Latitudinal distribution of bryozoan-rich sediments in the Ordovician

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Most bryozoans have calcareous skeletons that locally contribute large amounts of carbonate sediment to the sea floor. Whereas Recent bryozoans are diverse in shelf seas pan-globally, it is only in mid to high latitudes that they are potential limestone producers; tropical bryozoans invariably have too small a biomass relative to other carbonate producers (corals, algae and molluscs) to be important sources of sediment. During the Palaeozoic, however, bryozoan-rich deposits were formed at all palaeolatitudes, including the tropics. Extending the work of Taylor & Allison (1998), we have compiled data on 42 occurrences of bryozoan-rich deposits of Ordovician age to determine whether the Palaeozoic distributional pattern extends back to their earliest appearance in the fossil record. Estimated palaeolatitudes of deposition ranged from 10–75°, but the majority (71%) were found to be tropical, *i.e.* < 23.5°. Of the 14 reefal occurrences, 11 (79%) were formed in tropical palaeolatitudes. No significant trend in depositional palaeolatitude could be detected with time through the Ordovician. The most persuasive explanation for the broader palaeolatitudinal distribution of bryozoan-rich deposits (including reefs) in the Ordovician than at the present day is that durophagous predators were ecologically unimportant, allowing large erect, sediment-producing bryozoan colonies to grow in the tropics where today they are vulnerable to grazing fishes, decapods and echinoderms. • Key words: Bryozoa, Ordovician, carbonates, palaeolatitudes.

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Fossil occurrences of organisms and associated sedimentary facies are commonly used as a guide to ancient climates, and by extension, palaeolatitudes. Classic examples include reef limestones as indicators of warm, low latitudes, glacial sediments of cold, high latitudes, and evaporites of the subtropics (Hallam 1994, p. 12). The doctrine of uniformitarianism is usually crucial to such interpretations, with ancient patterns of distribution assumed to have been essentially the same as those in the modern world. However, there are limits to uniformitarianism, not least those caused by evolutionary ecological changes. Noting the latitudinal displacement of some carbonate-producing groups, Kiessling *et al.* (2003, p. 199) remarked "...uniformitarian approaches to pre-Mesozoic carbonate platforms have to be handled with care". Here we compare the latitudinal distribution of bryozoan-rich communities at the present day with that of the Ordovician period.

Bryozoans are colony-forming, mostly marine, benthic suspension feeders. The majority of species have calcareous skeletons, usually made of calcite, and this accounts for the excellent fossil record of the phylum. Locally, bryozoan skeletons occur in rock-forming abundances, resulting in bryozoan marls or bryozoan limestones (Fig. 1). The oldest unequivocal bryozoans come from the Lower Ordovician Tremadocian Fenghsiang Formation of the East Yangtze Gorges, China (Xia *et al*. 2007, Zhang *et al*. 2009), although putative bryozoans have been described recently from the Tremadoc (Landing *et al*. 2010). Bryozoans played a prominent role in the Great Ordovician Biodiversification Event, rapidly attaining a family-level diversity that was to persist throughout much of the Palaeozoic (Taylor & Ernst 2004).

Taylor & Allison (1998) drew attention to the striking contrast between the latitudinal distributions of Palaeozoic and post-Palaeozoic bryozoan-rich deposits (see also Allison *et al.* 1999). Nearly all post-Palaeozoic deposits in which bryozoans comprise a significant proportion (*ca* > 20%) of the sediment were deposited in mid- to high-latitudes, outside the tropics (defined as 23.5° north or south of the equator). This is not the case in the Palaeozoic

