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Epipelagic chitinozoan biotopes map a steep latitudinal temperature gradient for earliest Late Ordovician seas: Implications for a cooling Late Ordovician climate

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ABSTRACT

The Early–Mid Ordovician has long been considered a super-greenhouse world, based largely on high relative global sea levels and light stable oxygen isotope data from bulk carbonates. An alternative and largely untested hypothesis has suggested that, at least in equatorial palaeolatitudes, there was a steady cooling trend through the Early Ordovician reaching the range of modern equatorial sea surface temperatures by the Mid Ordovician. This hypothesis, though controversial, is supported by palaeobiogeographical studies of the early Late Ordovician (Sandbian) zooplankton (graptolite) biotopes. These are comparable to the modern planktonic foraminifera 'provinces' and suggest a latitudinal temperature gradient that is similar to the modern one.

Chitinozoans are also an important group of Palaeozoic marine microfossils, but with a poorly known biological affinity. Here we present an analysis of chitinozoan species palaeobiogeography for the early Late Ordovician (Sandbian *c.* 460 Ma), which confirms that these microfossils, and likely their parent organisms, were epipelagic. Unlike the graptolites, chitinozoans had their highest diversity and abundance south of ~35°S during this time, which strongly suggests adaptation to temperate to cold waters. The distribution of chitinozoan biotopes during the *gracilis* time-slice allows us to identify the austral Subtropical, Subpolar and Polar belts; key oceanographic boundaries are identified as the Subtropical–Subpolar Transition at ~35°S and tentatively, the Polar Front at ~55°–70°S. Again, these are in a similar position to those in the modern Southern Ocean. Chitinozoan biotopes also map a steep latitudinal faunal gradient that is comparable to that of the graptolites and that of modern plankton. This likely indicates a steep latitudinal temperature gradient for early Late Ordovician seas and questions the notion that this interval of Earth history had a greenhouse climate.

1. Introduction

The Early–Mid Ordovician has long been considered a super-greenhouse world (Brenchley et al., 1994, see references in Armstrong, 2007; Trotter et al., 2008), based on high relative global sea levels and light marine $\delta^{18}O_{carb}$ values from limestones and brachiopods (mean values roughly from −10‰ to −5‰), though the fidelity of the latter record is still debated (Shields et al., 2003; Trotter et al., 2008, also see references in Armstrong, 2007). The established paradigm then saw climate cooling rapidly towards a short-lived Hirnantian glaciation (Brenchley et al., 1994). A new interpretation of Ordovician glaciation has emerged from General Circulation Modelling (Herrmann et al., 2004) and new stable isotope data (e.g. Saltzman and Young, 2005). In this scenario, the Early Palaeozoic Ice Ages started at the Guttenberg Positive Carbon Isotope Excursion (GICE; Guttenberg Glaciation) in the Katian Stage of the Late Ordovician (*c.* 454 Ma; Saltzman and Young, 2005; Page et al., 2007; dates from Webby et al., 2004). Short-lived drops in sea level have been recorded during the Katian, tentatively interpreted as first glacial pulses by Bourahrouh et al. (2004, Fig. 8) and Loi et al. (in press). The ice age then proceeded with a series of likely discrete glaciations into the Hirnantian and Llandovery–Wenlock (Page et al., 2007; Armstrong, 2007). Trotter et al. (2008) have also suggested that there was a steady cooling trend in equatorial palaeolatitudes through the Early

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Ordovician reaching the range of modern equatorial Sea Surface Temperatures (SSTs) by the Mid Ordovician (*c.* 468 Ma) and posited a link between cooling and the Great Ordovician Biodiversification Event.

This latest interpretation contrasts with a Mid–early Late Ordovician greenhouse, and would require mechanisms other than climatological warming to explain the high sea levels during this interval, such as increased Mid Ocean Ridge volumes. Although greenhouse climates are still poorly understood and although absolute SSTs in greenhouse periods, especially in the tropics, remain elusive (e.g. Pearson et al., 2001), it is still generally accepted that during a greenhouse climate mode, higher heat transfer to the poles and reduced polar icesheets would result in a relatively shallower SST gradient from equator to pole. This in turn would result in broader plankton provinces particularly in low and mid-latitudes. For example, planktonic foraminifera distribution during the latest Albian (Hart, 2007, also see Hart, 2000, references therein, and Huber et al., 2002) shows a global five-fold subdivision, in contrast to the nine provinces in modern oceans. The different scenarios for the early Late Ordovician can therefore be tested with fossil plankton distributions.

Studies of graptolite palaeobiogeography for the early Sandbian (*c.* 460 Ma; Vandenbroucke et al., 2009), post-dating the onset of cooling suggested by Trotter et al. (2008), indicate zooplankton biotopes comparable to modern planktonic foraminifera ‘provinces’. These biotopes confirm SST estimates from the Global Climate Models (GCMs) for the Sandbian (Herrmann et al., 2004) and hence suggest a steeper latitudinal temperature gradient than would be predicted for a greenhouse climate state. By comparison with the earlier Ordovician, this is probably indicative of an early Sandbian “cool world”. Graptolite biotopes allow the tentative identification of the Subtropical–Subpolar Transition at ~35°S: a critical boundary in the ocean–atmosphere system (Vandenbroucke et al., 2009). In this paper we demonstrate that chitinozoans were also epizooplankton and these microfossils also provide further palaeobiogeographical evidence for an early Late Ordovician cool world. A coherent pattern of zooplankton distribution that can be linked to SST is therefore now emerging for the early Late Ordovician.

2. Chitinozoan palaeontology

Chitinozoans represent an extinct group of organisms, widely distributed in Ordovician to Devonian marine deposits as organic-walled microfossils. Their stratigraphic utility has resulted in a stable taxonomy and a high-resolution, spatial and temporal record of their occurrences. In comparison with the graptolites, the biology and ecology of this group is poorly known. Chitinozoans are considered to be the eggs of a soft-bodied, at present unknown, marine metazoan (Paris and Nõlvak, 1999). Environmentally, the highest abundance of chitinozoans (measured as the number of specimens per gram of rock) has been suggested to occur in high latitude, cold water, and locally in outer shelf settings (Paris, 1996 and references therein). Chitinozoan data could therefore be complementary to the dominantly low-mid latitude graptolite data of Vandenbroucke et al. (2009) for the analysis of Late Ordovician plankton biogeography.

Some authors have postulated that a part of the chitinozoan-producing fauna belonged to the (nekto)benthos, mainly based on lateral and facies differentiation of chitinozoans on regional shore-to-basin transects (Grahn, 1981, 1982; Grahn and Bergström, 1984; Bergström and Grahn, 1985; Nestor, 1998). However, the majority of species are facies independent (e.g. see our data below). Also, lateral differentiation has been identified as an important ecological control for clearly zooplanktonic groups such as the planktonic graptolites (Finney, 1984, 1986; Finney and Berry, 1997; Williams et al., 2003), and is therefore not restricted to nektobenthonic species.

Most authors now agree that chitinozoans, and likely their parent organisms, had a pelagic mode of distribution, with a palaeolatitudinal

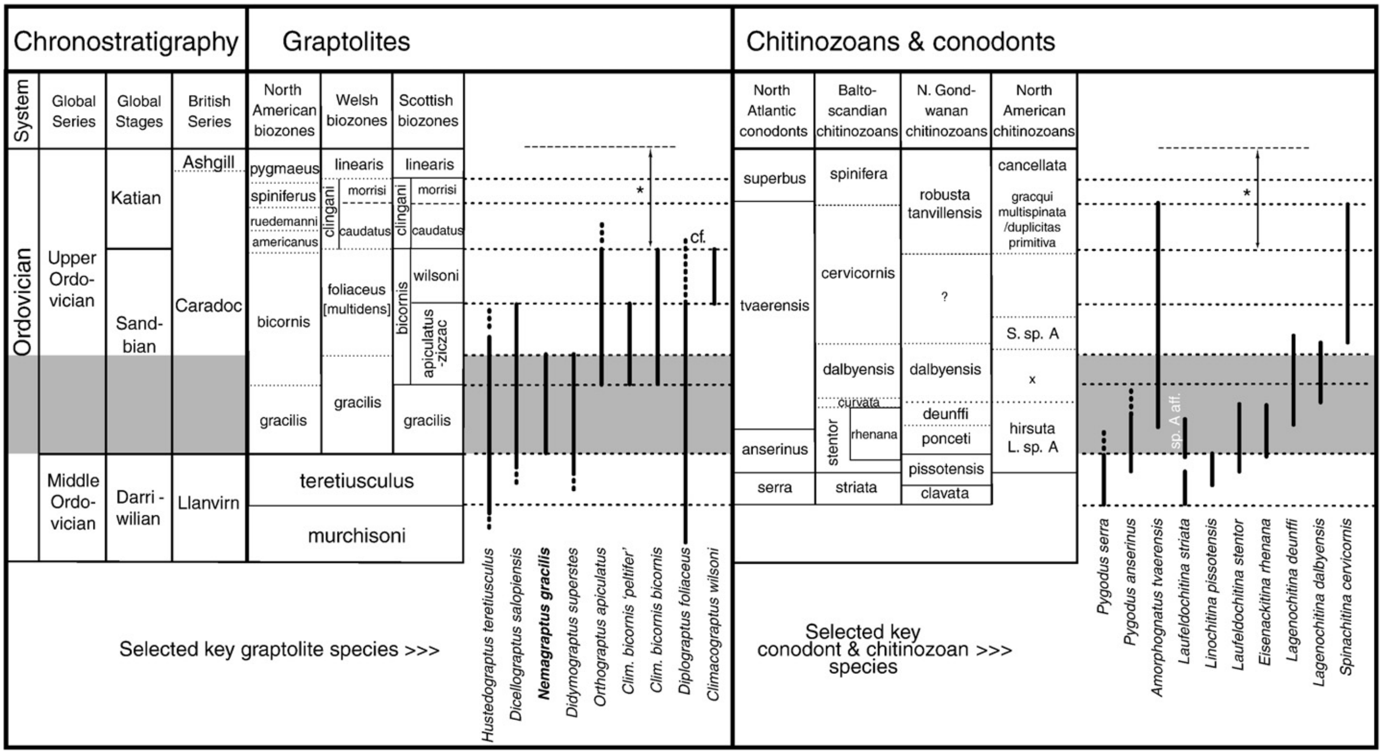


Fig. 1. Definition of the ‘*gracilis* time-slice’ (shaded), between the first (FAD) and last appearance data (LAD) of *N. gracilis*, summarised after Vandenbroucke et al. (2009). The graptolite data are after Bergström et al. (1998, 2000), Finney and Bergström (1986), Hede (1951), Hughes (1989), Williams et al. (2003, 2004) and Zalasiewicz et al. (2009). The conodont and chitinozoan ranges plotted on the figure are the combined longest ranges vis-à-vis the chitinozoan/conodont biozonal boundaries, as reported by Bergström (1983), Bergström et al. (2000), Nõlvak and Grahn (1993); Paris (1990) and Vandenbroucke (2004). The correlation between the graptolite biozones and the conodont/chitinozoan biozones follows Webby et al. (2004). The Scottish graptolite biozones follow the revision by Williams et al. (2004). *Species originating in this interval are not shown.

