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Paleogeographic, paleoceanographic, and tectonic controls on early Late Ordovician graptolite diversity patterns

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ABSTRACT

The Katian Age (early Late Ordovician) was a time of significant decline in marine biodiversity, but whether this decline was a real phenomenon or an artifact of the relatively few studies devoted to this interval requires further research. We examined the pattern of graptolite faunal changes across the boundary between the *Climacograptus bicornis* and *Diplacanthograptus caudatus* graptolite zones in North America and on several other continents. A sharp decline in species diversity occurs in the Appalachian Basin. Scores for normalized diversity dropped from 20 in the *C. bicornis* Zone to 7 in the *D. caudatus* Zone. Only 11% of the species present in the *C. bicornis* Zone carry over into the *D. caudatus* Zone. A similar pattern occurs in central Oklahoma. Regions at higher paleolatitude, such as Wales and Baltoscandia, exhibit low graptolite diversity in lower Katian strata, and then diversity declines further in higher strata. In other regions at low paleolatitude, such as Australasia and Scotland, however, diversity is fairly constant across this interval (although the percentage of carryover taxa remains low). We conclude that seawater temperature change or disruption of the oceanic density structure, which might accompany temperature change, provides explanations for the similarity between Laurentian and higher paleolatitude diversity patterns. Flooding of the Laurentian craton through the Sebree Trough by cool, subpolar Iapetus seawater may have adversely affected graptolite diversity there. Regions at high paleolatitudes likely underwent cooling associated with Katian climate deterioration. Thus seawater cooling, albeit driven by different mechanisms, may have produced similar diversity patterns at different paleolatitudes.

INTRODUCTION

Ordovician biodiversity studies have overwhelmingly focused on two remarkable features of the fossil record, the nearly fourfold increase in marine biodiversity that occurred during the Ordovician and the catastrophic mass extinction that marked the end of the period. Considerably less attention has been paid to

the smaller peaks and valleys that make up the overall curve, although Sepkoski (1995) pointed out an interesting upper Caradoc (Katian Stage) diversity drop among marine invertebrates (Fig. 1) and noted that more research was needed to discover if this decline was a real phenomenon or an artifact of fewer studies and fewer workers devoted to this interval.

Over the past decade a series of studies has examined faunal turnover and biodiversity changes during the late Sandbian and early Katian. In North America, Patzkowsky and Holland (1993,

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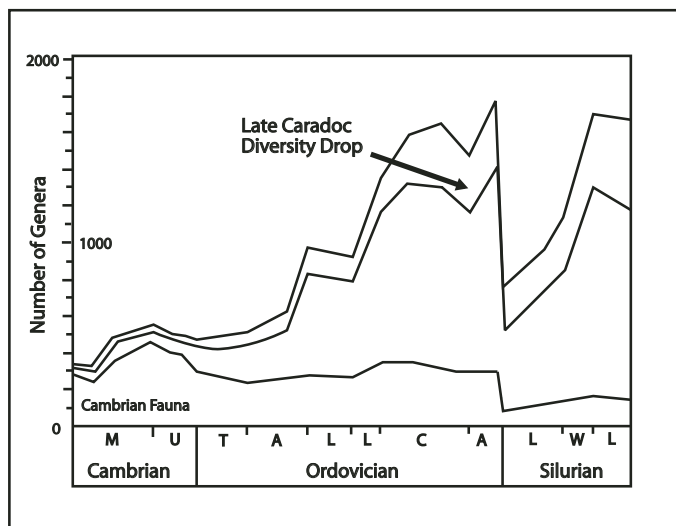


Figure 1. Lower Paleozoic marine diversity patterns. Note the prominent diversity decline prior to the Late Ordovician mass extinction. X-axis division abbreviations are (in order) M—Middle; U—Upper; T—Tremadoc; A—Arenig; L—Llanvirn; L—Llandeilo; C—Caradoc; A—Ashgill; L—Llandovery; W—Wenlock; L—Ludlow. Adapted from Sepkoski (1995).

1996) documented a regional brachiopod extinction in the lower Chatfieldian strata of the Appalachian Basin (Fig. 2), and Emerson et al. (2001) described a similar decline in brachiopod faunal diversity in rocks of similar age from the Upper Mississippi Valley. In Baltoscandia, Kaljo et al. (1995, 1996) and Ainsaar et al. (1999) recognized a precipitous decline in organic-walled microfossils across the Keila-Oandu regional stage boundary and referred to this diversity crash as the *Oandu Crisis* (Fig. 3). All of these regional events occur in a similar stratigraphic position relative to a suite of K-bentonite beds (Bergström et al., 2004; Huff et al., 1992), the prominent Guttenberg carbon isotope excursion (GICE; Fig. 4 herein; Young et al., 2005), a widely correlated stratigraphic sequence boundary (M3-M4 sequence boundary of Patzkowsky and Holland, 1996), and a graptolite zonal boundary (Goldman, 2004). Indeed, the similar timing of these local events and their proximity to a $\delta^{13}\text{C}$ excursion suggests that they may be part of a global bio-event.

All of the previously mentioned studies examined the diversity patterns of benthic fossil organisms from carbonate platform successions. In this study we examine Upper Ordovician diversity data from a group of planktonic fossil organisms generally found in offshore, deeper water deposits—graptolites. Graptolites are an ideal group for Ordovician biodiversity studies because they are widely distributed around the globe, are well represented in numerous relatively continuous black shale sections, and have been intensively sampled for biostratigraphy (Cooper et al., 2004). In addition to gathering data from a group of fossils that had a different lifestyle (planktonic) and are found in a different biofacies, this study examines graptolite faunal turnover across regions, in most of the key Upper Ordovician successions around the world.