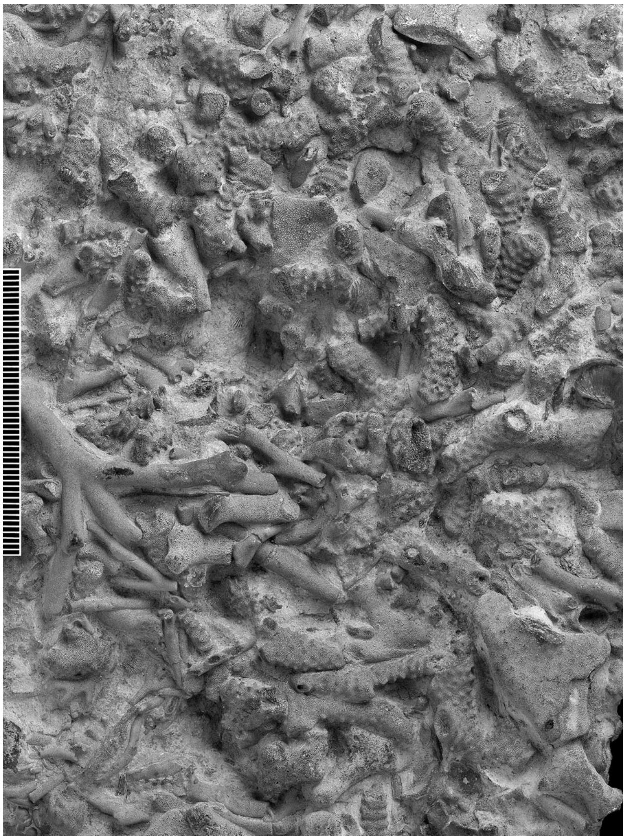

Figure 1. Bryozoan limestone from the Cincinnatian (Upper Ordovician) of the Cincinnati region, USA (NHM R223). The bedding plane is strewn with broken branches from bushy colonies of mostly trepostome bryozoans.

where the pattern of latitudinal distribution is essentially pan-latitudinal, with a large number of occurrences of bryozoan-rich deposits in the palaeotropics.

Our aim here is to describe the palaeolatitudinal distribution of bryozoan-rich deposits during the Ordovician, immediately after the first appearance of the phylum in the fossil record and during their initial evolutionary radiation. We add new occurrences to the database of bryozoan palaeolatitudes utilized by Taylor & Allison (1998) and consider reasons why bryozoans had a proportionally higher biomass in the Ordovician tropics than they do in the modern tropics.

Methods

Data for this analysis was gathered in the same way as described by Taylor & Allison (1998), except that online literature searches were undertaken in addition to trawling through printed sources such as the large collection of bryozoan reprints in the Department of Palaeontology at the Natural History Museum, London (NHM). Very few papers actually quantify the abundance of bryozoans in Ordovician deposits. Therefore judgements were made to include data based on the descriptive terms employed, for example, 'bryozoan limestone', 'bryozoan marl' or 'bryozoan reef'. In addition, phrases such as 'bryozoans abundant' and 'rich in bryozoans' were taken to indicate that bryozoans make a volumetrically significant contribution to the sediment. A few of the datapoints were identified on the basis of samples in the collections of the NHM rather the literature. In total, 42 records of bryozoan-rich deposits of Ordovician age could be recognized. These are summarized in Table 1. It must be emphasized that a record of bryozoans simply being present at a locality does not qualify this as a bryozoan-rich deposit; there must be evidence that bryozoans occur in rock-forming abundance. For information on the biogeographical distribution of Ordovician bryozoans, see Tuckey (1990) and references therein.

For all deposits accepted as bryozoan-rich, details of lithostratigraphy, chronostratography and location were recorded in a spreadsheet. In addition, any information provided about sedimentary facies and the types of bryozoans present were noted, in particular whether the unit containing the bryozoans was reefal or non-reefal. Stratigraphical information was used to estimate the age of the deposit as precisely as possible. In instances when only an age range was available (*e.g.* stage), the median age of the interval specified was calculated and used when estimating palaeolatitude.