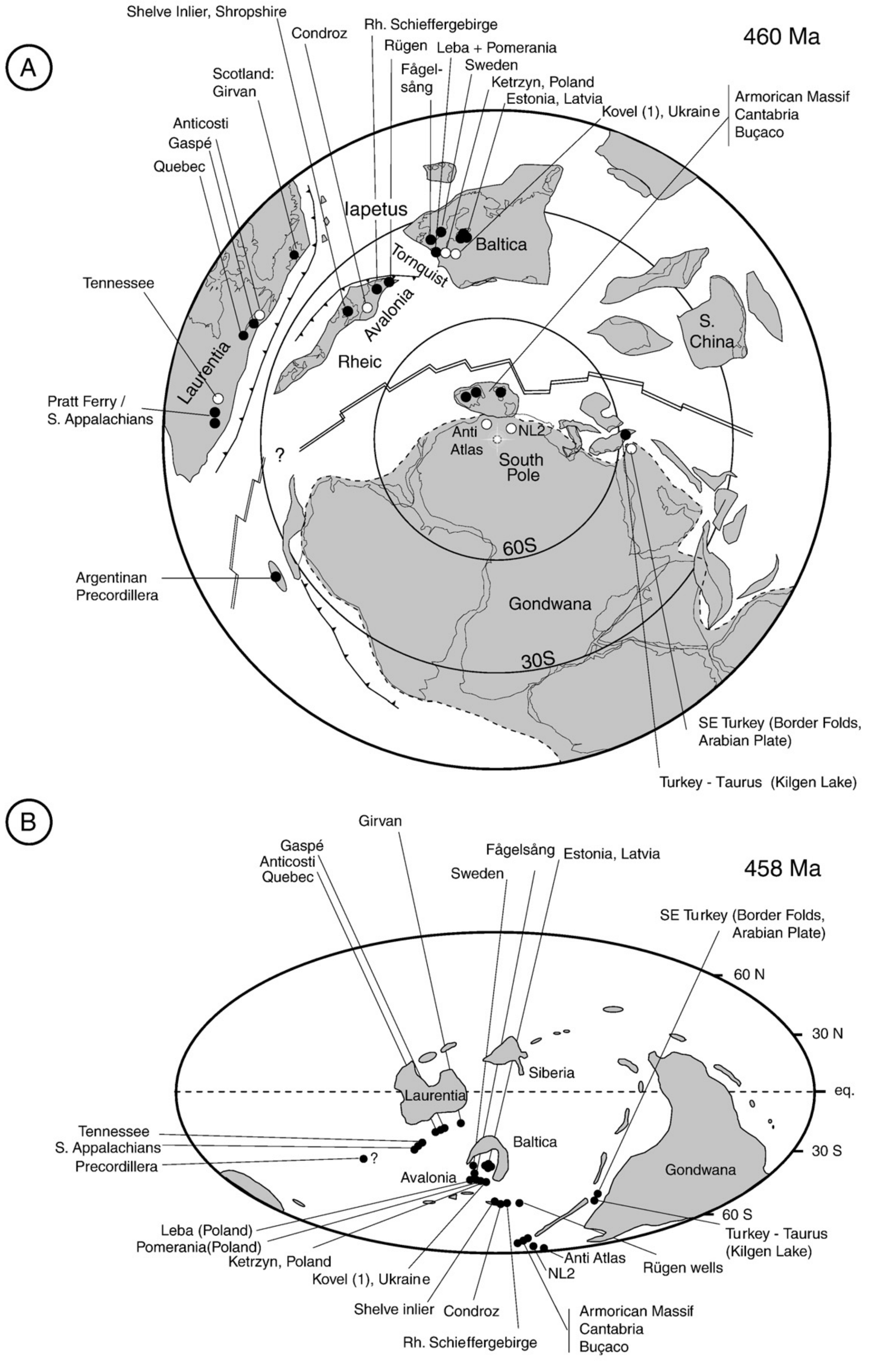


Fig. 2. Late Ordovician palaeogeographical reconstructions showing the distributions of the sections in this study: (A) Palaeogeographic terrane map of Cocks and Torsvik (2004). Filled circles indicate localities that have also been used in a parallel graptolite study (Vandenbroucke et al., 2009) whereas open circles represent localities exclusively yielding chitinozoans; (B) Palaeogeographic map after Scotese [www.scotese.com]. The grey areas are landmasses (but note that this is not the case in map 'A' where the shaded areas represent areas of continental crust). The actual 'Point Tracker' coordinates of the sections, as used in the analyses, are in the Supplemental Files.

(i.e. SST) control, subsequently modified by palaeocurrents (Paris et al., 1999, p. 291, and references therein). This consensus is not yet quantified and is mainly based on the wide and largely facies-independent distribution of species. Further key evidence to support a zooplanktonic mode of life for the chitinozoans is their occurrence in widespread anoxic deposits. For example, the early Silurian of high-latitude northern Gondwana is characterised by black graptolitic shales (i.e., the so-called 'hot shales') including beds in the Tannezzuft Fm. in Libya, the Qusaiba Shales in Saudi Arabia, the Ain Delliouine Fm. in Morocco and many lateral equivalents, that are devoid of trace fossils or benthic fauna (see Armstrong et al., 2005; Page et al., 2007; Zalasiewicz et al., 2007; Armstrong et al., 2009). These hemipelagic shales yield abundant graptolites (either as mature rhabdosomes, or as siculae), numerous leiospheres and tasmanitids (i.e., Prasinophyta, pelagic green algae), a few epiplanktonic bivalves and rich and diverse assemblages of chitinozoans including *Ancyrochitina*, *Cyathochitina*, *Linochitina*, *Cingulochitina*, *Plectochitina* and *Margachitina* (e.g. Paris, 1981; Paris et al., 1995, 1998, 2008; Zalasiewicz et al., 2007). Here, chitinozoans co-occurred exclusively with organisms that were dwelling in the upper oxic part of the water column. All the elements of this fauna must have had an epipelagic/nektonic mode of distribution, considering the inhospitable anoxic sea floor conditions over a vast area. The same species of chitinozoans, graptolites and leiospheres are distributed over an area covering over 20 (to 30) million km^2 (Paris, 1981; Dufka and Fatka, 1993; Paris et al., 1995, 1998; Bourahrouh, 2002). Another example supporting this interpretation is found in the Lower Palaeozoic deposits of Scotland and Wales where chitinozoans are known from widespread anoxic facies (e.g. Vandenbroucke et al., 2008), such as in parts of the Southern Uplands of Scotland where they are found in association with graptolites, radiolarians and radiolarian cherts (e.g. Zalasiewicz et al., 2004).

3. Methodology

Few chitinozoan studies have been specifically designed to elucidate chitinozoan palaeoecology. All previous studies were either (i) region-specific (e.g. Paris, 1993), (ii) global, but for a restricted number of taxa (e.g. Achab, 1989; Servais et al., 2005), (iii) part of biostratigraphically-focused research, or (iv), spanning too long a time interval (e.g. Achab, 1991). Here, we provide the first detailed, global-scale palaeobiogeographical analysis through a short, well-defined time-slice during which the climate was stable. Our main objectives are, first, to establish that chitinozoans were part of the zooplankton and, if so, to compare species distributions with those of the graptolites and hence to test and refine the palaeoclimatological models based on graptolite palaeobiogeography (Vandenbroucke et al., 2009). Our methodology therefore follows Vandenbroucke et al. (2009). To a considerable degree this is based on that of the USGS PRISM group, pioneers in effecting global, deep time reconstructions of biotopes and climate (see Dowsett, 2007).

3.1. The chitinozoan data

The *gracilis* time-slice of the early Sandbian is defined by the total range of the graptolite *Nemagraptus gracilis* (Fig. 1; Williams et al., 2004; Vandenbroucke et al., 2009). It differs from the Sa1 stage-slice (Bergström et al., 2009), as *N. gracilis* is known to range into the overlying Sa2 stage-slice, where it co-occurs with *Climacograptus bicornis*. Chitinozoans do not always co-occur with the biozonal indicator graptolites. In sections lacking characteristic graptolites we have followed Webby et al. (2004) and used the coeval chitinozoan biozonations (see Fig. 1). Taxa have been included from: (i) the *Lagenochitina ponceti* Biozone (Gondwana) and/or, (ii) the *Lagenochitina deunffi* Biozone (Gondwana/Baltica) and/or, (iii) the lower part of the *Lagenochitina dalbyensis* Biozone (Gondwana/Baltica) and/or, (iv) the *Eisenackitina rhenana* subzone (Gondwana/Baltica/Avalonia) and/or, (v) the upper 2/3rds of the *Laufeldochitina stentor* Biozone (Gondwana/Baltica/Avalonia) and/or, (vi) the *Lagenochitina* sp. A Biozone (Laurentia). However, for reasons of pragmatism, occurrences of *L. stentor* are also taken to be indicative of the *gracilis* time-slice, although this species appears slightly below the FAD of *N. gracilis*. Care has been taken to select contemporary species, excluding possibly reworked ones (see supplementary material, Table 1).

Our presence–absence data are taken predominantly from the literature, supplemented by our own unpublished data (TVDB, FP and JN). All locality information and literature sources are summarised in the supplementary information (Table 1). We have constructed a representative, though non-exhaustive, database from key sections. These, for historical reasons, are mainly located in the circum-Iapetus region. The palaeogeography and stratigraphy are shown in Figs. 2 and 3.