Cooper et al. (2004) compared graptolite diversity changes through the entire Ordovician in three regions (Australasia, Baltica, and Avalonia) that represented different paleolatitudes. The present study focuses on a much shorter stratigraphic interval, the upper Sandbian to Katian Stages (lower Upper Ordovician), but more comprehensively surveys graptolite diversity across the globe (eight regional successions) in that interval. The localities examined in this study are (1) the Appalachian Basin (Laurentia); (2) Ouachita Mountains, southeastern Oklahoma (Laurentia); (3) Southern Uplands, Scotland (Laurentia); (4) Newfoundland (Laurentia); (5) Trail Creek region, Idaho (Laurentia); (6) Victoria, Australia (northeast Gondwana); (7) Scania, Sweden (Baltica); and (8) South Wales (Avalonia) (Fig. 4). Breaking down the global pattern of lower Upper Ordovician graptolite biodiversity into regional patterns that can be compared and contrasted may help answer the question of whether the upper Caradoc biodiversity decline represents a global bio-event or a composite of different regional patterns that have regional explanations.

Finally, this study examines the possible links between graptolite faunal turnover and paleoenvironmental changes during the late Sandbian to early Katian. Several (and not mutually exclusive) explanations for the individual regional declines in lower Katian benthic diversity have been proposed. These include eustatic sea-level change (Patzkowsky and Holland, 1996), extensive volcanic ash deposition (Sloan, 1997), ocean temperature changes (Jaanusson, 1973; Patzkowsky et al., 1997), and changes in paleoceanographic circulation (Zalasiewicz et al., 1995). The pattern of graptolite faunal change provides additional data that can be used to evaluate these competing hypotheses, and also fuels some speculation on the relationship of biodiversity to pre-Hirnantian Late Ordovician global climate.

METHODOLOGY

Measuring biodiversity through geologic time and across different geographic regions presents a number of difficulties that need to be taken into consideration. Some of the problems stem from sampling biases and a lack of taxonomic consistency in data sets compiled by different workers, whereas others result from the process of converting stratigraphic range data derived from biostratigraphic studies into diversity measures. For many of the successions in this study we have personally examined the graptolite collections, thus reducing the problem of taxonomic inconsistency. In other cases, however, species lists were compiled from the literature with taxonomic updates and revisions where possible. Sampling differences among regions can be the most difficult bias to overcome. No attempt was made to standardize the sampling. However, as we demonstrate below, because the most densely sampled region in this study (in terms of both sections and collections), the northern Appalachian Basin of the eastern United States, also showed the greatest diversity decline across the upper Sandbian to lower Katian (Chatfieldian), we conclude that diversity decline in less intensively sampled sections is not the result of under-sampling.

