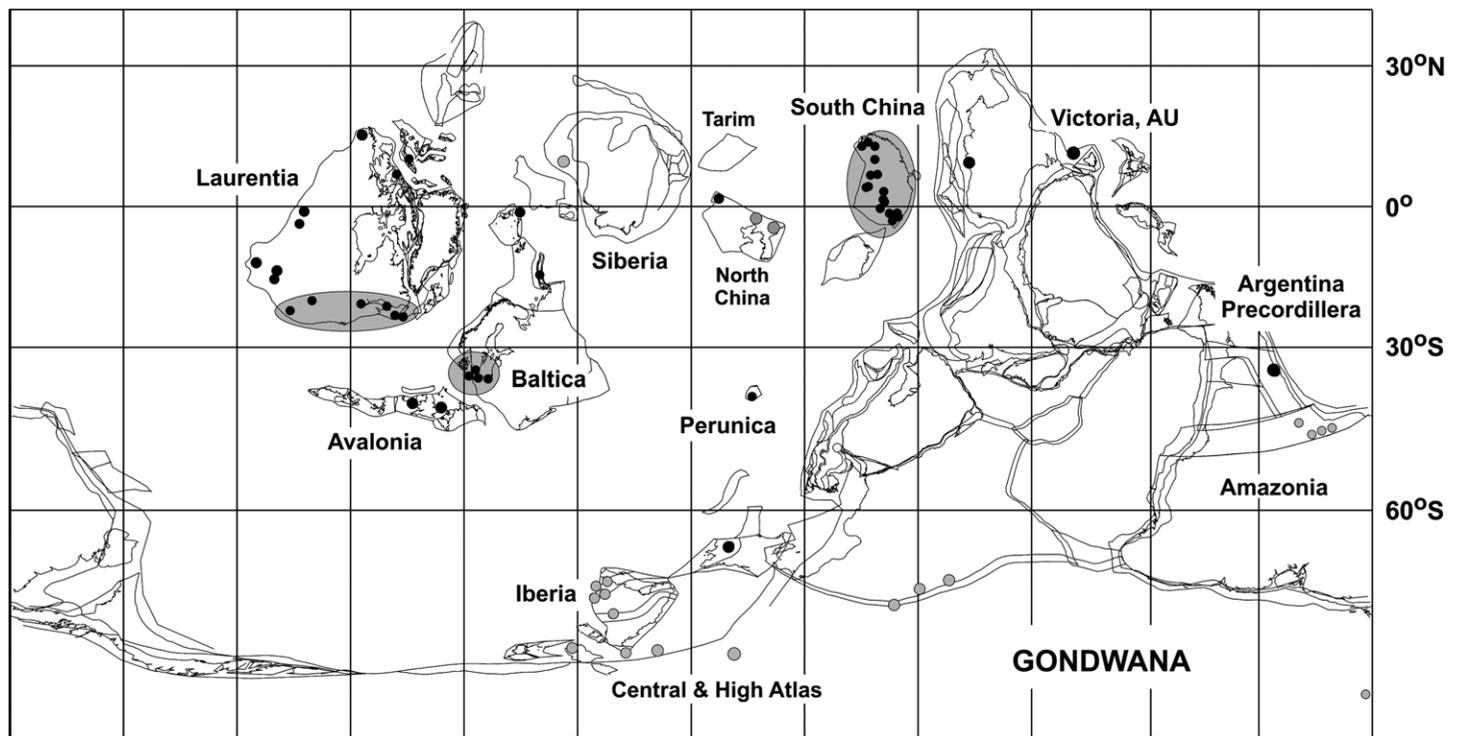
Provinciality began to increase again in the late Sandbian, when a number of graptolite species that are restricted to middle and high palaeolatitude localities such as Baltoscandia and Avalonia appear. Taxa not found in low-palaeolatitude localities include *Oepikograptus bekkeri*, *Hustedograptus uplandicus*, *Archiclimacograptus rugosus* (= *Diplograptus molestus* Thorslund), *Archiclimacograptus compactus*, *A. vasaе*, *A. skagensis*, *Normalograptus rotundatus* and *N. kukersianus* (e.g. Elles & Wood 1908; Hadding 1913; Hede 1951; Jaanusson & Skoglund 1963; Nilsson 1977; Williams *et al.* 2003). Generally, this fauna is dominated by a distinctive sub-group of archiclimacograptids, a few morphologically unusual taxa (e.g. *O. bekkeri*) and species of *Normalograptus*. As noted above, recent work by Vandenbroucke *et al.* (2009) also suggests that provinciality and a distinct onshore–offshore differentiation of faunas occurred in the Sandbian.

### Katian

Provinciality increased throughout the Katian, perhaps in response to the onset of Late Ordovician climate change. Graptolites from low-palaeolatitude regions such as Victoria (Australia), Scotland, South China and western Laurentia (including Trail Creek, Idaho; west Texas; and the Canadian Cordillera) consist primarily of species of *Orthograptus*, *Rectograptus*, *Dicranograptus*, *Dicellograptus*, *Amplexograptus* and *Climacograptus*, with a small radiation of archiretiolids (Berry 1960; Carter & Churkin 1977; Lenz & Chen 1985; Vandenberg & Cooper 1992; Zalasiewicz *et al.* 1995). In Baltoscandia, the rich faunas characteristic of the Darriwilian and Sandbian disappear, and are overlain by a relatively graptolite-poor lower Katian interval of grey shale and carbonate (Hede 1951; Nilsson 1977). This interval, however, does contain small sub-clades of *Diplograptus* and derived *Archiclimacograptus*, the diversity of which is not well understood. Faunal differences make it increasingly difficult to correlate between high- and low-palaeolatitude localities (e.g. Wales and Scotland) in the lower and middle Katian, although better sampling and the recovery of less abundant taxa has led recently to more precise correlations (e.g. Zalasiewicz *et al.* 1995; Williams *et al.* 2003).