Whereas the earlier paper of Taylor & Allison (1998) used the palaeogeographical reconstructions of Scotese & McKerrow (1990) to estimate Palaeozoic palaeolatitudes, we employed the more up to date maps of Cocks & Torsvik (2006). Datapoints were plotted as accurately as possible onto the palaeogeographical map closest in age to the deposit concerned (Fig. 2).

Results

When the palaeolatitudinal data is split into 10° bins (Fig. 3), the most populated bin is between 11° and 20° containing 21 bryozoan-rich deposits, *i.e.* 50% of the datapoints. Next is the 21–30° bin with 10 datapoints (23%). All other bins contain 5 or fewer datapoints. The lowest estimated palaeolatitude for a bryozoan-rich limestone in the Ordovician is 10°, and the highest 75°. All of the occurrences were in the southern hemisphere during the Ordovician, with the exception of two sites from present-day Australia which were situated just north of the Ordovician equator and very close together.

Considering reef occurrences separately, these are also concentrated in the 11–20° palaeolatitudinal bin. All apart from one were formed at palaeolatitudes of 25° or less, *i.e.* in the tropics or subtropics. The single exception is a mud mound in which bryozoans are the main skeletal component, deposited at a palaeolatitude of 62° S (Buttler *et al.* 2007).

The latitudinal distribution of bryozoan-rich deposits did not change through the Ordovician: there is no significant correlation between palaeolatitude and estimated age of the deposit (R^2 0.0253).

Discussion

As expected from the earlier study of Taylor & Allison (1998), the great majority (71%) of Ordovician bryozoan-rich deposits were formed in the palaeotropics, *i.e.* between 23.5° N and 23.5° S. However, bryozoan-rich deposits were formed at most palaeolatitudes to a maximum of 75°. Unfortunately, data available in the literature is strongly biased towards European and particularly eastern North American occurrences. Bryozoan-rich Ordovician deposits certainly occur elsewhere in the world but useable information about them is difficult to obtain. Systematic papers seldom give an indication of the relative abundance of bryozoans in the deposits from which they are described.

The broad latitudinal spread, but with a tropical focus, of bryozoan-rich deposits in the Ordovician at this early stage in the evolutionary history of the phylum contrasts with the pattern seen at the present-day. Incipient bryozoan limestones are forming today almost entirely outside the tropics, and this pattern seems to have been characteristic for most or all of the post-Palaeozoic (too few bryozoan-rich deposits are known in the Triassic to establish a pattern, although Baud *et al.* (2008) recently described some high latitude, Early Triassic bryozoan-rich deposits). Consequently, straightforward uniformitarian principles cannot be applied to infer palaeolatitude of deposition from the occurrence of bryozoan-rich deposits in the Ordovician.

Recent and ancient shelf carbonates are frequently subdivided into warm- and cool-water types. These two categories have been given a variety of names depending on the principal organic constituents, *e.g.* ‘foramol’ for a cool-water carbonate dominated by foraminifers and molluscs, and ‘coralgal’ for a warm-water carbonate dominated by corals and algae. James (1997) introduced a simpler terminology, categorizing carbonate grain associations as either photozoan or heterozoan. The term photozoan refers to the dominance of autotrophs, such as algae or zooxanthellate corals and foraminifera, depending on light for photosynthesis. Heterozoan refers to a more diverse assemblage of mostly heterotrophic organisms, including molluscs, bryozoans, benthic foraminifera and barnacles. Photozoan associations are typical of low latitude, warm water environments, heterozoan associations of colder water