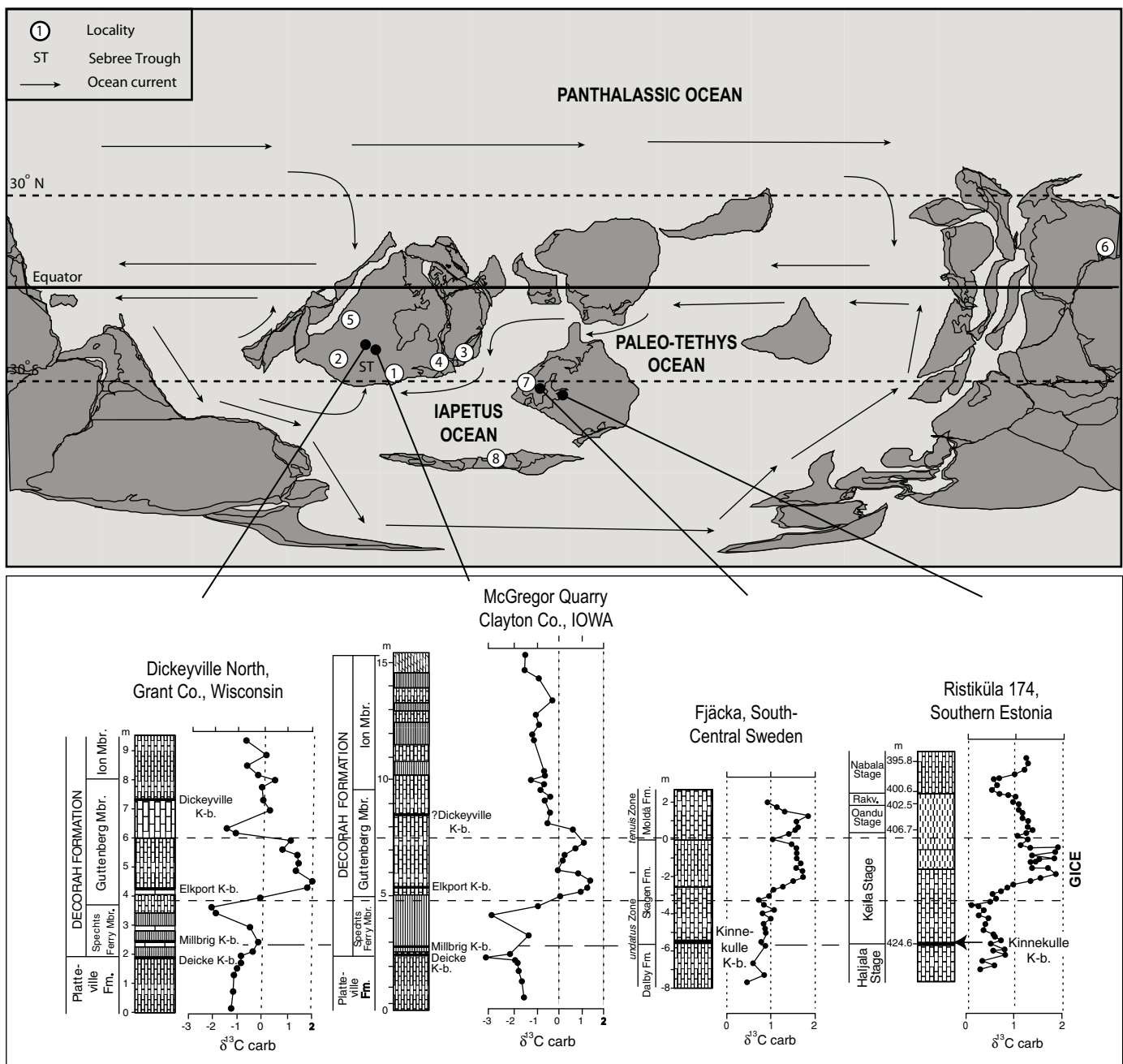


Figure 4. Locality map for regional graptolite diversity studies and lower Upper Ordovician carbon isotopic ($\delta^{13}\text{C}$) excursions. Black arrows indicate Late Ordovician oceanic circulation patterns and are adapted from Barnes (2004). Graptolite localities are (1) Appalachian Basin (Laurentia); (2) Ouachita Mountains, southeastern Oklahoma (Laurentia); (3) Southern Uplands, Scotland (Laurentia); (4) Newfoundland (Laurentia); (5) Trail Creek region, Idaho (Laurentia); (6) Victoria, Australia (northeast Gondwana); (7) Scania, Sweden (Baltica); and (8) South Wales (Avalonia). Base map produced from the paleogeographic map software ESH-GIS 1.0, The Paleomap Project (www.scotese.com). Carbon isotopic ($\delta^{13}\text{C}$) excursion data adapted from Bergström et al. (2004). K-b. indicates K-bentonites.

Converting taxon range data into diversity measures presents another type of problem. Cooper (2004) noted that when estimating the mean standing diversity (MSD) of species over a specified interval of time, there are several different ways in which taxa can be counted and biases introduced. The simplest method, *total*

diversity, is to just tally the total number of taxa within a time interval. Alternatively, one can divide the total diversity by the interval duration to produce *species per time unit* measures. Foote (2000) noted that counting taxa that do not cross the study interval boundaries but are restricted to the interval itself (“singletons”)

produces a number of undesirable effects and should be avoided. Unfortunately, adopting this recommendation would mean eliminating a substantial portion of the available data. Sepkoski (1975) proposed a diversity measure (called *normalized diversity* by Cooper, 2004) that assigns a full score to a species whose range crosses both the lower and upper boundaries of the study interval, a half score to species whose ranges cross only the upper or lower boundary of the study interval, and a half score to “singletons.” Cooper (2004) used model data sets to compare three diversity measures—total diversity, species per time unit, and normalized diversity—with actual MSD. Generally, Cooper (2004) found that total diversity measures tend to overestimate MSD, species per time unit measures tend to underestimate MSD, and normalized diversity scores best estimate MSD. Hence, we follow Cooper (2004) in using normalized diversity to calculate graptolite species diversity in lower Upper Ordovician strata.

Last, we must be sure that we are actually comparing diversity scores in coeval intervals at each locality. Thus, the study intervals must be correlated precisely enough around the globe to be sure that the diversity measures are calculated from coeval stratigraphic intervals. The diversity decline in benthic faunas in North America and Baltoscandia occurs just above the Millbrig and Kinnekulle K-bentonite beds, respectively (Bergström et al., 2004), and nearly coincident with the prominent GICE carbon isotope ($\delta^{13}\text{C}$) excursion (Young et al., 2005). This stratigraphic level also closely approximates the *Climacograptus bicornis*–*Diplacanthograptus caudatus* graptolite zonal boundary (Bergström et al., 2004) or the boundary between the Sandbian and Katian Stages (Fig. 5). Thus, whenever possible, graptolite diversity is calculated in four subequal intervals that symmetrically span the *C. bicornis*–*D. caudatus* graptolite zonal boundary (two below and two above). These intervals precisely correlate with the Gisbornian (*N. gracilis* and *O. calcaratus* Zones) and lower Eastonian (*D. lanceolatus* and *D. spiniferus* Zones) Stages in the Australasian succession (Fig. 5). The key horizon in each section is the base of the *Diplacanthograptus caudatus* graptolite Biozone, a level that can be confidently correlated around the world (Goldman, 2004).

GRAPTOLITE DIVERSITY PATTERNS

Appalachian Basin

Upper Ordovician black shale crops out along the extent of the Appalachian Mountains from Newfoundland to Alabama in series of northeast- to southwest-trending foreland basins that developed along the eastern margin of Laurentia during the Taconic orogeny (Finney et al., 1996; Hatcher et al., 1990). We have divided the Appalachian Basin into two regions on the basis of geography and faunal differences. These are the Appalachian Basin outcrops in the United States and Quebec (Fig. 6A), and those in Newfoundland that are treated separately (Fig. 6D). Graptolite diversity data for the United States and Quebec comes from the classic Utica Shale and Mount

System	Stages	Australasian Stages	Australasian Graptolite Zonation	Eastern N.A. Graptolite Zonation		
Upper Ordovician	Katian	Eastonian	Ea 4	<i>gravis</i>	<i>manitoulinensis</i>	450.8 Ma
			Ea 3	<i>kirki</i>	<i>pygmaeus</i>	452.0
		Ea 2	<i>spiniferus</i>	<i>spiniferus</i> <i>ruedemanni</i>	453.3	
		Ea 1	<i>lanceolatus</i>	<i>caudatus</i>	454.5	
	Sandbian	Gisbornian	Gi 2	<i>calcaratus</i>	<i>bicornis</i>	457.3
			Gi 1	<i>gracilis</i>	<i>gracilis</i>	460.5

Figure 5. Lower Upper Ordovician chronostratigraphic chart, showing global and Australasian stages, eastern United States and Australasian graptolite zones, and interpolated radiometric dates. The interval of our diversity study is shaded. Adapted from Sadler and Cooper (2004) and Bergström et al. (2006).