As previously mentioned, a few endemic species belonging to the genus *Geniculograptus* evolved and thrived in eastern and southeastern Laurentia (northern Appalachian basin, North American mid-continent and the Arbuckle Mountains of Oklahoma). The absence of these species in western Laurentia resulted in a long-standing controversy over correlations between eastern and western Laurentia (Riva 1969, 1974; Berry 1970, 1971, 1977; Finney 1986). The controversy was largely solved by the recognition of an unconformity that spans the lower Katian in the Marathon, west Texas succession (Bergström 1978; Goldman *et al.* 1995), but *Geniculograptus* is nonetheless absent from all low-palaeolatitude localities that have lower Katian graptolite successions.

Middle- and high-palaeolatitude faunas from Avalonia and Baltoscandia contain a subset of species different from those found in tropical successions, including such provincial taxa as *Climacograptus styloideus*, *Pseudoclimacograptus clevensis* and



**Fig. 26.3.** Late Ordovician (Katian, 450 Ma) palaeocontinent reconstruction map showing the distribution of localities with graptolite successions. Black dots are localities that have graptolite successions during the Katian; grey dots are localities without Katian graptolites. Grey shaded ovals indicate regions with endemic species. The base map is from BugPlates (Torsvik 2009) and the localities are listed in the Appendix.

*Normalograptus pulchellus*. The distribution of localities with well-known Katian graptolite successions is illustrated in Figure 26.3.

In Wales, Williams *et al.* (2003) described an interesting Middle Katian differentiation of faunas along an onshore–offshore transect. At Cardigan (south Pembrokeshire), shale and mudstones representing an open marine environment contain a moderately diverse graptolite fauna in the *Dicranograptus clingani* and *Pleurograptus linearis* biozones. At Whitland, a section thought to represent a near-shore environment, the Mydrim (or *Dicranograptus*) Shales contain a low-diversity *Dicranograptus clingani* Zone fauna generally similar to that found at Cardigan (Zalasiewicz *et al.* 1995). Higher in the section, however, faunal diversity decreases even further, and the fauna becomes completely dominated by several species of *Normalograptus*. Zalasiewicz *et al.* (1995) noted that the Mydrim to Sholeshook transition represents a shallowing-upwards sequence and that, even in the lowermost beds, most offshore or deep water taxa are absent. They also suggested that the marked diversity decline in post-*D. clingani* Zone age rocks might be related to either decreasing water depth or water temperatures, postulating that the transition from laminated graptolitic mudstones to bioturbated, nearly barren mudstones, and then to shallow shelf carbonates may record a preglacial climatic deterioration. Thus, both the sedimentological changes that occur up-section at Whitland and the faunal changes are consistent with the end-Ordovician extinction model of Chen *et al.* (2005), even though they occurred during the Katian.

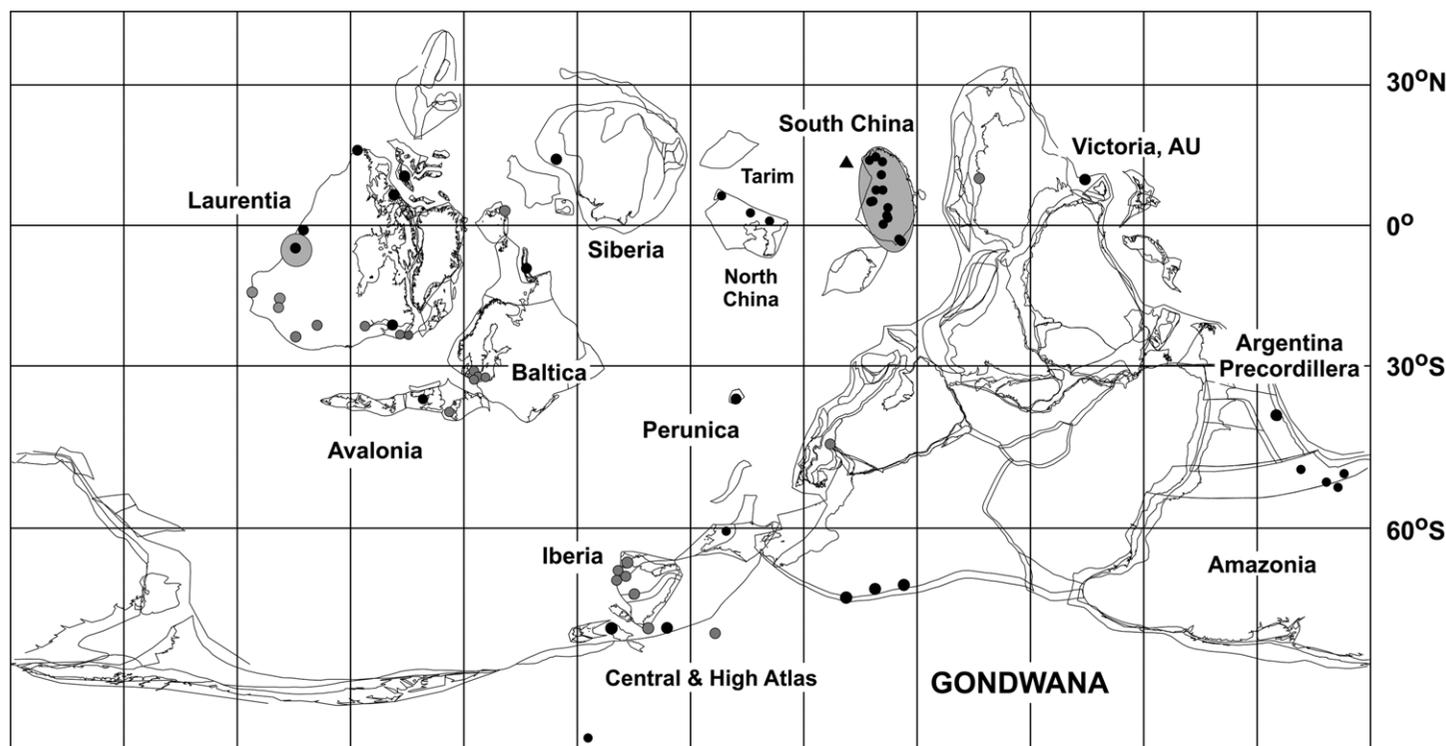
Diverse faunas were widespread in the low palaeolatitudes during the late Katian (*Paraorthograptus pacificus* Zone) but higher latitude successions are poorly known and those that have been described are of low diversity (Storch 2006). Some endemism may occur, particularly in South China faunas (e.g. species of *Tangyagraptus*, Chen *et al.* 2005), although recent intensive sampling efforts outside of South China have decreased the number of species that previously appeared to be endemic (Goldman *et al.* 2007; Storch *et al.* 2011).