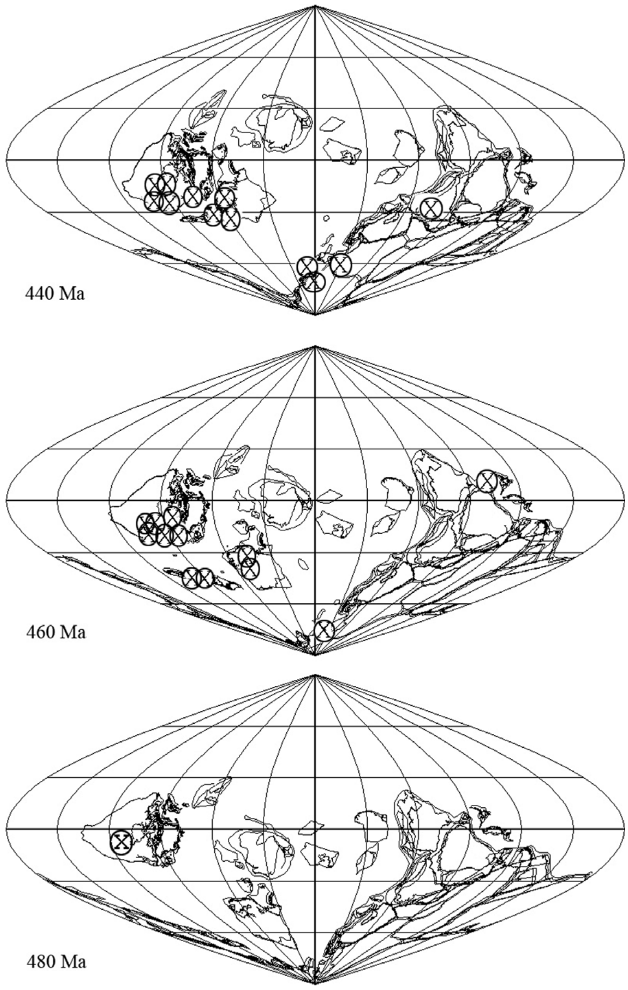

Figure 2. Distribution of Ordovician bryozoan-rich deposits plotted onto the Cocks & Torsvik (2006) 440, 460 and 480 Ma palaeogeographical reconstructions.

associations, either at higher latitudes or in deeper water. High abundances of bryozoans occur only in heterozoan associations.

In order to explain the contrasting latitudinal patterns between Ordovician and modern bryozoan-rich sediments it is necessary to examine factors that result in sufficiently high abundances of bryozoans for their skeletons to be sediment formers. Bryozoans are suspension feeders consuming phytoplankton, predominantly dinoflagellates (*e.g.* McKinney 1990). An adequate supply of phytoplankton is therefore necessary for their existence, as well as the presence of firm or hard surfaces onto which the larvae can settle and the adult colonies remain anchored during their life. Deleterious to bryozoans are high sediment loads as they both increase the likelihood of burial and adversely affect suspension feeding. Bryozoans are prey items for a large diversity of animals (see Lidgard 2008). They also suffer mortality, or partial mortality, as a result of overgrowth by competitors for space.

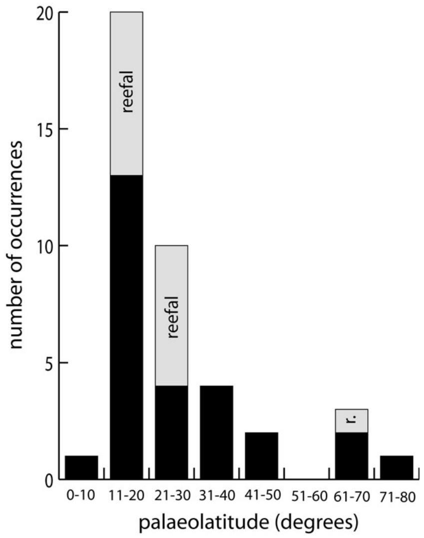

Figure 3. Palaeolatitudinal frequency distribution of bryozoan-rich deposits of Ordovician age. Data is divided into 10° palaeolatitudinal bins. Reefal occurrences are shown separately in grey.