Merino Shale outcrops in the Mohawk and Hudson River Valleys of New York State and the Saint Lawrence Lowlands of Quebec (Berry, 1962; Hall, 1847, 1865; Goldman et al., 1994; Riva, 1969, 1972, 1974; Ruedemann, 1908, 1912, 1947), and from the Athens Shale of the southern Appalachian Mountains (Decker, 1952; Finney et al., 1996; Grubb and Finney, 1995). Graptolite diversity is constant in the *Nemagraptus gracilis* and *Climacograptus bicornis* Zones (normalized diversity scores of 20) and then declines precipitously in the overlying *Diplacanthograptus caudatus* Zone (normalized diversity score of 7). In addition to the steep decline in taxonomic diversity, morphologic diversity declines as well. Reclined (dicellograptid) and partially reclined (dicranograptid) taxa, as well as species with cladia and scopulae, all disappear or are greatly reduced in number at the base of the *D. caudatus* Zone. Diversity declines further in the *Orthograptus ruedemanni* Zone before rebounding in the *Diplacanthograptus spiniferus* Zone (Fig. 6A). Graptolite diversity never attains lower Upper Ordovician levels higher in the Appalachian Basin succession; as the Taconic orogeny waned, black shales bearing graptolites were replaced by coarse clastic deposits derived from the eroding Taconic highlands (Ruedemann, 1925; Fisher, 1977).

Because no single section spans the *Climacograptus bicornis*–*Diplacanthograptus caudatus* zonal boundary in the Appalachian Basin, the possibility exists that the dramatic drop in graptolite diversity is in part an artifact of an unconformity at that level. However, a complete section that is conformable through this interval does exist in the Ouachita Mountains of southeastern Oklahoma.

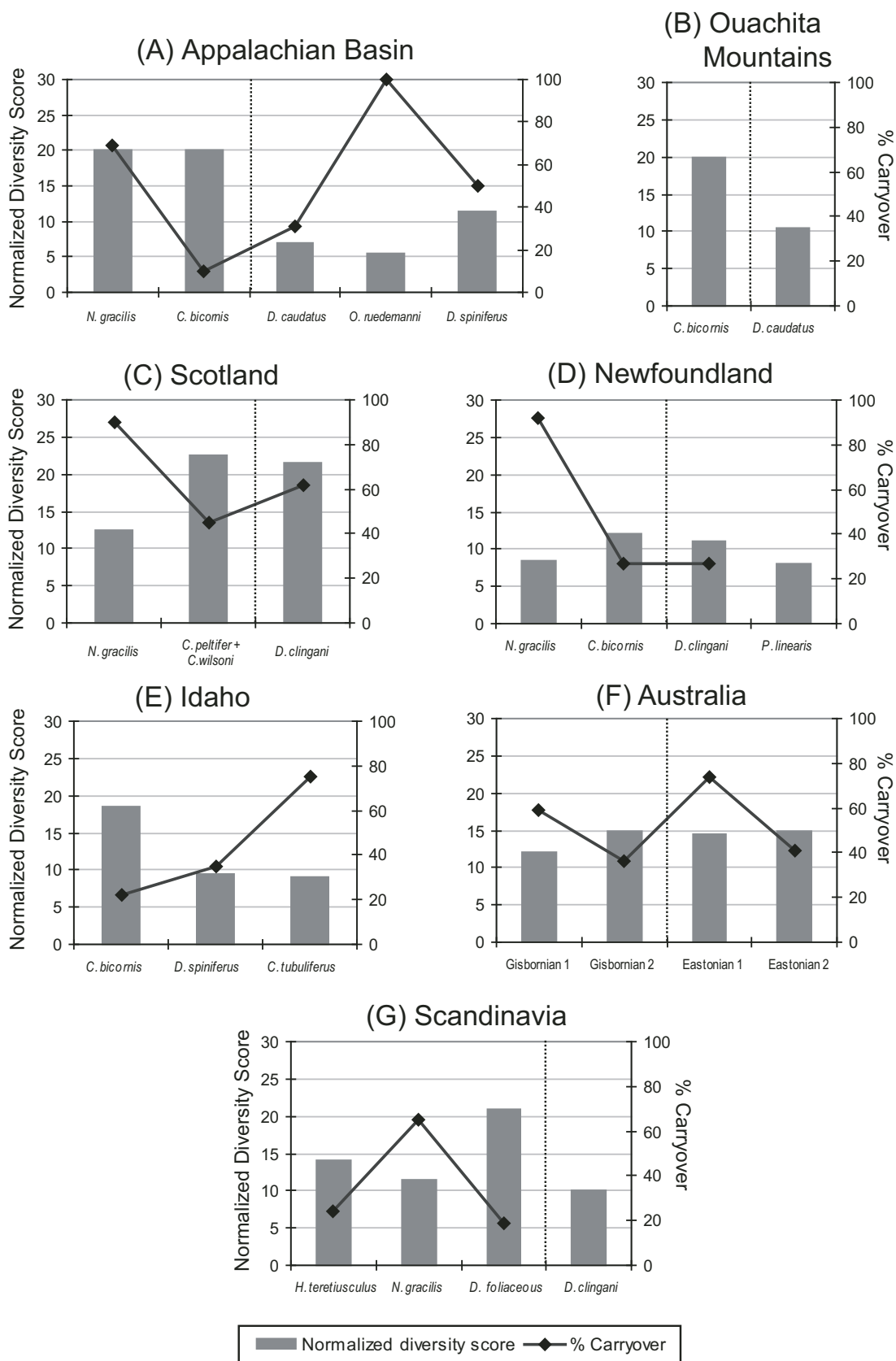


Figure 6. Early Late Ordovician diversity histories from eight key graptolite successions (see Fig. 4). Histograms illustrate normalized diversity scores (see text for explanation of normalized diversity), and the superimposed line graph shows the percentage of carryover taxa from one zone to another. The dashed vertical line in each histogram represents the boundary between the Sandbian and Katian Stages. Data such as regional species lists, scores for total diversity, normalized diversity, and holdover taxa are available from the authors upon request.