#### Hirnantian

One of the greatest ecological and evolutionary replacements to affect graptolites occurred within the Hirnantian Age. The diverse low-palaeolatitude Diplograptina faunas were rapidly replaced by species of Normalograptidae and their descendants (the Neograptina) that invaded from the southern high latitudes (Chen *et al.* 2005). Most of the Diplograptina extinction and replacement occurred at the base of the *Normalograptus extraordinarius* Zone, but in South China, a few Diplograptina faunal elements lasted well into the *Normalograptus persculptus* Zone (Chen *et al.* 2005) before becoming extinct prior to the beginning of the Silurian Period. The Diplograptina extinction was coincident with the radiation of Neograptina, which continued on into the Early Silurian. Chen *et al.* (2005) also noted the possibility that the South China platform represented a geographical refugium for certain members of the Diplograptina, as shown by their longer duration there than anywhere else in the world. However, the Yangtze region of South China is rich in graptolite-bearing sections and has been intensively sampled, and new data from Nevada based on similarly intensive sampling (Mitchell *et al.* 2007b; Storch *et al.* 2011) show that some of the Diplograptina persist through much of the Hirnantian there as well, indicating that South China was not the sole refugium for these typically pre-extinction forms during the Hirnantian (Fig. 26.4), or that the effects of sampling on palaeobiogeographical patterns are critically important and must be taken into consideration.

#### Silurian graptolite biogeography

Silurian graptolite faunas have been widely regarded as showing a lower degree of provincialism than those of the Ordovician. This has been most apparent in the fact that the historically ‘standard’ graptolite biozonations of Britain (e.g. Rickards 1976) could be readily applied through much of the Silurian record in many parts of the world. As more detailed regional biostratigraphical



**Fig. 26.4.** Latest Ordovician (Hirnantian, 445 Ma) palaeocontinent reconstruction map showing graptolite localities. Both high- and low-palaeolatitude localities now contain graptolite faunas dominated by species of *Normalograptus* and its descendants. Black dots are localities that have graptolite successions during the Hirnantian; grey dots are in our database but have no Hirnantian graptolites. Grey shaded ovals indicate regions where a remnant *Diplograptina* fauna persists into the *Normalograptus persculptus* Zone. The base map is from BugPlates (Torsvik 2009) and the localities are listed in the Appendix.

studies began to emerge from several different parts of the world, however, significant faunal differences began to emerge.

Legrand (2009) recently summarized the results of over three decades of study of the strongly endemic late Hirnantian–early Rhuddanian graptolite faunas of the NW African part of Gondwana. Štorch (1998) considered the North African part of Gondwana to represent a distinct palaeobiogeographical region of cool-water faunas through the Llandovery and Wenlock. The degree of endemism of these faunas, however, appears to be strongest in the late Hirnantian–Rhuddanian (Legrand 2009) and declines somewhat later in the Llandovery and Wenlock, when the North African graptolite faunas bear somewhat stronger affiliations with those of peri-Gondwanan Europe (Štorch & Massa 2003). Maletz *et al.* (2002), however, showed that small endemic faunas remained in the South American part of Gondwana within the Ludlow.