The palaeolatitude of the sections (Supplementary Information; Fig. 2) is derived from Scotese (utilising his Point Tracker software [www.scotese.com]). The palaeolatitudinal error for a single

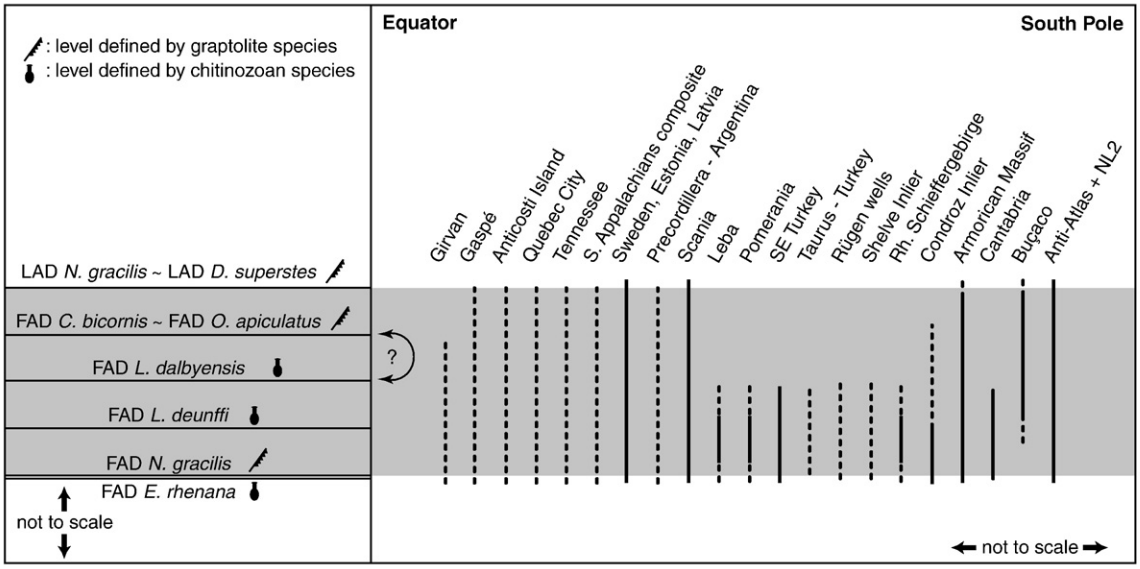


Fig. 3. Stratigraphical sources for the sections used (for references, see Supplemental Materials and Fig. 1. caption). The exact stratigraphical order of the FAD's of *L. dalbyensis* and *Climacograptus bicornis* is slightly unclear.

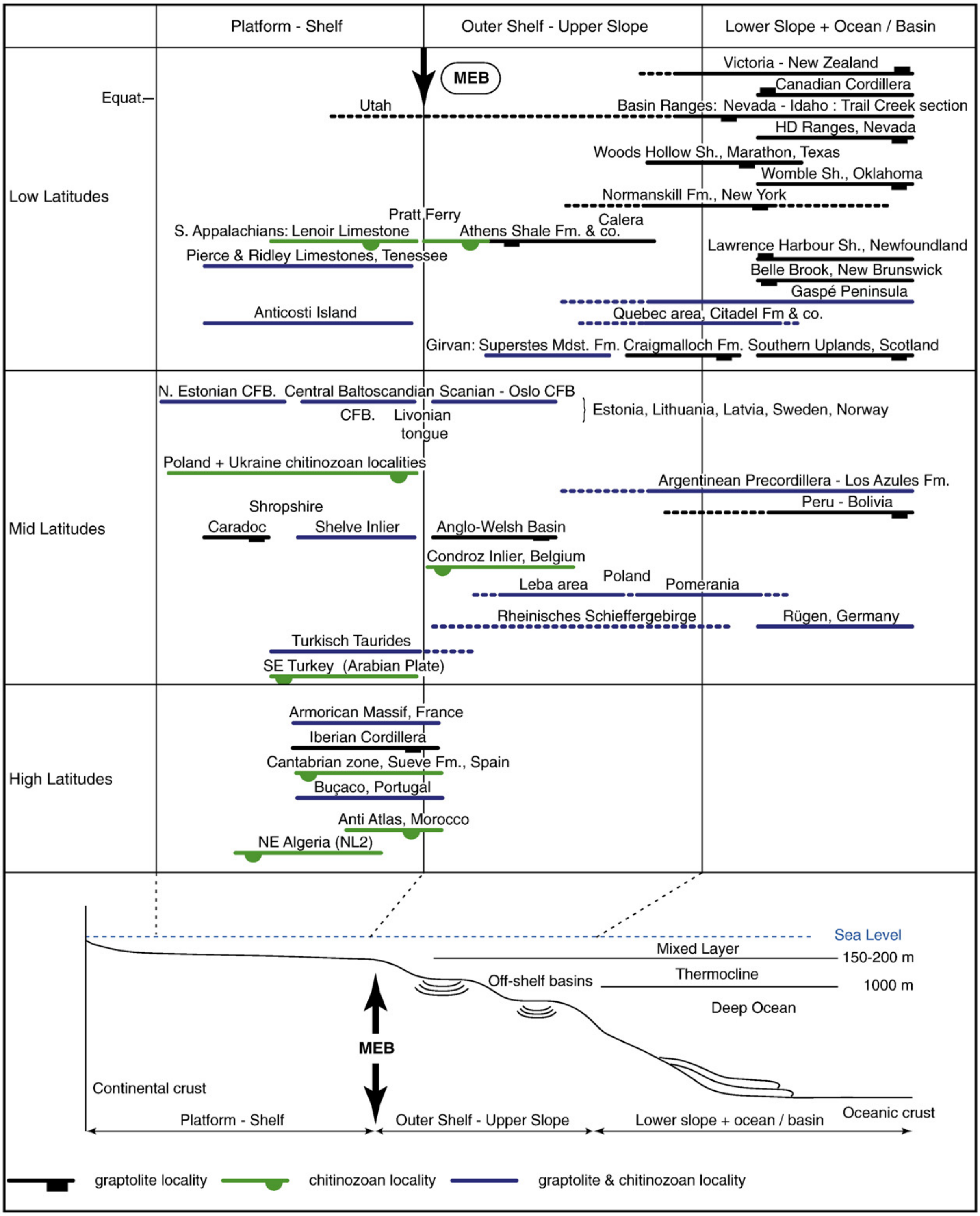


Fig. 4. Shelf-to-basin transect versus latitude (based on Cooper et al. (1991), fig. 2), plotting all the localities used, as well as those from the parallel graptolite study (Vandenbroucke et al., 2009). The arrow indicates the main ecological boundary (MEB) used in this study, dividing the localities into an on-shelf and an off-shelf group. Shelfal sections are generally considered to lie in up to 200 m water depth but there is currently no independent measure of depth, and these may have been considerably shallower or deeper.

location is defined by comparing its location in Point Tracker to that from the palaeogeographical reconstruction of Cocks and Torsvik (2004). Typically this error is less than 5° of latitude and this has been used to define our 'bin size'. There are more pronounced differences in the palaeolatitudes of some sections (up to 15°) mostly due to the differences in the positions of Avalonia and Laurentia. For the analyses, we have defaulted to the palaeolatitudes calculated using Point Tracker [www.scotese.com] as these are closest to the palaeogeographical reconstructions of Scotese and McKerrow (1990) used by Herrmann et al. (2004) to develop their climate simulations.

All of the sections have been assigned a position relative to the inferred position of the shoreline (Fig. 4). Examples of shelf localities include the limestone successions of the Estonian shelf, the Gondwanan shelf in Brittany (France), the Shelve Inlier in Shropshire (UK), and Anticosti Island (Canada). The remaining localities that represent "off-shelf" facies (outer shelf, slope and basin settings) include the more siliciclastic successions of the Scanian–Oslo Confacies Belt in Scandinavia, the Superstes Mudstone Formation in Girvan, Scotland, the Southern Uplands, Scotland, and Rügen, Germany. We have therefore separated "shelf" and "off-shelf" locality groups defining one ecological boundary ("Main Ecological Boundary, MEB" on Fig. 4). The complete list of localities is given in the supplemental material (Table 1).

Taxonomic filtering has been limited to revisions at the generic level and the synonymy of species listed in Table 1 of the supplementary information, based on the personal experience of TVDB, FP and JN. In general, the dataset includes species in open nomenclature ("?" and "cf."), with the exception of material not identified to species level, or identified as "aff." Exceptions are species from the latter category that were considered to be well-described, such as *Lagenochitina* sp. A aff. *capax* (Grahn et al., 1996) which is reported from several localities. All species are given a taxonomic weight: easily recognisable species (clear diagnosis and obvious characteristics) are weighted highly (5), while easily misidentified species are down-weighted (poor diagnosis, ubiquitous morphology or frequently misidentified taxa). Species with a taxonomic weight of '1' have been excluded from the analysis but are listed in the appendix for completeness. Repeated analysis that excluded species with a taxonomic weight of '2' (and/or all open nomenclature species, including cf./?), did not significantly alter the patterns and these species have all been included in the analysis.

3.2. Analytical methods

A preliminary ordination analysis (Detrended Correspondence Analysis - DCA) of our dataset revealed a gradient length>4, which suggests that species turnover in the dataset is considerable and that unimodal ordination methods such as Correspondence Analysis (CA), or methods based on unimodal ordination methods (e.g. TWINSPAN) should be used (Lepš and Šmilauer, 2003). The species presence/absence matrix was first subjected to TWINSPAN, "two way indicator species analysis" (Hill, 1979). TWINSPAN differs from other clustering methods in that it is based on an initial sample ordination (i.e. CA) and that it provides a simultaneous, hierarchical classification of both species and sites. Major groupings (clusters) of species and samples were recognised down to division level 3 (Fig. 5); they are discussed in Section 4.2. CA (Fig. 6) was used to construct an ordination diagram, which allows visualizing inter-sample distances (i.e. species turnover distances among samples) between and within the TWINSPAN clusters. Division level 3 is the point in the analysis where there is a stable number of groups and an interpretable ecological structure. Cutting a tree at a lower level results in more but lower diversity groups (see Supplementary Information). Doing so in this particular case only results in duplication of patterns: the supplementary data has a figure that shows the tree cut at level '4', creating a number of additional groups with duplicated patterns that are identical to those illustrated in Fig. 5.

The (high-level) TWINSPAN species clusters were then used in a constrained seriation analysis (Hammer and Harper, 2006 for details). The palaeolatitude of the localities was constrained allowing a re-ordering of species into biotopes ('the smallest biogeographical unit of the biosphere or of a habitat that can be delimited by convenient boundaries and is characterised by its biota' as defined by Lincoln et al. (1998) p. 42 and also used in Vandenbroucke et al. (2009)). The results have then been simplified by the grouping of localities into bins of 5° palaeolatitude (Figs. 7 and 8).