Ouachita Mountains of Oklahoma

In southeastern Oklahoma, Upper Ordovician strata are exposed along Black Knob Ridge, a low, narrow ridge at the extreme western end of the Ouachita Mountains (Hendricks et al., 1937; Finney, 1988). These strata are composed primarily of graptolite-rich shales associated with deep-water limestones and cherts (Ethington et al., 1989) and were deposited in the deep marine environment of the Ouachita Geosyncline off the southern margin of Laurentia (Finney, 1988). The units exposed along Black Knob Ridge are, in ascending order, the Womble Shale, Bigfork Chert, and Polk Creek Shale. Graptolites from the Womble Shale and Bigfork Chert at Black Knob Ridge have been comprehensively described by Finney (1986) and more recently by Goldman et al. (2007). Only graptolites from the *C. bicornis* and overlying *D. caudatus* zones were counted at this section. At Black Knob Ridge the Womble Shale contains a diverse assemblage of *C. bicornis* Zone graptolites (normalized diversity score of 20) that is nearly identical in its faunal composition to that of the Appalachian Basin. The boundary between the *C. bicornis* and overlying *D. caudatus* Zones occurs 4 m above the base of the Bigfork Chert, which conformably overlies the Womble Shale. With a pattern similar to that of the Appalachian Basin, normalized diversity in the *D. caudatus* Zone at Black Knob Ridge drops by nearly 50% to 10.5 (Fig. 6B).

Southern Uplands, Scotland

Another important low paleolatitude graptolite locality in the environs of Laurentia is Hartfell Score in the Southern Uplands of Scotland. It was in this region that Lapworth's (1876, 1878) pioneering work demonstrated the stratigraphic utility of graptolites by using them to help work out the geologic structure of the uplands. In the Southern Uplands, Upper Ordovician to Silurian mudstones and graywackes are exposed in a series of structurally repeated, thrust-bounded slices that dip steeply to the northwest (Leggett et al., 1979; Rushton et al., 1996). At Hartfell Score near Moffatt, ~20 m of graptolite-rich black mudstones conformably span the *Climacograptus wilsoni* (= *C. bicornis*)–*Diplacanthograptus caudatus* zonal boundary (Williams, 1982; Zalasiewicz et al., 1995). The graptolite biostratigraphy was recently updated by Zalasiewicz et al. (1995), and we have used their detailed range chart for our diversity analysis (Fig. 6C).

The normalized diversity score for the *C. wilsoni* Zone at Hartfell Score is 22.5, and the score for the overlying *D. caudatus* Zone is 21.5. In stark contrast to the Appalachian Basin, graptolite diversity in southern Scotland remains nearly constant across the *C. bicornis*–*D. caudatus* zonal boundary. Also noteworthy is the fact that dicellograptinids and dicranograptinids remain an important part of the *D. caudatus* Zone fauna in southern Scotland, whereas they disappear almost entirely from the Appalachian Basin in the strata above the *C. bicornis* Zone. Although we only counted species from the single section at

Hartfell Score, the data indicate a much more diverse *D. caudatus* Zone than in the Appalachian Basin or Ouachita Mountains of Oklahoma.

Newfoundland

Late Ordovician graptolites from the Lawrence Harbour Formation (Exploits Zone) in central Newfoundland were described and figured by Erdtmann (1976) and Williams (1995). We have used the species list and range chart provided by Williams (1995), because it covers a greater number of collection localities and uses updated graptolite taxonomy. The Lawrence Harbour Formation outcrops are structurally complex, and no single exposure contains a complete succession of zones; hence Williams' (1995) range chart does not illustrate the stratigraphic ranges of taxa, only the zones in which they occur. Normalized diversity scores for graptolites from the Lawrence Harbour Formation are *N. gracilis* Zone, 9; *C. bicornis* Zone, 12; *D. clingani* Zone, 11; *P. lineariz* Zone, 8 (Fig. 6D). As in Scotland, graptolites in central Newfoundland exhibit no notable decrease in species diversity across the *C. bicornis*–*D. caudatus* zonal boundary.

Trail Creek, Idaho

The Trail Creek Summit section within the Phi Kappa Formation of central Idaho, northwestern United States, exposes an ~200-m-thick succession of black siliceous shale and argillite that has yielded biostratigraphically important graptolites for nearly a century. Surveys of the local biostratigraphy in this area, conducted by Churkin (1963), Carter (1972), and Carter and Churkin (1977), established a set of zones that have been employed as a standard reference for the North American Cordillera. More recent studies by Mitchell et al. (2003), Maletz et al. (2005), and Motz et al. (2006) have updated the graptolite taxonomy and substantially revised the biostratigraphic zonation. The new data indicate that the Trail Creek succession is similar to the Australasian and South China (Chen et al., 2005) successions (low paleolatitude, tropical regions) and is also more incomplete than previously thought.

At Trail Creek the normalized diversity score for the *C. bicornis* Zone is 14 (Fig. 6E). Mitchell et al. (2003) noted that a succeeding *D. caudatus* Zone fauna could not be unambiguously identified at Trail Creek. The strata that overlie the *C. bicornis* Zone were called *passage beds* by Carter and Churkin (1977), who were unable to precisely define their biostratigraphic age. Although *D. caudatus* does occur within the "passage beds," its first appearance is above that of *D. spiniferus* (which was misidentified as *C. bicornis* by Carter and Churkin), the index for the overlying *D. spiniferus* Zone. Additionally, J.F.V. Riva (2005, personal commun.) claims to have found evidence of a prominent unconformity just below the first appearance of *D. spiniferus* at the summit section. The normalized diversity score for the zone succeeding the *C. bicornis* Zone is 6, indicating a large drop in diversity, but because we cannot differentiate between a

D. caudatus and a *D. spiniferus* Zone at Trail Creek the data must be viewed with caution.

Victoria, Australia

The Australasian region of Gondwana lay in low latitudes during the Ordovician (Scotese and McKerrow, 1990), and its graptolite succession is one of the most complete and finely divided in the world. It is considered to be the standard for the Pacific Faunal Province (VandenBerg and Cooper, 1992). Graptolite biostratigraphy and biodiversity in the Victorian succession were comprehensively reviewed by VandenBerg and Cooper (1992) and Cooper et al. (2004), and we relied on their range charts for our data. These data, which are similar to Williams' (1995) Newfoundland data, do not illustrate the exact stratigraphic range of each species from measured sections but only the biozones in which they occur. Graptolite diversity increases from the Gisbornian 1 (*Nemagraptus gracilis* Zone, normalized diversity of 12) to a nearly constant level in the three succeeding zones—Gisbornian 2 (nearly equivalent to the *C. bicornis* Zone), normalized diversity of 15; Eastonian 1 (nearly equivalent to the *D. caudatus* Zone), normalized diversity of 14.5; and Eastonian 2 (*D. spiniferus* Zone), normalized diversity of 15 (Fig. 6F).