Durophagous fishes, decapod crustaceans and grazing echinoids may all consume bryozoans as parts of their diets. According to Lidgard (2008), selective pressure imposed by predators can be a strong determinant of the distribution of bryozoans at the present day, at least on a local scale, with many bryozoans surviving better in cryptic microhabitats. In general terms, predator pressures are greater in the tropics than they are in higher latitudes at the present day (Vermeij 1978). Assemblage diversities of bryozoans can be at least as high in the modern tropics, including in coral reefs (*e.g.* Winston 1986), as they are at higher latitudes (Clarke & Lidgard 2000). However, bryozoan skeletal biomass is invariably small when compared with other organisms possessing calcified skeletons, and large, erect species capable of generating appreciable quantities of carbonate sediment are typically uncommon in the tropics. For example, Freestone *et al*. (2009) deployed settlement panels at a range of latitudes and found the resulting communities to contain bushy bryozoans, except for the panel in Belize where the bryozoans were "very small, delicate, and rare" (p. 255).

In respect to their minor biomass in the tropics, bryozoans resemble brachiopods which, in contrast to their abundance in the tropics and subtropics during the Palaeozoic-Jurassic, are generally rare in the tropics today and when present tend to be small, cryptic and contribute negligible quantities of carbonate sediment (Zuchsin & Mayrhofer 2009). Levels of predation are believed to have been lower during the Palaeozoic than they are today, and durophagous predators were certainly less diverse during the Ordovician than they are in modern seas (*e.g.* Vermeij 1987). It is therefore conceivable that large, sediment-producing bryozoans were able to survive in the palaeotropics where today they cannot. This could explain the existence of bryozoan-rich deposits at low latitudes during the Ordovician.

A second hypothesis is that nutrient levels in the Ordovician tropics were higher than they are in the modern tropics, promoting phytoplankton growth and favouring suspension feeders such as bryozoans and also brachiopods.

Warm water, photozoan associations, including coral reefs, characterize nutrient-deficient carbonate environments today (Hallock & Schlager 1986). Holland & Patzkowsky (1996) studied facies changes in the Upper Ordovician of the eastern USA, an area located close to the palaeoequator. They identified a change from 'tropical-type' to 'temperate-type' carbonates at approximately the Mohawkian-Cincinnatian sequence boundary, coinciding with an increase in siliciclastics and phosphatization. This was interpreted as a result of transgression, allowing the introduction of cool, nutrient-rich waters onto the craton. In other words, enrichment in nutrients facilitated the development of heterozoan carbonates, rich in bryozoans, at a low palaeolatitude. Other studies have also correlated sedimentary rocks rich in bryozoans with increased nutrient levels, often due to upwelling, as in the case of mounds from the Pleistocene (James *et al.* 2004) and Ordovician (Buttler *et al.* 2007). However, optimal nutrient levels for dense growths of carbonate-producing bryozoans remain unclear. According to Lidgard *et al*. (1997), 'bryozoan gardens' at the present day are generally correlated with nutrient levels between oligotrophic shelf conditions and offshore upwelling. On the other hand, McKinney & Hageman (2006) and McKinney (2007) proposed that modern communities in the eastern Adriatic Sea dominated by Palaeozoic-like epifaunal suspension feeders rich in bryozoans were explained by the low nutrient, oligotrophic conditions here compared with the western Adriatic where higher nutrient levels correlate with dominantly infaunal communities (see also Zuchsin & Stachowitsch 2009). More research needs to be done before the role of nutrient level on bryozoan abundance can be evaluated.

Future research is needed to enlarge the database of bryozoan-rich deposits of Ordovician age, especially outside present-day North America and Europe. It would also be instructive to compare the facies and taxonomic compositions of Ordovician bryozoan limestones from different palaeolatitudes. A study of bryozoans in the Late Palaeozoic of Gondwana showed that cystoporate and rhabdomesine bryozoans in low latitude settings were replaced by trepostomes at higher latitudes (Reid & James 2008). It is not known whether such palaeolatitudinal patterns of taxonomic dominance within the phylum also existed during Ordovician times.