3.3. Hypothetical plankton model

We have used the concept of a hypothetical plankton model (see Vandenbroucke et al. (2009) for further details) to better understand the distribution of chitinozoan biotopes. This is based on the hypothetical distribution of modern planktonic foraminifera provinces (temperature boundaries taken from Kucera (2007)), mapped onto the Sandbian SST maps from the GCMs for ×8 and ×15 PAL (present atmospheric level) $p\mathrm{CO_2}$ (Herrmann et al., 2004). The hypothetical plankton model is summarised in Fig. 9 (B–C). The terminology (Sub)tropical and (Sub)polar used in this paper refers to that applied for modern planktonic foraminifera provinces (Kucera, 2007) and now their Ordovician equivalent biotopes. The oceanographic boundaries between the water masses they occupied are referred to as 'fronts', e.g. the Polar Front at the equator-ward edge of the Polar waters and biotopes in the Southern Hemisphere.

4. Results

4.1. Onshore to offshore differentiation

Mapping the position of our localities onto a lateral onshore–offshore transect (Fig. 4), at a local (e.g. Athens Shale versus the Lenoir Limestone and Fågelsång versus North Estonia, see Fig. 2) and on a global scale results in the following chitinozoan distribution patterns during the *gracilis* time-slice (Fig. 10). Very few species (4%) occur exclusively in an off-shelf setting. All other species have been observed on the shelf even if they have off-shelf occurrences. The majority of the species, 57% of the matrix, occur in both shelf and off-shelf localities. 39% of species are restricted to shelf localities.

4.2. TWINSPAN and constrained seriation

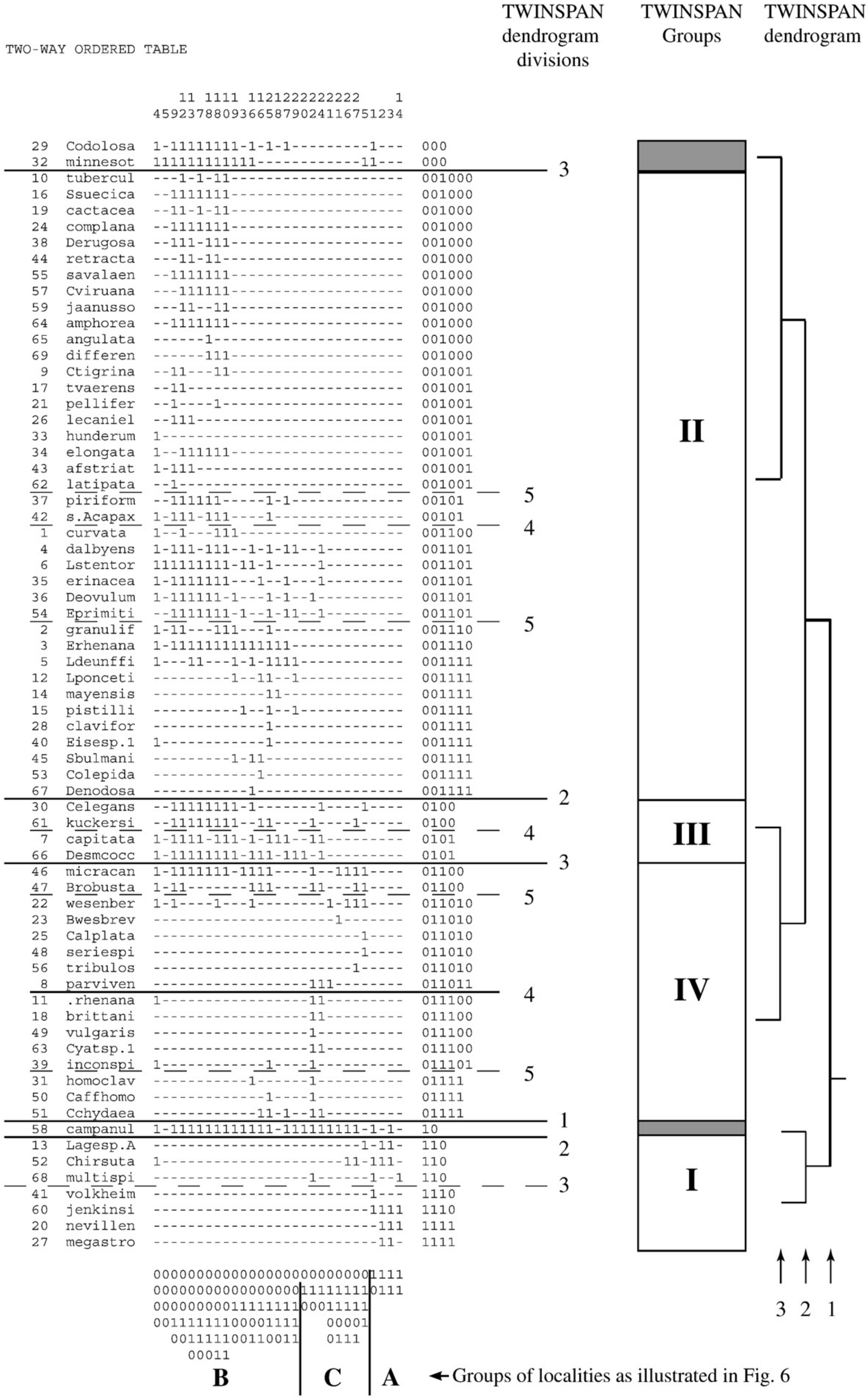
TWINSPAN analysis (down to the third division level) divides the chitinozoan data for the *gracilis* time-slice into six groups of species (Figs. 5 and 7), of which four are retained for palaeobiogeographical interpretation (see below). These groups are further subdivided by constrained seriation into subgroups, here considered equivalent to biotopes (but in practice these would be equivalent to present-day foraminifera "provinces"; also see definitions in Lincoln et al. (1998)). The full faunal composition of the TWINSPAN groups and biotopes is given in Fig. 7 and in the Appendix A.

TWINSPAN Group I is mainly defined by species such as *Belonechitina nevillensis*, *Calpichitina megastrophica*, and *Lagenochitina* sp. A *sensu* Achab. These have narrow latitudinal ranges from 25°S to 30°S. TWINSPAN group I contains too few taxa and samples to allow constrained seriation and therefore, it also represents 'Biotope I'.

TWINSPAN Group II. This group includes two biotopes (Fig. 7). Biotope IIa comprises 35 species, including those with a narrow latitudinal range around 35°S and 40°S, such as *Conochitina tigrina*, *Spinachitina tvaerensis*, and *Conochitina tuberculata*, and wider-ranging species such as *Lagenochitina deunffi* (35°S to 82°S), *Laufeldochitina stentor* (35°S to 70°S), *Eisenackitina rhenana* (35°S to 75°S) and *Lagenochitina dalbyensis* (35°S to 82°S). Grouped localities at 35°S and 40°S are not separated in our interpretation; they represent a number of localities in the same general region on or near the Baltoscandian carbonate ramp. Biotope IIb contains four species with a more narrow latitudinal distribution, the most prominent species, *Linochitina mayensis*, appearing at 70°S and *Pistillachitina pistillifrons* ranging somewhat wider, from 60°S to 82°S.

TWINSPAN Group III comprises species which all have a comparable, relatively wide latitudinal range from 30° or 35°S to 60–80°S. The four species are *Conochitina elegans*, *Cyathochitina kuckersiana*, *Belonechitina capitata* and *Desmochitina cocca*. TWINSPAN group III is not further subdivided and thus also represents Biotope III.

TWINSPAN Group IV. Constrained seriation divides this group into three biotopes. As explained below, the validity of Biotope IVa is doubtful. Biotope IVb comprises 3 species only, appearing around 40°S and ranging south to 55°–70°S. Its most characteristic species are *Eisenackitina ?rhenana* and *Eisenackitina inconspicua*. Biotope IVc



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TWO-WAY ORDERED TABLE

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 44  retracta  ---11-11---------------------  001000
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 56  tribulos  -----------------------1-----  011010
  8  parviven  ------------------111--------  011011
 11  .rhenana  1-----------------11---------  011100
 18  brittani  ------------------11---------  011100
 49  vulgaris  ------------------1----------  011100
 63  Cyatsp.1  ------------------11---------  011100
 39  inconspi  1------------1----1----------  011101
 31  homoclav  -----------1------1----------  01111
 50  Caffhomo  -------------1----1----------  01111
 51  Cchydaea  ------------11-1--11---------  01111
 58  campanul  1-111111111111-111111111-1-1-  10
 13  Lagesp.A  ------------------------1-11-  110
 52  Chirsuta  1---------------------11-111-  110
 68  multispi  ------------------1------1--1  110
 41  volkheim  -------------------------1---  1110
 60  jenkinsi  -------------------------1111  1110
 20  nevillen  --------------------------111  1111
 27  megastro  --------------------------11-  1111