A detailed survey of low paleolatitude graptolite localities reveals that the precipitous declines observed in the Appalachian Basin and the Ouachita Mountains of Oklahoma are clearly not pervasive phenomena but are restricted to certain parts of Laurentia. One important low paleolatitude locality that we have not analyzed is the Marathon region of West Texas (Berry, 1960). Riva (1969), Bergström (1978), and Goldman et al. (1995) all noted that a prominent unconformity corresponds to much of the Katian Stage (upper Caradoc) in the Marathon succession.

Scania, Sweden

Scania (southern Sweden) belonged to the paleocontinent Baltica, which was at mid-latitudes during the early Late Ordovician (Scotese and McKerrow, 1990; Mac Niocall et al., 1997). The Ordovician rocks of Baltoscandia are subdivided into subparallel, generally SE-NW-trending confacies belts that maintained fairly constant geographic positions through time (Jaanusson, 1976, 1995). The Middle and Upper Ordovician strata in Scania (studied from both core and outcrop) are predominantly black to gray shales and mudstones representing outer shelf or foreland basin deposition (Bergström et al., 2000). Our diversity data come from the Koängen and Fågelsång cores described by Nilsson (1977) and Hede (1951), respectively, and Pålsson (2001). The senior author of this paper has personally examined the graptolites from both cores and has revised and updated the taxonomy and taxon ranges.

Graptolite diversity in Scania increases from the *Nemagraptus gracilis* Zone to the *Diplograptus foliaceus* Zone (= *C. bicornis* Zone) and drops dramatically into the *Dicranograptus clingani* Zone (approximately equivalent to the *D. caudatus* Zone), with

normalized diversity scores of 11.5, 21, and 10, respectively (Fig. 6G). Thus, the graptolite diversity pattern in Scania is similar to that found in the Appalachian Basin and the Ouachita Mountains.

South Wales (Avalonia)

Another classic location in the history of graptolite studies is Wales, which, along with England, was part of Avalonia, a mid- to high-latitude paleocontinent during the early Late Ordovician (Mac Niocall et al., 1997). Elles and Wood (1901–1918) provided the first comprehensive descriptions of Welsh graptolites, and Elles (1939) later elucidated the stratigraphic ranges of many Llandeilo and Caradoc graptolite species. These early classic works were updated by Hughes (1989).

The graptolite-bearing strata in Wales are generally older than the intervals examined in this paper, but Zalasiewicz et al. (1995) described a new section in Whitland, South Wales, that has its base in the *Dicranograptus clingani* Zone. Although we cannot compare diversity changes across the base of the Katian Stage because the underlying *Diplograptus foliaceus* Zone is absent from this section, we believe that the pattern of graptolite faunal change that is exhibited in these rocks provides some insight into understanding the global pattern of Katian (late Caradoc) diversity changes.

At Whitland, nearly 60 m of laminated dark-gray graptolitic mudstones and silty mudstones of the Mydrim (or *Dicranograptus*) Shales is exposed (Zalasiewicz et al., 1995). In its upper part, the Mydrim Shales exhibit less pronounced lamination and become interbedded with thin muddy limestone bands before finally grading upward into the Shoeshook Limestone. Based on brachiopods and trilobites, the Shoeshook Limestone at Whitland is Ashgillian in age (Zalasiewicz et al., 1995). Between 12.5 and 39 m above the base of the section, the Mydrim Shales contain a low diversity *Dicranograptus clingani* Zone fauna. This fauna contains elements (*Diplacanthograptus spiniferus*, *Neurograptus margaritatus*, *Dicranograptus nicholsoni*, *Dicellograptus flexuosus*, and *Orthograptus quadrimucronatus*) that indicate a correlation with the *D. caudatus* to *D. spiniferus* zones in North America and Eastonian 1–Eastonian 2 in Australia. Above 39 m, faunal diversity decreases even further, and the fauna is completely dominated by several species of *Normalograptus* (Fig. 7). Zalasiewicz et al. (1995) note that the Mydrim to Shoeshook transition represents a shallowing upward sequence and that even in the lowermost beds most offshore or deep water taxa (deep water biotope of Cooper et al., 1991) and the cosmopolitan mesopelagic biotope of Goldman et al. (1995) are absent from the Whitland section. They also suggest that the marked diversity decline in post-*D. clingani*-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.