Conclusions

1. Bryozoan-rich carbonates, including bryozoan limestones and bryozoan marls, were mostly formed in the tropics during the Ordovician. Thus, the pattern of tropical dominance that was to characterize the entire Palaeozoic was established early in the evolutionary history of phylum Bryozoa.

2. There is no appreciable difference between the latitudinal distributions of reefal and non-reefal bryozoan-rich deposits in the Ordovician: bryozoan reefs or mounds were formed at both low and relatively high latitudes. Although low latitude occurrences are more abundant, this may reflect the greater number of records of bryozoan-rich deposits in the Ordovician tropics.

3. Modern sediments with high bryozoan skeletal contents are found almost entirely outside the tropics. This extra-tropical pattern of distribution has characterized most or all of post-Palaeozoic time.

4. The present-day distribution of bryozoan carbonates cannot be used as a guide to their latitude of formation during the Ordovician, or indeed for any period in the Palaeozoic.

5. Control/s over the latitudinal distribution of bryozoan-rich sediments are unknown, both today and in the geological past. Higher nutrient levels in the Ordovician tropics are one possible explanation for the abundance of bryozoans. However, the most attractive hypothesis is that calcareous bryozoans of sufficient biomass to contribute significant quantities of carbonate could exist in the Ordovician tropics due to the low pressure from durophagous predators.

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Appendix

Database of Ordovician bryozoan-rich deposits arranged in order of increasing palaeolatitude of formation.

A	Stratigraphy	B	Locality	C	References
10° S	Arenig, Kanosh Fm.	473	Ibex, Utah, USA	no	Li & Droser (1999)
12° N	Upper Ordovician (Gisbornian, Eastonian and Bolindian), Benjamin Limestone Fm.	453	Western Tasmania, Australia	no	Ross & Ross (2008)
12° S	Chazyan, Mingan Fm.	466	Mingan Islands, Quebec, Canada	no	Desrochers & James (1989), Bolton & Cuffey (2005)
12° S	Chazyan, Mingan Fm.	466	Mingan Islands, Quebec, Canada	yes	Desrochers & James (1989)
13° S	Cincinnatian, Maysvillian, Bellevue Fm.	450	Brookville Dam Spillway, southeastern Indiana, USA	no	Hay & Cuffey (1998)
15° N	Upper Ordovician, Upper Gisbornian, Gleesons Limestone Member	468	Cliefden Caves, New South Wales, Australia	no	Webby & Packham (1982)
15° S	Cincinnatian, Whitewater Fm.	441	Caesar Creek etc., Cincinnati area, Ohio, USA	no	Rockwell & Cuffey (1996)
15° S	Maysville Stage, Corryville Member, Grant Lake Fm.	441	Maysville, Kentucky, USA	yes	Cuffey & Pursell (1995), Cuffey (1998), Dettmers (2009)
15° S	Cincinnatian, Dillsboro Fm.	441	SE Indiana, USA	no	Brown & Daly (1985)
15° S	Trenton Group	454	Quebec, Canada	no	Harland & Pickerill (1984)