               00000000000000000000000001111
               00000000000000000111111110111
               00000000011111111000111111
               00111111100001111   00001
                 001111100110011   0111
                   00011
```

comprises 6 species, appearing around 55°S; its most characteristic species are *Conochitina parviventer* and *Belonechitina brittanica*.

Three further groupings have been excluded from our interpretation (Fig. 7): these include two low-diversity TWINSPAN groups, one consisting only of *C. campanulaeformis* and a second which has only two species, *C. minnesotensis* and *C. dolosa*. These species have very wide ranges; they occur in samples typical of several high-level TWINSPAN groups and may represent previously poorly diagnosed species or may be super-generalists that could live in a wide range of conditions. In either case, they have little biogeographical significance.

Biotope IVa includes *Belonechitina wesenbergensis brevis* occurring around 25°S, and *Belonechitina seriespinosa*, *Calpichitina lata* and *Conochitina tribulosa*, occurring around 30°S, in addition to wider-ranging species. Though superficially apparently sound species, those defining Biotope IVa at 30°S were described with low-quality illustrations (Siesser et al., 1998) that make comparison of material difficult, or have an anomalously disparate distribution, occurring only in the Southern Appalachians and Baltoscandia (Fig. 7; see Grahn and Bergström, 1984). We have been unable to independently check the validity of these identifications and have not considered this grouping further.

5. Discussion

Our results (Section 4.2) show that early Late Ordovician chitinozoans occupy a series of discrete biotopes, the distribution of which is notably latitudinally differentiated. This section now discusses how such latitudinal differentiation is seen in contemporaneous planktonic graptolite faunas and is also recorded in Recent and fossil epiplanktonic foraminifera. By analogy, this most likely reflects the latitudinal temperature gradient with different biotopes inhabiting warmer or cooler water masses (see Section 5.2). A corollary is that chitinozoans can be confirmed to have been epiplanktonic as there is little latitudinal variation in seawater temperature below the mixed layer. Meanwhile, comparison with graptolite biotope distribution and hypothetical plankton provinces derived from GCM estimates of Late Ordovician SST (in Section 5.2) allows the recognition of the Subpolar–Subtropical transition and of the Polar Front. As the Ordovician plankton provinces resemble those seen in Recent oceans more closely than those of the Albian, it seems that the Late Ordovician climate may have been more similar to that of the Quaternary icehouse than that of the Late Cretaceous greenhouse (Section 5.3).

Before we can use chitinozoans for palaeoclimatology, it is key to demonstrate that they were indeed part of the zooplankton, using a method that is independent from our biotope-methodology. Apart from arguments already formulated in Section 2 of this paper, this is further detailed in the next section.

5.1. Implications for chitinozoan palaeoecology

Chitinozoans and graptolites have been widely interpreted as being ecologically similar, occupying similar environments and water depths and being found in similar lithologies (see e.g. Achab and Paris, 2007). Vandenbroucke et al. (2009) recognised a regional onshore–offshore differentiation in graptolite assemblages, identifying two assemblages, one being restricted to off-shelf localities of species and a second group of species that ranged from shelf to off-shelf localities. They also identified similar latitudinally restricted biotopes within these two groups of species. This led them to support the graptolite ecological model proposed by Finney and Berry (1997) that used lateral differentiation on a shelf-to-basin transect.

Fig. 10, and our calculations in Section 4.1, show that chitinozoan species occur in shelf to off-shelf deposits. However, there is no evidence in our analysis that chitinozoan species show a pattern of lateral differentiation across the continental shelf comparable to that of the graptolites during the *gracilis* time-slice. Only 4% of the chitinozoan species occur exclusively in an off-shelf setting (Fig. 10), compared to 82% for the graptolites. In contrast, 39% of the chitinozoan species are exclusively shelf, which is many more than for graptolites (just 1%). These different distribution patterns, and especially the virtual absence of exclusively off-shelf chitinozoan species, challenges the notion that both groups were occupying the same ecological space during the *gracilis* time-slice.

Almost all chitinozoan species occur in shelf deposits and the majority of those (i.e. 57% of all the species) also occur in off-shelf settings during the *gracilis* time-slice. We suggest the chitinozoan animal lived within the shallow "mixed layer" of the ocean, independent of any seafloor facies control.

5.2. *Gracilis* time-slice chitinozoan biotope distribution patterns compared to graptolite biotopes and GCMs

Modern plankton provinces and *gracilis* time-slice graptolite biotopes have a broadly similar distribution (Fig. 9 A–D; also see Vandenbroucke et al., 2009). Modern plankton species can be distinguished as having broad or narrow biogeographical ranges. Factors accounting for the wide latitudinal range of modern planktonic species include, amongst others, redistribution of taxa in sea surface currents, association with zones of upwelling, and wide environmental tolerances of certain taxa (Cifelli and Stern Benier, 1976; Kucera, 2007; see also Armstrong and Brasier, 2005 for a review). Recent work on the Ordovician (Vandenbroucke et al., 2009) indicates that these factors were equally important in controlling the distribution of graptolite species. Species with narrow biogeographical ranges suggest a limited range of SST tolerance in discrete water masses.

The chitinozoan biotopes defined in this study also contain a mixture of species with both narrow and wide geographical ranges and we assume that similar ecological and biological factors controlled their distribution. In keeping with our previous studies of graptolites (Vandenbroucke et al., 2009) and those of the modern plankton, we use species with the most narrow latitudinal ranges to define the latitudinally restricted biotopes.

Chitinozoan Biotope I is defined by the first split in the Twinspan analysis (Fig. 5), which sets it apart from all remaining species. This split therefore represents the highest ecological structure in the data. Chitinozoan Biotope I ranges from 25°S to 35°S (Fig. 8) and corresponds to the Tropical–Subtropical Province in the hypothetical plankton model (at ×15 $p\text{CO}_2$), to the Subtropical Province (at ×8 $p\text{CO}_2$) and is equivalent to subtropical graptolite Biotopes C4–D4 (Fig. 9). We will refer to it as the Subtropical chitinozoan biotope.