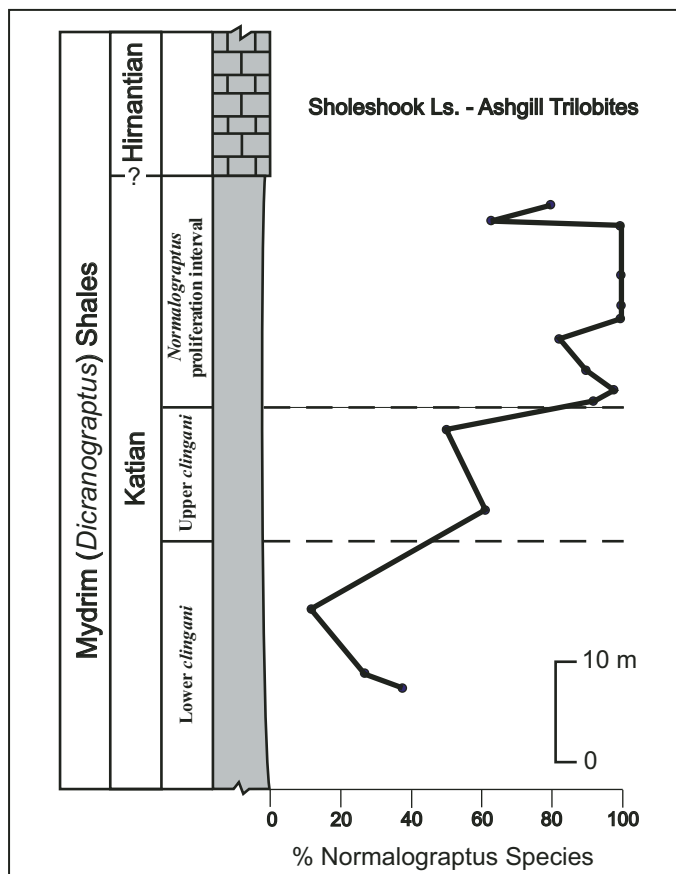


Figure 7. Percentage of *Normalograptus* species in the Whitland, South Wales, graptolite succession. Note the increasing percentage of normalograptids with time. Adapted from data in Zalasiewicz et al. (1995).

Summary of Regional Upper Sandbian to Katian Graptolite Diversity Patterns

The preceding regional review of graptolite diversity change through the upper Sandbian and Katian Stages reveals a varied pattern. In the low paleolatitudinal localities of the eastern and southern United States, graptolite diversity declines precipitously across the *Climacograptus bicornis*–*Diplacanthograptus caudatus* zonal boundary. However, other former tropical localities such as Scotland, Newfoundland, and Australia, exhibit nearly static diversity across this same interval. The mid-paleolatitude succession in Scania records a sharp diversity drop, and the mid- to high-paleolatitude Whitland section in South Wales contains a low diversity lower Katian assemblage followed by nearly complete domination by a single genus, *Normalograptus*. These results, however, are consistent with data from other fossil groups—regional brachiopod extinctions in the Appalachian Basin and Upper Mississippi Valley (Patzkowsky and Holland, 1996; and Emerson et al., 2001, respectively) and organic-walled microfossil declines in Baltoscandia (Kaljo et al., 1995, 1996;

Ainsaar et al., 1999). Thus, each region has its own local diversity history, and although the sum of these regional histories likely produces the global decline recognized by Sepkoski (1995), no global pattern that might warrant a comprehensive explanation is immediately evident. Nevertheless, we do see an interesting relationship between the regional diversity histories and paleo-latitude, as well as a possible connection between these patterns and the changing Late Ordovician climate.

PALEOENVIRONMENTAL CONTROLS ON GRAPTOLITE DIVERSITY

Graptoloids are one of the fossil groups that were decimated by the end-Ordovician mass extinction. In several regions, particularly those at higher latitudes, graptolite diversity began declining in the Katian, well before the Hirnantian climate deterioration and glaciation. Zalasiewicz et al. (1995) proposed that because Wales lay at a higher latitude than Scotland during the Late Ordovician it may have been subject to more rapid climatic deterioration during a cooling event. Additionally, the density-stratified setting that seems to have favored graptolite proliferation and fossilization (Berry et al., 1987) may have been disrupted by an influx of cooler, oxygen-rich polar waters (Zalasiewicz et al., 1995).

Cooper et al. (2004) also noted that graptolite diversity in Avalonia (and perhaps Baltica) began to decline well before it declined in Australasia, and they speculated on similar causal mechanisms (that higher latitude localities may have undergone surface water temperature changes or breakdowns in ocean density structure from an earlier onset of global cooling than at lower latitude localities). They also noted, based on the paleo-plate reconstructions of Cocks and Torsvik (2004), that Avalonia and Baltica had already drifted into near-tropical latitudes by the end of the Katian, making latitude an unlikely determinant of diversity change. It appears to us, however, that on the basis of the paleocontinental reconstructions of Scotese and McKerrow (1990), Mac Niocall et al. (1997), and even Cocks and Torsvik (2004), a distinct latitudinal gradient did exist among the regions discussed here during the early Late Ordovician.

We re-propose the hypothesis that a pre-Hirnantian episode of global cooling took place and that this climate change negatively affected graptolite diversity at middle and high latitudes but was not a major factor at low latitudes. However, the steep decline in diversity exhibited by several Laurentian successions requires a separate causal mechanism.

Several workers (e.g., Berry et al., 1987; Cooper, 1998) proposed that graptolites thrived during times of sluggish oceanic circulation and that their preferred habitat was in a nutrient-rich layer above an oxygen minimum zone (OMZ) that produced the anoxic conditions necessary for graptolite preservation—generally deep shelf to slope settings. During the end-Ordovician regression and glaciation, the formation of cold, oxygen-rich polar waters and their sinking and spreading toward the equator would have intensified, increasing the ventilation of the ocean and disrupting the density-stratified water that

graptolites favored (Berry et al., 1987). *Normalograptus*, the only graptolite genus to survive the Ordovician mass extinction and diversify in the Silurian was an epipelagic species and occupied one of the shallowest, most oxygen-rich zones of the upwelling region. Finney and Berry (2001) and Chen et al. (2005) noted that the normalograptids therefore were the species least likely to be affected by deep ocean ventilation and disruption of a density stratified water column.

As noted above, the lower Katian (*D. clingani* Zone) in South Wales has a low-diversity graptolite fauna. Near the top of the *D. clingani* Zone the graptolite fauna becomes almost entirely dominated by the genus *Normalograptus*. Thus, both the sedimentological changes that occur up section at Whitland—transition from laminated, graptolitic mudstones to bioturbated, barren mudstones and finally shelf carbonates—and the faunal changes are consistent with the end-Ordovician extinction model, even though they occurred during the Katian.