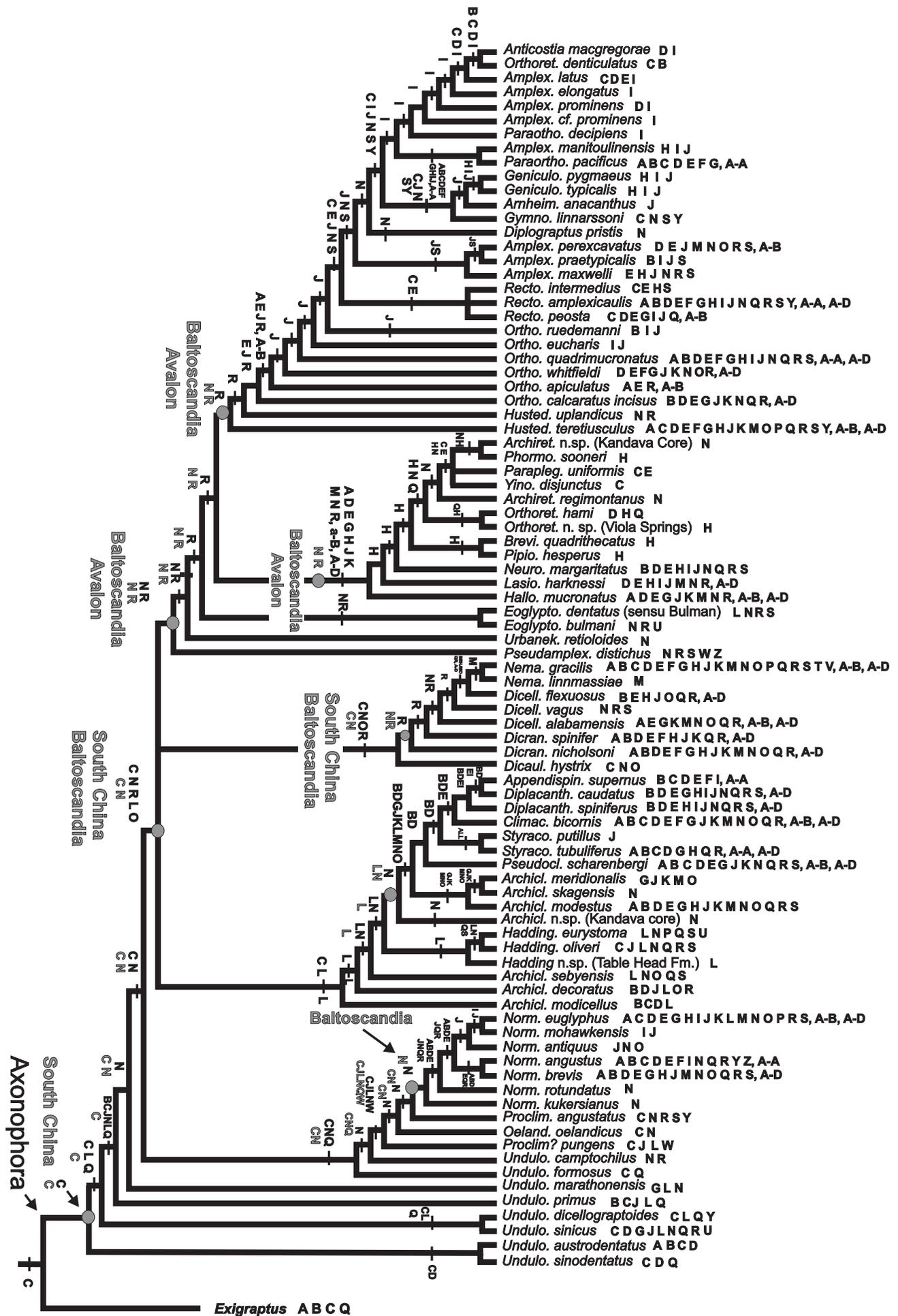
Melchin (1989) made comparisons between the Llandovery faunal assemblages of Arctic Canada and those of many other regions and found that a number of taxonomic groups were restricted to the palaeotropical regions of Laurentia, Baltica, Siberia, Kazakhstan and China. Melchin found that the distribution of these taxa could be used to recognize a circum-equatorial faunal province. This same faunal region was referred to as the ‘Pacific Province’ by Rickards *et al.* (1990). Both Rickards *et al.* (1990) and Lenz & Melchin (1991) suggested that this circum-equatorial or Pacific faunal province could be recognized in the Wenlock. The data provided by Lenz & Melchin (1991), with recent updates summarized by Lenz & Kozłowska-Dawidziuk (2001, 2002) and Lenz *et al.* (2012), indicate that faunal differences between Arctic Canada and the Iapetus/Rheic Ocean regions are relatively strong in the mid-Sheinwoodian, but weaker in the late Sheinwoodian to late Homerian.

Rickards *et al.* (1990) and Štorch (1998) described the patterns of faunal differentiation within the Iapetus and Rheic Ocean systems. Both studies concluded that there appears to be

some degree of latitudinal control on the faunas within these regions. In particular, Štorch (1998) noted that the lower palaeolatitude regions of Avalonia and southern Baltica represented transitional faunas between the cooler-water faunas of the peri-Gondwanan and circum-equatorial regions. In addition, however, both Rickards *et al.* (1990) and Štorch (1998) suggested that there are also significant differences within these regions owing to differences in palaeoenvironment – particularly along a gradient from shelf to basin (Štorch 1998, fig. 2). We refer readers to Štorch (1998, fig. 3) for a palaeogeographical map that displays the most current ideas on graptolite provinciality in the Silurian Period. In addition to these studies, there have been a number of papers that deal with the patterns of faunal distribution of particular taxonomic groups (e.g. Koren’ & Suyarkova 1994; Loydell *et al.* 1997; Loydell & Maletz 2002; Chokey-Jones *et al.* 2003; Williams & Zalasiewicz 2004; Melchin 2007).