A	Stratigraphy	B	Locality	C	References
17° S	Trenton Limestone Group	445	Ontario, Canada	no	Brookfield (1988)
17° S	Chazyan, St Martin Member, Laval Fm.	466	Caughnawaga, Montreal area, Quebec, Canada	yes	Pratt (1989)
18° S	"St James-Beecher Mbr contact, Dunleith Fm., Galena Gp."	458	Guttenberg, Iowa, USA	no	Sanders *et al*. (2002)
20° S	Pin Formation	443	Spiti Valley, Northern India	yes	Suttner & Ernst (2007)
20° S	Champlainian, Trentonian, Laframboise Mbr, Ellis Bay Fm.	444	Natiscotec, Anticosti Island, Canada	yes	Ernst & Munnecke (2009)
20° S	Middle Ordovician, Mountain Lake Mbr, Bromide Fm.	450	Chicasaw, Arbuckle Mts, Oklahoma, USA	yes	Cuffey & Cuffey (1995)
20° S	Upper Ordovician	452	Butler Co., Ohio, USA	no	Horowitz & Potter (1971)
20° S	Middle Ordovician Tanglewood Mbr, Lexington Limestone Fm.	457	Kentucky, USA	no	Horowitz & Potter (1971)
20° S	Champlanian, Rockland Fm.	460	NW New York State, USA	no	Ross (1972)
20° S	Champlanian, Rockland Fm.	460	Ontario, Canada	no	Ross (1972)
20° S	Cincinnatian, Grant Lake Fm.	460	Southwestern Ohio, USA	no	Schumacher *et al*. (1991)
20° S	Middle Ordovician, Carters Limestone	462	Central Tennessee, USA	yes	Alberstadt *et al.* (1974)
21° S	Shermanian, Grier and Tanglewood mbrs, Lexington Limestone Fm.	453	Central Kentucky, USA	yes	Lambert *et al.* (2001)
21° S	Upper Ordovician, Hull Limestone Mbr, Bobcaygeon Fm.	453	Eastern Ontario, Canada	no	Kiernan & Dix (2000)
21° S	Middle Ordovician, Chaumont Fm.	458	Bonnechere River, Ottawa Valley, Canada	yes	Steele-Petrovich (1988)
21° S	Middle Ordovician, Millersburg Mbr, Lexington Limestone Fm.	454	Kentucky, USA	no	Cressman & Peterson (2001)
22° S	Cincinnatian, Late Edenian McMicken Mbr, Kope Fm.	449	Miamitown, Ohio, USA	no	Cuffey (1998)
22° S	Middle Ordovician, New Market – Benbolt fms	462	Virginia, USA	yes	Read (1982)
23° S	Hirnantian, Boda Limestone	439	Dalarna, central Sweden	yes	Brood (1981)
23° S	Shermanian, Sulpher Well Member, Lexington Limestone Fm.	453	Central Kentucky, USA	no	Ettensohn *et al*. (1986)
25° S	Middle Ordovician, Bowen Fm.	450	SW Virginia, USA	yes	McKinney *et al*. (2001)
25° S	Middle Ordovician, Chickamauga Group	450	Central Alabama, USA	yes	Crow (1985, 1997), Stock & Benson (1982), Gault & McKinney (1980)
31° S	Ashgill, Fosses Fm.	447	Cocriamont, Condroz area, central Belgium	no	Tourneur *et al.* (1993)
31° S	Caradoc, Rakvere Stage, Wesinberg Limestone	451	Slantsy, Leningrad Oblast, Russia	no	Dronov (1997)
32° S	Middle Ordovician, D3, Wassalem Limestone	454	Sack, south of Reval, Estonia	no	NHM material
36° S	Upper Rawtheyan, Slade and Redhill Beds	440	Whitland, Dyfed, Wales, UK	no	Buttler (1991)
50° S	Caradoc, Costonian, Hoar Edge Limestone	463	Evenwood-Harnage area, Shropshire, England, UK	no	Ross (1963)
50° S	*Marrolithus favus* Biozone, 'Llandeilo Limestone'	463	Clog-y-fran, Dyfed, Wales	no	Buttler (1997)
61° S	Lower-Middle Ashgill, Cystoid Limestone Fm.	449	Badules, Iberian Chains, NE Spain	no	Vennin *et al*. (1998), Jiménez-Sánchez & Villas (2007), Jiménez-Sánchez (2009)
62° S	Lower Ashgill, Jifarah Fm.	447	Tripolitania (subsurface), NW Libya	yes	Buttler *et al*. (2007)
62° S	Ashgill, Khabt-el-Hajar Fm.	449	Erfoud, Morocco	no	Álvaro *et al.* (2007)
75° S	Upper Caradoc, Unit C	453	Southern Sardinia	no	Conti (1990)

Abbreviations: A – palaeolatitude, B – estimated age (Ma), C – reefal.