Is there any independent evidence that an episode of global cooling occurred prior to the Hirnantian? Patzkowsky et al. (1997) suggested that positive excursions in carbon isotope compositions in both carbonate and organic carbon from lower Katian strata in the eastern and midcontinental United States—the prominent GICE carbon isotope ($\delta^{13}\text{C}$) excursion (Fig. 4)—indicate increased productivity and rates of organic carbon burial that may have drawn down atmospheric $p\text{CO}_2$ and precipitated global cooling. Pope and Steffen (2003) noted that Upper Ordovician carbonates from the southern and western margins of Laurentia contained abundant chert and phosphate, which they interpreted as evidence of widespread upwelling and vigorous thermohaline circulation related to early Gondwanan glaciation. They also point out that this period of upwelling corresponded with cool surface waters in the Appalachian Basin (Railsback et al., 1990), a northward expansion of cool-water trilobite faunas in North America (Shaw, 1991), and a transition to cooler water benthic faunas across eastern North America (Patzkowsky and Holland, 1993). Finally, several workers claimed that Katian (middle to upper Caradoc) siliciclastic deposits in northwestern Gondwana display clear evidence of glacial transport and deposition (e.g., Barnes, 1986; Theron, 1994; Hamoumi, 1999). It is also worth noting, however, that Brenchley et al. (1994) and Marshall et al. (1997) consider there to be little substantive isotopic evidence for a long-lived glacial episode that substantially preceded the Hirnantian.

If climatic cooling occurred during the early Katian it clearly did not affect graptolite faunal diversity in all the low latitude tropical regions. Southern and eastern Laurentian graptolite faunas were severely depleted, but faunas from northeast Laurentia (Scotland and Newfoundland) and northeast Gondwana (Australia) do not exhibit a pronounced diversity decline. Interestingly, the percentage of taxa that carry over from the upper Sandbian into the lower Katian is similarly low in all areas, suggesting that where a diversity drop is observed, it is the result of reduced origination rate and not elevated extinction rate.

Zalasiewicz et al. (1995) and Finney (1986, 1988) noted that prominent regressions, as evidenced by distinct facies changes,

occurred in South Wales and southwestern Laurentia during the early to mid-Katian. Perhaps the different regional diversity patterns could be attributed to unique water-depth histories of individual basins. Although we agree that sea level was an important factor that affected the graptolite biotope, as a single causal mechanism, sea level alone could not be responsible for Katian graptolite diversity decline in Laurentia because the Appalachian Basin underwent a relative sea-level rise at that time (Holland and Patzkowsky, 1996). Indeed, the nadir of graptolite diversity in the northern Appalachian Basin occurred within the *Orthograptus ruedemanni* Zone, an interval considered by Joy et al. (2000) to represent a transgressive system.

Patzkowsky and Holland (1996) and Pope and Steffen (2003) provided evidence for the incursion of cool oceanic waters onto the Laurentian continent. Kolata et al. (2001) suggested that cool, subpolar Iapetus seawater may have flooded the Laurentian craton through a narrow depressed corridor, the Sebree Trough. This trough is filled with a succession of dark brown to gray shales that contain a very low diversity graptolite fauna of Katian age (Kolata et al., 2001; Mitchell and Bergström, 1991). These shales are similar in age and faunal composition to the classic Utica Shale of the northern Appalachian Basin (Mitchell and Bergström, 1991). We think that if cool, well-oxygenated subpolar waters flooded the Laurentian craton, it may have adversely affected graptolite diversity. Thus, physical and chemical seawater changes, albeit driven by different mechanisms, may have produced similar diversity patterns at different paleolatitudes.

Finally, Finney and Berry (1997) proposed that graptolites thrived in a denitrification layer above an OMZ that developed where vigorous upwelling occurred along continental margins. They attribute changes in graptolite diversity to fluctuations in upwelling conditions and that the OMZ loss of upwelling conditions resulted in destruction of the preferred graptolite habitat and declines in both abundance and diversity. The upwelling model was proposed to explain the relationship between vertical changes in facies patterns and graptolite diversity and abundance in the Vinini Formation of north-central Nevada (Finney and Berry, 1997). This model is seemingly at odds with the interpretation of widespread Late Ordovician upwelling in North America (Pope and Steffen, 2003) and coincident graptolite diversity decline. We agree that upwelling produces the nutrient-rich conditions necessary for high productivity, but it is not clear that plankton abundance and species diversity respond similarly to circulation changes. The phosphate-rich, dark shale of the Late Ordovician Maquoketa Group crops out extensively in the Upper Mississippi Valley of the United States (Templeton and Willman, 1963). Witzke (1987) noted that in its southeastern outcrop area the lower Maquoketa was deposited in an epicontinental seaway with well developed density and oxygen stratification. Interestingly, the lower Maquoketa Formation is rich in graptolites but exhibits very low species diversity (Goldman and Bergström, 1997). We think that more research on the relationship between plankton abundance, species diversity, and upwelling is still needed.

CONCLUSIONS

The early Late Ordovician (Katian) was a time of significant decline in benthic marine biodiversity. In this study we compiled Upper Ordovician diversity data for graptolites, a group of fossil organisms that had a different lifestyle (planktonic) and are generally found in a different biofacies. We investigated the pattern of graptolite faunal changes across the *Climacograptus bicornis*–*Diplacanthograptus caudatus* graptolite zonal boundary in North America and on several other continents. In the Appalachian Basin a sharp decline in species diversity occurred. Scores for normalized diversity dropped from 20 in the *C. bicornis* Zone to 7 in the *D. caudatus* Zone. Only 11% of the species present in the *C. bicornis* Zone carry over into the *D. caudatus* Zone. A similar pattern occurs in the Ouachita Mountains of Oklahoma. High and middle paleolatitude regions such as Wales and Baltoscandia exhibit low diversity in the lower Katian and then further decline in graptolite diversity at higher stratigraphic levels. In other low paleolatitude regions such as Australasia and Scotland, however, diversity is fairly constant across this interval (although the percentage of carryover taxa is low).

Climatic cooling during the Katian may have directly affected graptolite faunas at mid- to high latitudes but not at low latitudes. Parts of Laurentia were affected only because a depressed corridor, the Sebree Trough, allowed deep, cool Iapetus Ocean water to spread across the craton. Thus, different combinations of local tectonics, climate change, and water-depth history may have produced similar diversity patterns at different paleolatitudes.

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