There has been very little study of the palaeobiogeographical patterns of Ludlow and Pridoli graptolites. Most authors have noted that the degree of provincialism was relatively low and this has been attributed to the progressive closure of the Iapetus and Rheic Ocean systems and the northward movement of the peri-Gondwanan terranes that bear graptolitic records into progressively lower palaeolatitudes (e.g. Koren’ 1979; Berry & Wilde 1990). No recent studies have been undertaken that focus on the palaeobiogeography of Ludlow–Pridoli graptolites. Nevertheless, comparison of biostratigraphical data from Kazakhstan (Koren’ 1989), northern Laurentia (Lenz 1988, 1990) and Bohemia (Příbyl 1983) shows that there are significant differences in their faunal lists, suggesting that it may be possible to extend the recognition of the earlier Silurian graptolite faunal provinces into the Ludlow (Rickards *et al.* 1990) and possibly also the Pridoli.

In summary, it is now clear that there are important taxonomic differences between graptolite faunas of different parts of the world through all or most of the Silurian. In addition, at least some of these differences are consistent with faunal differentiation



along roughly palaeolatitudinally distributed belts. However, these patterns require considerably more analysis based upon: (1) comprehensive, quantitative documentation of taxon distribution patterns and comparison of faunal similarities between regions for successive time slices; and (2) distinction of those faunal differences that are the result of palaeogeographical patterns from those caused by regional differences in palaeoenvironment/biotope (e.g. Boucot & Chen 2009).

### Devonian graptolite biogeography

Devonian graptoloid faunas are of low diversity and, although found on nearly every continent, show no apparent biogeographical provinciality. Jaeger (1978) discussed a worldwide distribution of Lower Devonian graptolite faunas, but modern palaeogeographical reconstructions indicate an increasing restriction to equatorial regions (Berry & Wilde 1990). Lenz *et al.* (1996) noted that, at least in southwestern Europe, Lower Devonian graptolites are usually restricted to outer shelf regions and are not found in inner shelf areas, an indication that the last refuge of the planktic graptoloids may have been in the wide expanses of the Palaeozoic oceans and not the shelf regions in which they may have been exposed to stronger competition by other planktic organisms. Koren' (1979) suggested that this restriction of Devonian planktic graptolites, both in terms of biofacies and palaeogeographical extent, may have been a significant factor in their final extinction.

### Historical biogeography

Traditionally, the difference between historical and ecological biogeography was one of scale – historical biogeography analyses the distribution patterns of species and higher taxa over larger spatial and temporal scales than does ecological biogeography (Crisci 2001; Morrone 2009). With the advent of phylogenetic systematics (Hennig 1966), however, historical biogeographical approaches were adapted to consider phylogenetic hypotheses as the basis for inferring biogeographical history (see Posadas *et al.* 2006; and Morrone 2009 for a review of methods in historical biogeography). A pre-phylogenetic palaeontological approach would be to look for the oldest species in a group and assume that its area of occupation was the group's ancestral region (Lieberman 2000). Unfortunately, this approach assumes that the oldest species is the direct ancestor to the other species in the group, a problematic assumption because the incompleteness of the fossil record has generally made stratigraphical position a controversial choice for identifying ancestors.

Here we use a parsimony-based analysis in an initial attempt to trace the geographical roots of the Anoxophora and the main biserial sub-clades. It is important to note that higher-level graptolite taxonomy (supra-generic) is in the process of being substantially revised and many of the new clade names, although published, do not yet have widespread usage. Using the recent diplograptid phylogeny of Mitchell *et al.* (2007a) and a method known as modified Fitch parsimony analysis (Fitch 1971; Lieberman & Eldredge 1996; Lieberman 2000), we used geographical area as a multistate

character and optimized the states to the ancestral nodes of the Mitchell *et al.* (2007a) cladogram (Fig. 26.5). This algorithm assumes that multistate characters are unordered, or in this case that the transformations between geographical regions are all equally likely. Lieberman & Eldredge (1996) and Lieberman (2000) also modified the Fitch (1971) parsimony method to allow multiple geographical states to map to a node at the same time, a modification that allows ancestors to occupy multiple regions (as opposed to restricting widespread species to terminal branches). Ancestral geographical states are found by evaluating the overlap (or lack of) of geographical regions occupied by taxa above the node in question. If the taxa have one or more regions in common, the set of shared areas is mapped to the ancestral node (called an 'intersection'), but if there are no regions in common, the combined set of areas is applied to the node (called a 'union'; see Lieberman 2000, pp. 121–122, for a complete explanation of the modified Fitch parsimony method). Hence each node on the cladogram, representing a hypothetical ancestor, has a single or set of geographical regions mapped to it.