Fig. 5. TWINSPAN 'two-way ordered table' of species and localities. The names of the species (rows, numbers 1 to 69) can be deduced from the Appendix, but a list of species numbers and full taxon names is reproduced in the online supplemental materials. The localities (columns, numbers 1 to 29) are as follows: 1 Girvan (Superstes Mudstones); 2 Gaspé; 3 Anticosti Island; 4 Québec City; 5 Tennessee; 6 Southern Appalachians, Pratt Ferry: Athens Shale; 7 Southern Appalachians, Lenoir - Chickamauga Limestone; 8 North Estonia; 9 Sweden (excluding Scania); 10 West Estonia; 11 Precordillera (Argentina); 12 South Estonia; 13 Latvia; 14 Fågelsång (Sweden, Scania); 15 Leba; 16 Pomerania (Koszalin–Chojnice area); 17 Poland; 18 Ukraine; 19 Southeast Turkey (Border Folds area); 20 Taurus — Turkey (Kilgen Lake area); 21 Rügen Wells; 22 Shelve Inlier; 23 Rhenisches Schiefergebirge; 24 Condroz Inlier; 25 Armorican Massif; 26 Cantabria (Sueve Formation); 27 Buçaco; 28 NL 2 well; and 29 Anti-Atlas. All localities are detailed in Table 1 of the supplementary material. The divisions introduced by TWINSPAN are indicated with the columns (species) and rows (localities) of 1s and 0s. The divisions into groups of species are emphasized by full lines and numbered 1 to 5; the dendrogram has been cut at level '3', resulting in the four main TWINSPAN groups indicated on the figure (I to IV). These are in turn characteristic of the groups of localities A, B and C (see Fig. 6). Low-diversity groups of generalists (shaded) have not been retained (see text).

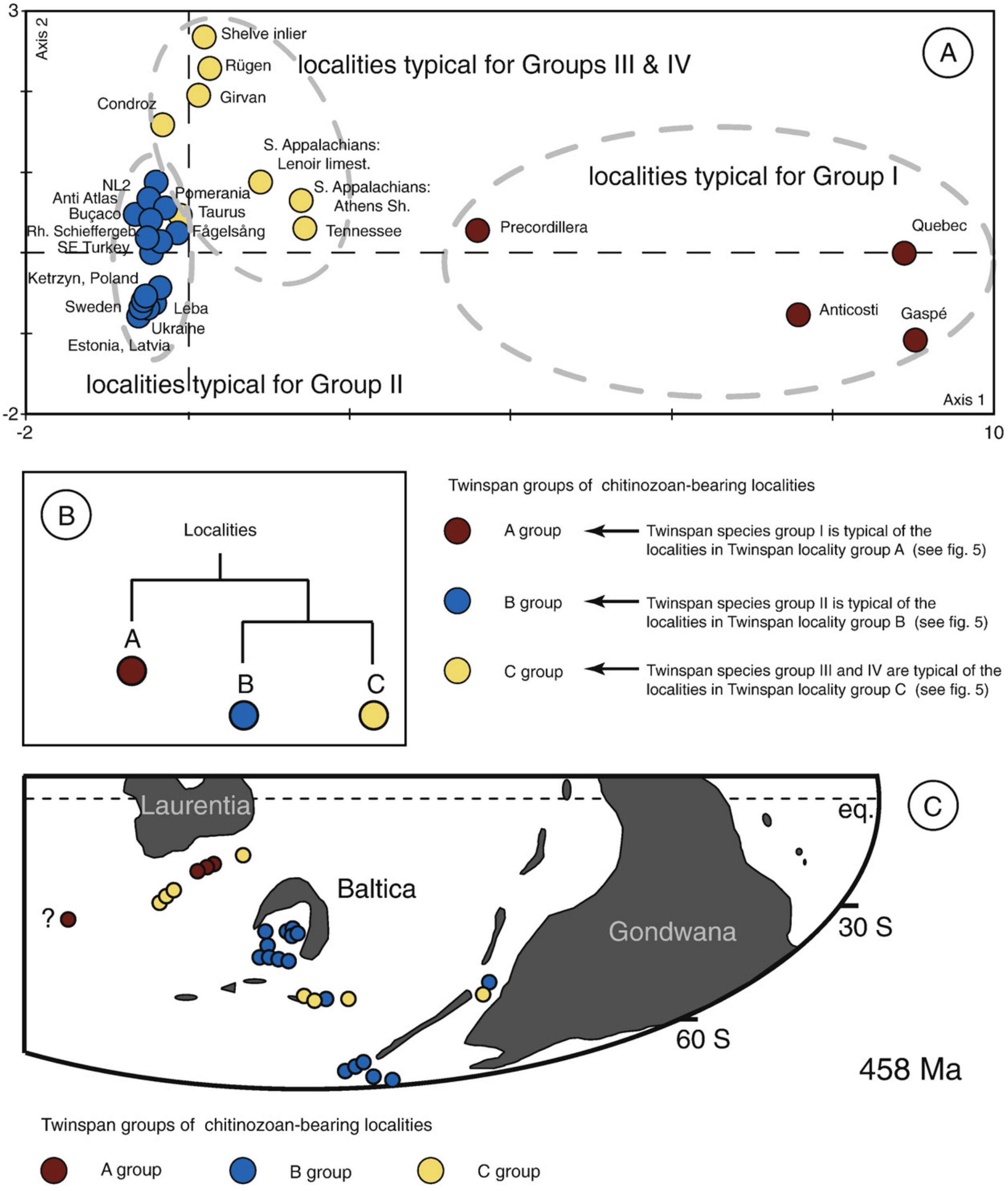
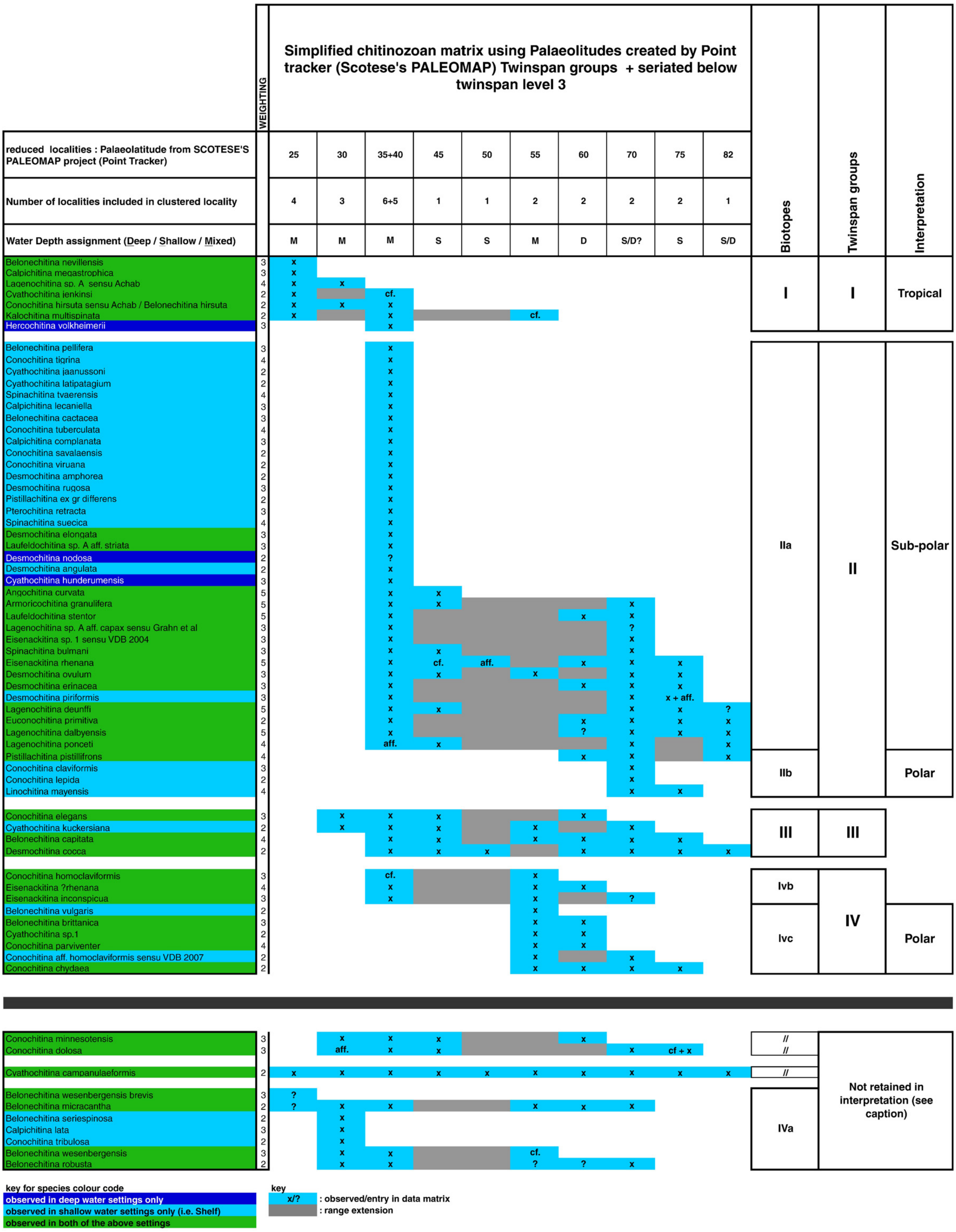


Fig. 6. (A) Correspondence Analysis (CA) of localities for a presence–absence chitinozoan dataset for the early Sandbian *gracilis* time-slice. Data filtered as explained in the Methodology section. (B) TWINSPAN dendrogram of localities, illustrating group hierarchy. (C) Localities as subdivided into TWINSPAN groups A–C (see Fig. 5), plotted on the palaeogeographic map after Scotese [www.scotese.com] of Fig. 2B.

Correspondence Analysis also groups this at low-latitude (Fig. 6), including species from Anticosti Island, Québec, Gaspé and the Argentinian Precordillera (Fig. 6). The repeated first-order clustering of subtropical Laurentian species and samples underlines the robustness of this grouping.

The remaining biotopes (in TWINSPAN groups II–IV) comprise species which are largely restricted polewards of ~35°S. Thus we interpret the highest ecological grouping in our analysis to separate warm and cool water taxa. Chitinozoan Biotope IIa is the most diverse of the biotopes: it first appears at 35°S, and corresponds with either the Transitional province in the hypothetical plankton model at ×15 $p\mathrm{CO_2}$, or with the Subpolar province (at ×8 $p\mathrm{CO_2}$). We refer to it as the Subpolar chitinozoan biotope (the overall distribution pattern of chitinozoan biotopes fits best that of the hypothetical plankton model at ×8 $p\mathrm{CO_2}$).

Chitinozoan Biotope IIb appears at 60° or 70°S, depending on whether one uses the occurrence of *Pistillachitina pistillifrons* at 60°S or of *Linochitina mayensis* at 70°S (Fig. 7), and corresponds in part with the Polar province in the hypothetical plankton model at ×8 $p\mathrm{CO_2}$ of Fig. 9, or with the Subpolar or Polar province at ×15 $p\mathrm{CO_2}$. This



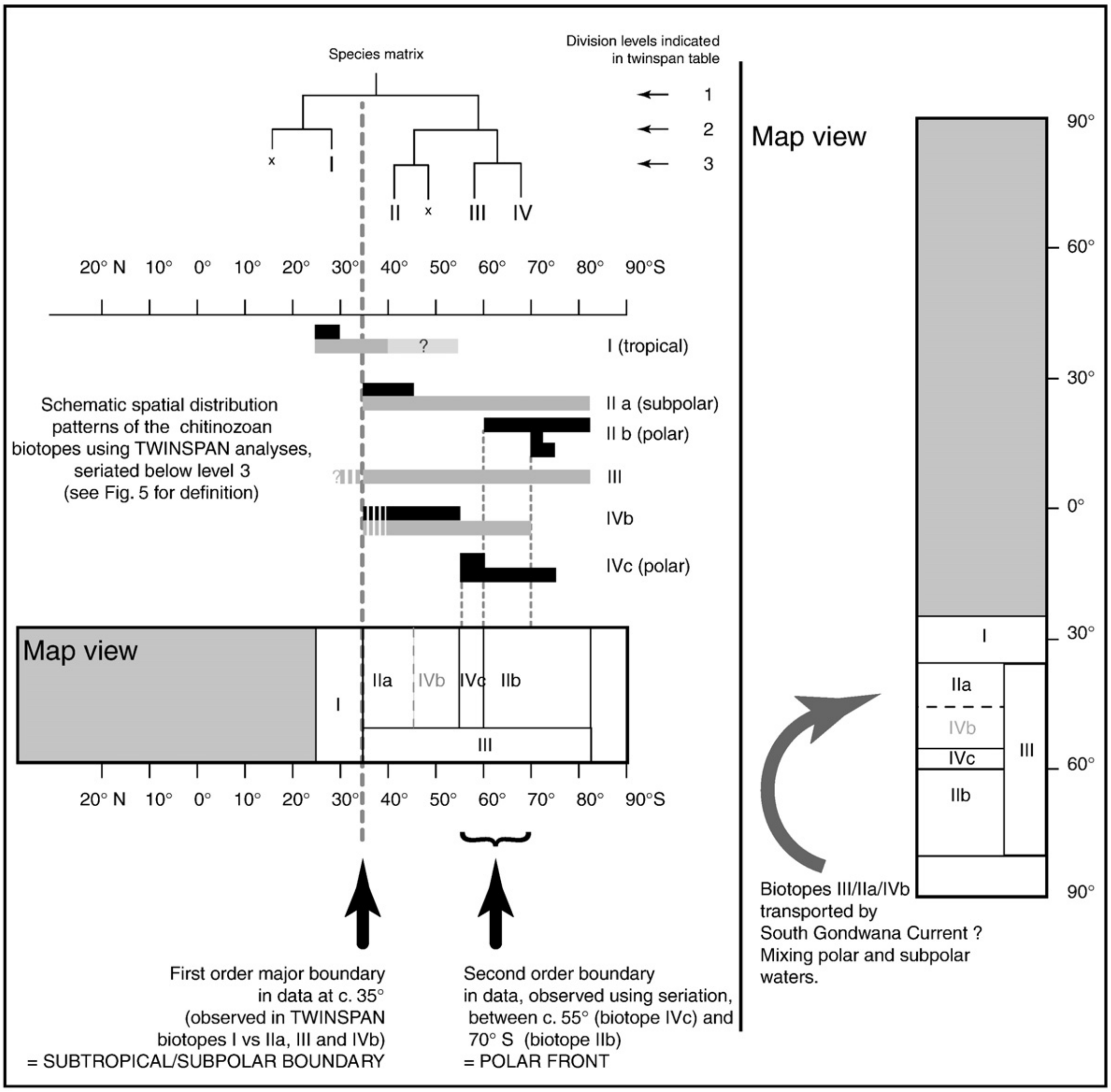
Simplified chitinozoan matrix using Palaeolitudes created by Point tracker (Scotese's PALEOMAP) Twinspan groups + seriated below twinspan level 3

reduced localities : Palaeolatitude from SCOTESE'S PALEOMAP project (Point Tracker)	WEIGHTING	25	30	35+40	45	50	55	60	70	75	82	Biotopes	Twinspan groups	Interpretation
Number of localities included in clustered locality		4	3	6+5	1	1	2	2	2	2	1			
Water Depth assignment (Deep / Shallow / Mixed)		M	M	M	S	S	M	D	S/D?	S	S/D			
Belonechitina nevillensis	3	x										I	I	Tropical
Calpichitina megastrophica	3	x												
Lagenochitina sp. A sensu Achab	4	x	x											
Cyathochitina jenkinsi	2	x	▨	cf.										
Conochitina hirsuta sensu Achab / Belonechitina hirsuta	2	x	x	x										
Kalochitina multispinata	2	x	▨	x	▨	▨	cf.							
Hercochitina volkheimerii	3			x										
Belonechitina pellifera	3			x								IIa	II	Sub-polar
Conochitina tigrina	4			x										
Cyathochitina jaanussoni	2			x										
Cyathochitina latipatagium	2			x										
Spinachitina tvaerensis	4			x										
Calpichitina lecaniella	3			x										
Belonechitina cactacea	3			x										
Conochitina tuberculata	4			x										
Calpichitina complanata	3			x										
Conochitina savalaensis	2			x										
Conochitina viruana	2			x										
Desmochitina amphorea	2			x										
Desmochitina rugosa	3			x										
Pistillachitina ex gr differens	2			x										
Pterochitina retracta	3			x										
Spinachitina suecica	4			x										
Desmochitina elongata	3			x										
Laufeldochitina sp. A aff. striata	3			x										
Desmochitina nodosa	2			?										
Desmochitina angulata	2			x										
Cyathochitina hunderumensis	3			x										
Angochitina curvata	5			x	x									
Armoricochitina granulifera	5			x	x	▨	▨	▨	x					
Laufeldochitina stentor	5			x	▨	▨	▨	x	x					
Lagenochitina sp. A aff. capax sensu Grahn et al	3			x	▨	▨	▨	▨	?					
Eisenackitina sp. 1 sensu VDB 2004	3			x	▨	▨	▨	▨	x					
Spinachitina bulmani	3			x	x	▨	▨	▨	x					
Eisenackitina rhenana	5			x	cf.	aff.	▨	x	x	x				
Desmochitina ovulum	3			x	x	▨	x	▨	x	x				
Desmochitina erinacea	3			x	▨	▨	▨	x	x	x				
Desmochitina piriformis	3			x	▨	▨	▨	▨	x	x + aff.				
Lagenochitina deunffi	5			x	x	▨	▨	▨	x	x	?			
Euconochitina primitiva	2			x	▨	▨	▨	x	x	x	x			
Lagenochitina dalbyensis	5			x	▨	▨	▨	?	x	x	x			
Lagenochitina ponceti	4			aff.	x	▨	▨	▨	x	▨	x			
Pistillachitina pistillifrons	4							x	x	▨	x	IIb		Polar
Conochitina claviformis	3								x					
Conochitina lepida	2								x					
Linochitina mayensis	4								x	x				
Conochitina elegans	3		x	x	x	▨	▨	x				III	III	
Cyathochitina kuckersiana	2		x	x	x	▨	x	▨	x					
Belonechitina capitata	4			x	x	▨	x	x	x	x				
Desmochitina cocca	2			x	x	x	▨	x	x	x	x			
Conochitina homoclaviformis	3			cf.	▨	▨	x					Ivb	IV	
Eisenackitina ?rhenana	4			x	▨	▨	x	x						
Eisenackitina inconspicua	3			x	▨	▨	x	▨	?					
Belonechitina vulgaris	2						x					Ivc		Polar
Belonechitina brittanica	3						x	x						
Cyathochitina sp.1	2						x	x						
Conochitina parviventer	4						x	x						
Conochitina aff. homoclaviformis sensu VDB 2007	2						x	▨	x					
Conochitina chydaea	2						x	x	x	x				