Based on the available data, the earliest biserial graptolites such as *Undulograptus sinodentatus*, *U. austrodentatus* and *U. marathonsensis* (stem axonophorans of Maletz *et al.* 2009) have a geographical origin in palaeotropical South China. This interpretation is congruent with the geographical distribution of more primitive stem axonophorans such as *Pseudisograptus* and *Exigraptus*, which share the single intersection region of South China. Graptolites belonging to the Axonophora (Maletz *et al.* 2009; Storch *et al.* 2011), which include the biserial 'diplograptids' (e.g. members of the Diplograptina), and the Neograptina (Storch *et al.* 2011), which include the Normalograptidae (e.g. *Undulograptus formosus*, *Normalograptus* species; Melchin *et al.* 2011) and all of their descendants (e.g. petalolithids, retiolitids and uniserial monograptids), were already latitudinally widespread occurring in both low and high palaeolatitudes (i.e. South China and the higher latitude Baltoscandia – Fig. 26.5).

Our analyses also indicate that a great deal of further biserial diversification seems to have taken place in the high to mid palaeolatitudes. Among axonophoran graptolites that are informally referred to as 'diplograptids' by Maletz *et al.* (2009) (the Diplograptina of Mitchell *et al.* 2007a), four main sub-clades (informally the diplograptid, lasiograptid, dicranograptid and climacograptid sub-clades; see Fig. 26.5) can be delineated and their ancestral roots traced. Of these, three have geographical origins at high palaeolatitude. The Diplograptidae of Mitchell *et al.* (2007a), which include the genera *Diplograptus*, *Amplexograptus*, *Orthograptus*, *Geniculograptus* and *Rectograptus*, appear to have evolved and diversified in Baltoscandia and Avalonia. Similarly the Lasiograptidae, which include *Lasiograptus*, *Hallograptus*, *Orthoretiolites* and *Archiretiolites* (among others) have an ancestry that can be traced to those high-palaeolatitude localities. The Dicranograptoida (Dicranograptacea of Mitchell *et al.* 2007a) have a broader geographical origin, South China and Baltoscandia, but the majority of clade members, *Dicranograptus*, *Dicellograptus* and *Nemagraptus*, also appear to have evolved in Baltoscandia and Avalonia. The fourth main 'diplograptid' sub-clade, the Climacograptoida, which include the genera *Archiclimacograptus*, *Pseudoclimacograptus*, *Climacograptus*, *Diplacanthograptus* and *Haddingograptus*, appear to have originated in low-palaeolatitude localities of South China and western Newfoundland (Laurentia).

**Fig. 26.5.** An area cladogram based on the phylogeny of Mitchell *et al.* (2007a) illustrating the geographical regions occupied at the nodes, which represent hypothetical ancestors. Geographical regions are as follows: (A) Canadian Cordillera; (B) Victoria, Australia; (C) South China; (D) West Laurentia (Nevada, Idaho); (E) Southern Uplands, Scotland; (F) Kazakhstan; (G) Marathon region, west Texas; (H) Arbuckle Mountains, Oklahoma; (I) Anticosti Island, Canada; (J) Appalachian Basin, Quebec and New York; (K) Ouachita Mountains, Oklahoma; (L) Western Newfoundland; (M) Appalachian Basin, Alabama; (N) Baltoscandia; (O) North China; (P) Rugen Borehole, Germany; (Q) Argentina, Precordillera; (R) Avalonia; (S) Tarim, China; (T) Southern Boliva; (U) NW Boliva; (V) Peru; (W) Argentina, Gondwana; (X) Turkey; (Y) Bohemia; (Z) Mauritania, North Africa; (A–A) Mirny Creek, Siberia; (A–B) Taimyr, Russia; (A–C) Canadian Arctic; (A–D) Central Newfoundland. Geographical regions occupied by hypothetical ancestors after final analysis are shown in grey (see Lieberman & Eldredge (1996) and Lieberman (2000) for discussions on using the modified Fitch (1971) parsimony method to map geographical states to ancestral nodes).

However, *Archiclimacograptus* is a polyphyletic taxon in the Mitchell *et al.* (2007a) phylogeny and a group of derived species (*A. modestus*, *A. meridionalis* and *A. skagensis*) originate in Baltoscandia.

Axonophoran graptolites that belong to the Neograptina (Štorch *et al.* 2011; Melchin *et al.* 2011; referred to as ‘monograptids’ by Maletz *et al.* 2009, and the Monograptina by Mitchell *et al.* 2007a) evolved from the stem axonophorans and seem to have spread from South China to Baltoscandia. Within the Neograptina the genus *Normalograptus*, which, together with its descendants eventually dominated Late Ordovician tropical faunas and became the only Ordovician generic group to survive the Hirnantian extinction (Chen *et al.* 2005), appears to have evolved in high-palaeolatitude Baltoscandia.

It is important to note that these results are based solely on the tree published in Mitchell *et al.* (2007a) and that certain biases may exist in the data. In order to construct a detailed character set for phylogenetic analysis Mitchell *et al.* (2007a) included only species that could be examined in isolated, relief or exceptionally well-preserved flattened specimens. This limited their dataset and probably imposed a facies and hence ecological bias in the analysis. We readily acknowledge that some of these results may change as more complete phylogenetic analyses are conducted.

### Examples of biogeographical patterns in graptolite evolution

One of the best documented patterns of a change in ecological preference during graptoloid evolution can be seen in the early evolution of the axonophorans as cosmopolitan, epipelagic species. The axonophorans originated in deep, offshore environments from isograptid and pseudisograptid ancestors (Maletz 2010) and subsequently migrated into shallow-water regions, as can be shown from their distribution in the Upper Yangtze Region (Zhang & Chen 2007, 2008). These authors, therefore, favour a ‘deep-water origin and shallow water dispersal’ model, which might be supported by the observation of the late arrival of early axonophorans, *Undulograptus austrodentatus* and related forms, in platform regions like Scandinavia (see Maletz 2005), but not in the slope successions of eastern North America (Maletz 1997b; Williams & Stevens 1988). It is also in agreement with the appearance of distinct endemic axonophorans originating in the early Darriwilian (see above). This model, however, is not a general pattern of origination and dispersal of graptolite faunas.

For example, the biogeographical history of expansograptids indicates that the origination of these graptolites was as shallow-water endemics, and was subsequently followed by their worldwide dispersal in the oceanic biofacies. The expansograptids (e.g. the genera *Expansograptus*, *Didymograptus*, *Baltograptus* and related forms) may have originated in the high palaeolatitudes, where the earliest two-stiped forms, presently included in *Kiaerograptus* as *Kiaerograptus supremus* Lindholm, occur, but later diversified and migrated into palaeotropical regions. Species of the genus *Cymatograptus* appear suddenly in the lower part of the *Tetragraptus phyllograptoides* Biozone at a level considerably before the origination of the cosmopolitan genus *Expansograptus* (Toro & Maletz 2008). They are present in most high-palaeolatitude regions, but have not been found in the low palaeolatitudes, except for a single record of *Cymatograptus* sp. cf. *Cymatograptus protobalticus* in the Cow Head Group of western Newfoundland (Toro & Maletz 2008, p. 981). A shallow-water shelf origin and initial dispersal must, therefore be suggested for this group. It may have taken the expansograptids several million years to establish a permanent presence in the cosmopolitan oceanic biofacies. Only with the evolution of the *Expansograptus holmi-suecicus* group in the later part of the

*Tetragraptus approximatus* Zone, did the expansograptids become successful on a global scale.

Similarly, the evolution of xiphograptids in the low palaeolatitudes also demonstrates a clear biogeographical pattern of graptoloid evolution. The earliest xiphograptids appear with the genus *Didymograptellus* in the *Tetragraptus akzharensis* Biozone of western Newfoundland (Maletz 2010) as low-palaeolatitude endemics. Further evolutionary changes accompanied a global dispersal and invasion of the genera *Xiphograptus* and *Pterograptus* into the cosmopolitan oceanic biofacies, where they enjoyed long-term success until the demise of the group in the late Darriwilian. However, the genus *Didymograptellus* was only moderately successful in the late Floian, as being represented only by the short-lived species *Didymograptellus bifidus*. The closely related *Yutagraptus*, originating in the late Floian, had greater species longevity, lasting until the early Darriwilian, but was also restricted to the low palaeolatitudes or was perhaps even endemic to Laurentia (Maletz 2010).

The evolution and radiation of the Neograptina also represents an excellent example of the biogeographical component of macroevolutionary processes – in this case extinction. Species of *Normalograptus* are generally uncommon in the Mid to mid Late Ordovician, an interval dominated by the Diplograptina. Generally, only high-latitude and relatively onshore successions contain faunas with common occurrences of *Normalograptus* species (e.g. late Mid Ordovician Baltic localities and early Late Ordovician strata in Wales; Goldman *et al.* 2011). During the early Hirnantian, however, species of *Normalograptus* and its descendants (i.e. the neograptines) invaded the palaeotropics and rapidly replaced Diplograptina species during the Late Ordovician extinction event (Melchin & Mitchell 1991; Chen *et al.* 2005). This clearly seems to represent an ecological replacement, where Late Ordovician climate deterioration produced changes in ocean chemistry and structure that gave a selective advantage to normalograptids (Zalasiewicz *et al.* 1995; Chen *et al.* 2005; Finney *et al.* 2007). Eventually, only species of the Neograptina survived the extinction and repopulated the Early Silurian oceans.

A final example pertains to the evolutionary history of the genus *Cyrtograptus* through the late Llandovery and Wenlock. The early history of *Cyrtograptus* shows that there were significant provincial differences of cyrtograptid species distributions in the late Telychian – Melchin (1989) used the distribution of *Cyrtograptus sakmaricus* and related forms as one of the indicators of the circum-tropical faunal province. More significant, however, is that *Cyrtograptus* appears to have disappeared completely from the southern palaeohemisphere in the mid-Sheinwoodian, and the genus is well documented in this interval only in the Canadian Arctic, albeit largely by rare species (Lenz & Melchin 1991; Lenz *et al.* 2012). In the upper Sheinwoodian (*Cyrtograptus rigidus* Zone), *Cyrtograptus* reappeared in Avalonia, Baltica and Bohemia.

### Conclusions

Recent work on graptolite biogeography suggests that several new ideas need to be incorporated into the seminal models of Skelvington (1973, 1974) and Cooper *et al.* (1991). First, we think that a synthesis of the depth stratification and surface temperature distribution control models that is based more directly on how the physical and chemical character of ocean water changes with latitude, depth and distance from shore is required to explain graptolite biogeographical patterns. Second, recent studies have demonstrated the existence of species that are endemic not just to a particular province but to an individual palaeocontinent or depositional basin. Hence, although graptoloids were pelagic organisms, some were apparently endemic to individual depositional basins or perhaps persistent but isolated oceanic circulation

cells. A third modification of existing models is the recognition that the biserial Axonophora also exhibit provinciality.