Conochitina minnesotensis	3		x	x	x	▨	▨	x				//	Not retained in interpretation (see caption)	
Conochitina dolosa	3		aff.	x	x	▨	▨	▨	x	cf + x		//		
Cyathochitina campanulaeformis	2	x	x	x	x	x	x	x	x	x	x	//		
Belonechitina wesenbergensis brevis	3	?										IVa		
Belonechitina micracantha	2	?	x	x	▨	▨	x	x	x					
Belonechitina seriespinosa	2		x											
Calpichitina lata	3		x											
Conochitina tribulosa	2		x											
Belonechitina wesenbergensis	3		x	x	▨	▨	cf.							
Belonechitina robusta	2		x	x	▨	▨	?	?	x					

key for species colour code
observed in deep water settings only
observed in shallow water settings only (i.e. Shelf)
observed in both of the above settings

key
x/? : observed/entry in data matrix
▨ : range extension

Fig. 7. Simplified chitinozoan matrix for the early Sandbian *gracilis* time-slice. TWINSPAN groups are identified above division level '3' in Fig. 5. Below that level, biotopes within the TWINSPAN groups are identified by constrained seriation. Baltoscandian ramp localities at 35°S and 40°S have been grouped (see text). Groups below the grey line at the bottom of the figure have not been considered further in the palaeobiogeographical analysis: super-generalists *C. campanulaeformis*, *C. minnesotensis* and *C. dolosa* have been assigned to separate TWINSPAN groups (// in the figure). The fidelity of Biotope IVa is doubtful; some of its defining species at 30°S are only poorly illustrated, which hampers comparison of the material. In addition the taxonomy of some species in common between the Southern Appalachians and the Baltoscandian shelf needs to be independently checked.



Schematic spatial distribution patterns of the chitinozoan biotopes using TWINSPAN analyses, seriated below level 3 (see Fig. 5 for definition)

First order major boundary in data at c. 35° (observed in TWINSPAN biotopes I vs IIa, III and IVb) = SUBTROPICAL/SUBPOLAR BOUNDARY

Second order boundary in data, observed using seriation, between c. 55° (biotope IVc) and 70° S (biotope IIb) = POLAR FRONT

Biotopes III/IIa/IVb transported by South Gondwana Current ? Mixing polar and subpolar waters.

Fig. 8. Schematic distribution of species with narrow (black) and wide (grey) latitudinal ranges for each biotope; the map view uses the narrowest ranges. The main boundaries in the distribution patterns are indicated. They occur at 35°S and between 55°–70°S. Very few species cross the main divide at 35°S, with the exception of the ones that have been questioned taxonomically (see caption of Fig. 7 and text) and the super-generalists of Fig. 5 that have not been considered in the further analysis. The interpretation of the biotopes (e.g. Polar, Subpolar) follows from Fig. 9.

is a low-diversity Polar chitinozoan biotope of which *Linochitina mayensis* and *P. pistillifrons* are considered characteristic. Chitinozoan Biotope IVc appears at 55°S and corresponds to the same hypothetical plankton provinces as Biotope IIb. Therefore we also consider it to represent the Polar chitinozoan biotope. These multiple indications of the northern edge of the Polar biotope imply that the position of the Polar Front remains somewhat ill-constrained between 55° and 70°S.

The data matrix also contains wide-ranging taxa with a comparable distribution, broadly south of 35°S and ranging up to 80°S, but these cannot be easily separated by constrained seriation. They also cluster together in the Correspondence Analysis based on localities (Fig. 6) and can be found in three of our biotopes (Fig. 7). Chitinozoan Biotope IIa comprises narrow- and wide-ranging species. Chitinozoan Biotope III has four species which all have a broad latitudinal range from 35°S to 70–80°S. Biotope IVb appears at 40°S but does not contain species that are truly latitudinally restricted. The distribution of all these wide-ranging species is directly comparable to those in the *Oepikograptus bekkeri* graptolite biotope (Vandenbroucke et al., 2009; Biotope 'A' in Fig. 9) and we speculate that this grouping may reflect a water mass associated with the South Gondwana Current (SGC; Herrmann et al., 2004). This current is modelled to flow from high to mid-latitude and thus provides a mechanism by which species could be transported into low latitudes. To the north of this, Vandenbroucke et al. (2009) already suggested that low latitude, tropical and subtropical graptolites have been transported by currents that formed part of the "South Panthalassic convergence" gyre (Wilde, 1991; Poussart et al., 1999; Herrmann et al., 2004). Taken at face value, this is reminiscent of the modern Southern Ocean sea surface current configuration, from which one could in principle infer its relation to palaeo-atmospheric circulation and the nature of the Hadley and Ferrel Cells in the *gracilis* time-slice.

There are clear similarities between the distribution of chitinozoan and graptolite biotopes (Fig. 9). The boundary between Subtropical (I) and Subpolar (IIa) chitinozoan biotopes lies at ~35°S, equivalent to the boundary between graptolite Biotopes A and C4/D4, and represents the position of the Transitional zone, between the hypothetical Subtropical and Subpolar plankton provinces (Vandenbroucke et al., 2009). In the modern ocean–climate configuration this

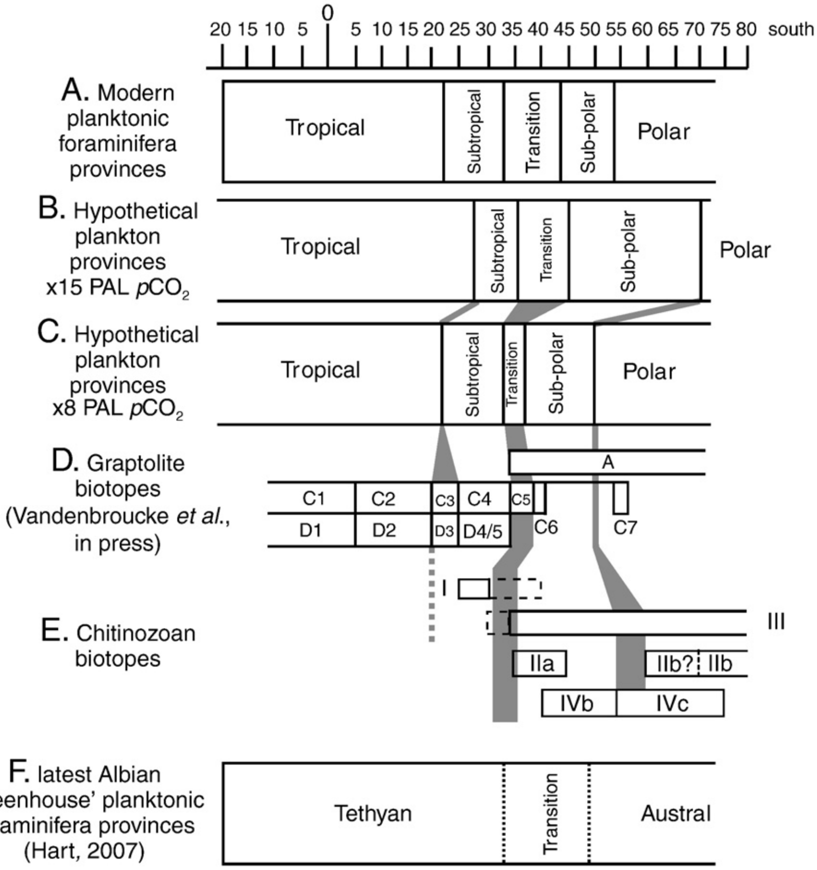


Fig. 9. (A) Recent planktonic foraminifera provinces; their boundaries are those defined in terms of SST by Kucera (2007), and their latitudinal position is obtained by plotting these boundaries on a present-day SST map (central Pacific Ocean, www.noaa.gov; Locarnini et al., 2006). (B) and (C) Hypothetical position of plankton provinces for the Sandbian, using climate simulations at ×8 and ×15 PAL pCO_2. The boundaries of these hypothetical plankton provinces are obtained by plotting the SST-definitions of modern boundaries on the Sandbian SST simulations of Herrmann et al. (2004) at ×8 and ×15 PAL pCO_2. (D) The graptolite biotope distributions from Vandenbroucke et al. (2009). (E) Chitinozoan biotope distributions from Fig. 8. (F) Late Albian planktonic foraminifera provinces from Hart (2007), here taken as an example of plankton patterns for a greenhouse scenario, which display a much shallower gradient. Figure after Vandenbroucke et al. (2009).

Transitional zone marks an important climatological boundary. Chitinozoan Biotope III has the same distribution as the *O. bekkeri* graptolite Biotope (A) that has an equivalent distribution to the hypothetical Transition to Polar plankton provinces (Vandenbroucke et al., 2009). The discrete chitinozoan Polar Biotopes (IIb and IVc) have no direct equivalent in the graptolites, but graptolite Biotope C7, at 55°S, occupies (Sub)polar waters (Vandenbroucke et al., 2009; Fig. 9). The northern edge of the Polar biotopes, i.e. the Polar Front, lies between 55° and 70°S in the chitinozoan dataset (Fig. 9).