There have been relatively few studies that have explored the geographical origin of graptolite sub-clades (both in a regional and environmental sense) and their subsequent migration and expansion. Important examples discussed above include the origination of axonophorans in deep, offshore environments from isograptid and pseudisograptid ancestors and their later expansion into shallow water regions; the replacement of Diplograptina by Neograptina in the low palaeolatitudes during the Late Ordovician extinction event; and the origination of expansograptids in the high palaeolatitudes as shallow water endemics followed by their worldwide dispersal into the oceanic biofacies.

Further work that documents the changing geographical distribution of species over time will be critically important in understanding the details of graptolite evolution. In addition to these geographical and stratigraphical studies, advances in graptolite phylogeny that use parsimony-based techniques will greatly improve our understanding of graptolite origins, both geographical and evolutionary.

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## Appendix

Table 26A.1 provides a list of important Ordovician graptolite successions that are plotted on the palaeocontinent reconstruction maps (Figs 26.2–26.4). The latitude, longitude and BugPlate palaeocontinent code (Torsvik 2009) are provided for each locality.

**Table 26A.1.** Locality list for palaeogeographical maps

Location	Latitude	Longitude	Plate code
1. Vinini Creek Nevada	39.512404	–115.96085	101
2. Anticosti Island	49.5	–63	101
3. Marathon Texas	30.2075	–103.24333	101
4. Oklahoma Arbuckle Mountains	35.4823	–97.5352	101
5. Oklahoma Ouachita Mountains	34.384167	–96.1275	101
6. Central Newfoundland	48.966667	–56.033333	101
7. North America, Midcontinent	39.153489	–84.542133	101
8. Quebec and New York	46.7	–71.583333	101
9. West Newfoundland	48.57	–59.05	101
10. North America, Alabama	33.653333	–86.808889	101
11. Canadian Cordillera, Peel River	66.999722	–134.98417	101
12. Trail Creek, Idaho, USA	43.696311	–114.269236	101
13. Cape Manning, Arctic Canada	75.44667	–94.33333	120
14. Argentina Precordillera	–31.534167	–68.526111	201
15. Southern Uplands Scotland	55.331944	–3.4419444	314
16. Khantank Otar, South Kazakhstan	43.5487	75.1966	402
17. Olmalik, Uzbekistan	40.847056	69.603136	402
18. Mirny Creek, Siberia	63.612832	150.022888	403
19. Taimyr	76.345833	105.68583	417
20. Tarim	40.508339	79.047292	580
21. Alashan, North China	41.649444	102.615	601
22. Honghuayuan, South China	28.066667	106.83333	602
23. Wangjiawan, South China	30.975	111.418	602
24. Changning, South China	28.380149	104.88115	602
25. Wuning, South China	29.28333	115.07833	602
26. Gaoluncun, Jurong, South China	31.93847	119.1583	602
27. NW Zhejiang	30.229549	119.710202	602
28. Yushan, Jiangxi, South China	28.67643	118.23701	602

(Continued)

**Table 26A.1.** Continued

Location	Latitude	Longitude	Plate code
29. Jiaodingshan, Hanyuan, Sichuan	29.35	102.711667	602
30. Bajiaokou, Pijiaba, Ziyang, Shaanxi	32.52301	108.518697	602
31. Chengkou, South China	31.94772	108.65955	602
32. Jiuxi, Taoyuan, Hunan	29.17809	111.2703	602
33. Yanjin, Yunnan	28.11075	104.22944	602
34. Luxi, West Yunnan	24.442421	98.5849887	602
35. Shahechang, Baoshan, Yunnan	25.11226	99.1565	602
36. Victoria, Australia	–37.813611	144.96306	801
37. Canning Basin, NW Australia	–17.961944	122.23611	801
38. Masealayta, NW Bolivia	–14.5629	–68.882997	201
39. Atocha, South Bolivia	–20.933	–66.233	201
40. Chaquimayo, Peru	–15.52889	–71.38944	201
41. Argentina Gondwana	–16.5	–68.15	201
42. Skåne, Sweden	55.990257	13.595769	302
43. Bornholm, Denmark	55.0198055	15.0050067	302
44. Leba Elevation, Poland	54.7962322	17.8673515	302
45. Rugen Wells, Germany	54.416667	13.4	302
46. Nevera Massif, Spain	40.588798	–1.76218987	304
47. Almaden, Spain	38.77523	–4.84016	304
48. El Centenillo, Spain	38.3380754	–3.7282966	304
49. Cerrondel Hornillo, Spain	37.81263	–5.4995155	304
50. Barrancos, Portugal	38.1315421	–6.9781849	304
51. Montaigne Noire, SW France	48.248731	1.669447	305
52. SW Sardinia, Italy	39.2154583	9.1092282	306
53. Avalonia	51.894444	–5.2958333	315
54. Brabant Massif, Belgium	50.62662	4.231181	315
55. Novaya Zemlya	73.744167	55.974894	373
56. Bohemia, Gondwana	50.083333	14.416667	374
57. Taurides, Turkey	38.417	36.57	504
58. Tassili, North Ajjer, Algeria	25.5	9	714
59. Eastern Anti-Atlas	31.51666	–5.53333	714
60. Tichitt and Hodh, Mauritania	18.442222	–9.4966667	714
61. Oued In Djerane, Algeria	23.4851	11.2223	714
62. Djado, Niger	20.95	12.35	714
63. Ougarta Mountains, Algeria	29.6658	–2.27109	714
64. Central High Atlas, Morocco	31.733333	–7	714

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