Chitinozoan biotopes therefore define SST-controlled water masses in much the same way as do the graptolites and modern planktonic foraminifera. Taken together with the other evidence (cf. Sections 1 and 5.1), the most parsimonious interpretation is that chitinozoans were part of the zooplankton and can be used in Ordovician palaeoclimatological studies. However, chitinozoans were largely restricted to the southern Subpolar to Polar waters, poleward of ~35°S during the *gracilis* time-slice. In contrast, graptolites had their greatest diversity and abundance in Subtropical and Tropical waters. It would therefore appear that during the *gracilis* time-slice, the chitinozoan animal was adapted to cool/cold waters, while graptolites were predominantly warm water specialists.

5.3. Implications for early Late Ordovician palaeoclimate

The chitinozoan palaeobiogeographical biotope map contains two important palaeo-oceanographic boundaries at *c*. 35°, and at 55°–70°S (Figs. 8 and 9). These coincide closely with the southerly edge of the subtropics and the austral Polar Front in the modern oceans. The former is also observed in the graptolite biotope map (Fig. 9) and represents the most robustly documented of the two. However it is not possible to further constrain the position of the Polar Front due to the sparse data from these palaeolatitudes and the potential palaeogeographical error on the location of Avalonia, which includes the most equator-ward localities of Biotope IVc. The equator-ward limit of Polar Biotope IIb lies between 60° and 70°S, Polar Biotope IVc appears south of 55°S. The Polar Front is a fundamental ecological barrier in the modern oceans defining the position where the thermocline shoals to the ocean surface. It may however be possible with further work on new and emerging collections from Eastern Gondwana to identify species indicative of the thermocline or Polar Front.

For the *gracilis* time-slice, chitinozoan and graptolite biotopes (in Vandenbroucke et al., 2009), display a steep faunal gradient from equator to pole that is broadly comparable to the present day. Hypothetical plankton provinces, retrofitted for the Ordovician using the SST reconstructions of Herrmann et al. (2004), conform to the distribution patterns of genuine Sandbian zooplankton, which corroborates these SST simulations. Sandbian zooplankton distributions are better matched to the SST predictions from the GCM at ×8 PAL pCO_2. Overall, the biotope distribution patterns of early Late Ordovician zooplankton appear to question the notion of a (super-) greenhouse climate during the earliest Sandbian (references in Vaughan, 2007; Trotter et al., 2008), despite the relatively high atmospheric modelled pCO_2 (Berner and Kothavala, 2001; Tobin and Bergström, 2002), and appear to suggest that climate started cooling towards the Hirnantian glacial maximum before or during the early Sandbian.

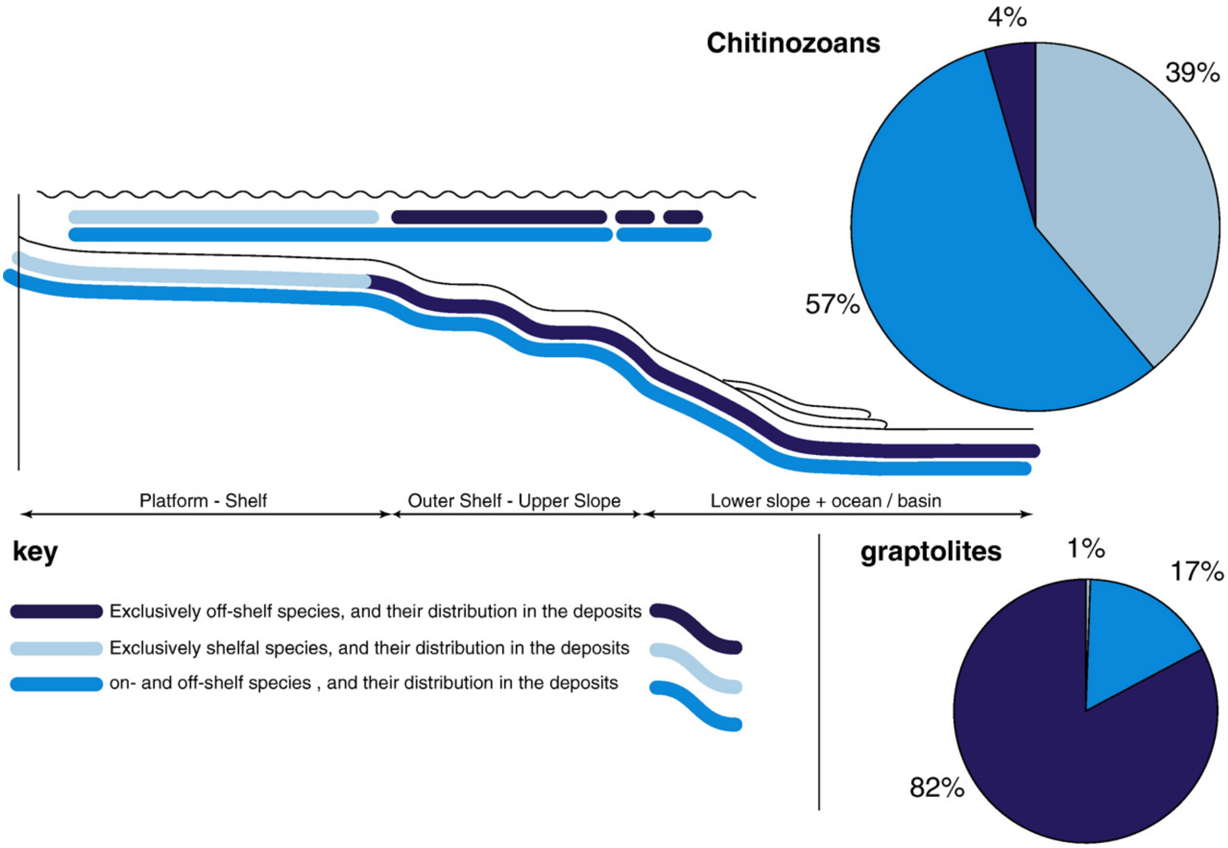


Fig. 10. Contrasting on-shelf to off-shelf lateral differentiation for chitinozoans and graptolites during the *gracilis* time-slice, based on the presence–absence data.

6. Conclusions

This is the first detailed, global-scale study of the palaeobiogeography of chitinozoans (through the well-defined *gracilis* time-slice). The following are documented.

- We confirm that chitinozoans and likely their parent organisms were epiplanktonic.
- Chitinozoan species define latitudinally restricted water masses that are inferred to be SST-controlled, and potentially chitinozoans allow us to trace sea surface currents, in much the same way that the plankton has been used for climate modelling in the Cenozoic.
- Our analysis suggests that graptolites and chitinozoans possessed broadly different ecological tolerances during the *gracilis* time-slice, graptolites thriving in the low latitude, warmer tropical and subtropical surface waters, whereas chitinozoans favoured the temperate and colder mid and high latitudes.
- Not only did they occupy latitudinally distinct temperature-defined water masses, chitinozoans also display an on-shelf to off-shelf lateral differentiation that was unlike that of the graptolites during the *gracilis* time-slice: almost all of the chitinozoan species that have been observed off-shelf also occur on-shelf. In addition, there is a large chitinozoan assemblage that is exclusively shelf. This contrasts with the graptolites that have a well-established, exclusively off-shelf group.
- Chitinozoan and graptolite biotopes can be used to define the position of climate-sensitive palaeoceanographical boundaries during the *gracilis* time-slice: the transition between the Subtropical and the Subpolar waters at ~35°S and the Polar Front between 55°S and 70°S.
- It is speculated that a number of chitinozoan and graptolite species with long latitudinal ranges may have been indicative of the equator-ward flowing Southern Gondwana Current.
- Our findings for the *gracilis* time-slice display a steep zooplankton gradient from equator to pole, more similar to that of the present oceans than that of a peak greenhouse. This likely indicates a steep latitudinal temperature gradient for the *gracilis* time-slice and supports a pre-Katian-cooling as suggested by Trotter et al. (2008), as well as the GCM Sandbian SST-reconstruction for 8 × PAL $p\mathrm{CO}_2$ by Herrmann et al. (2004).

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Appendix A

A.1. TWINSPAN *group I*

Belonechitina nevillensis, *Calpichitina megastrophica*, *Lagenochitina* sp. A *sensu* Achab, *Cyathochitina jenkinsi*, *Belonechitina hirsuta sensu* Achab, *Kalochitina multispinata*, and *Hercochitina volkheimerii*.

A.2. TWINSPAN group II

Biotope IIa: *Belonechitina pellifera*, *Conochitina tigrina*, *Cyathochitina jaanussoni*, *Cyathochitina latipatagium*, *Spinachitina tvaerensis*, *Calpichitina lecaniella*, *Belonechitina cactacea*, *Conochitina tuberculata*, *Calpichitina complanata*, *Conochitina savalaensis*, *Conochitina viruana*, *Desmochitina amphorea*, *Desmochitina rugosa*, *Pistillachitina* ex gr *differens*, *Pterochitina retracta*, *Spinachitina suecica*, *Desmochitina elongata*, *Laufeldochitina* sp. A aff. *striata*, *Angochitina curvata*, *Armoricochitina granulifera*, *Laufeldochitina stentor*, *Lagenochitina* sp. A aff. *capax sensu* Grahn et al. (1996), *Eisenackitina rhenana*, *Desmochitina ovulum*, *Desmochitina erinacea*, *Desmochitina piriformis*, *Lagenochitina deunffi*, *Euconochitina primitiva*, *Lagenochitina dalbyensis*, *Desmochitina angulata*, *Cyathochitina hunderumensis*, *Desmochitina nodosa*, *Eisenackitina* sp. 1 *sensu* Vandenbroucke (2004), *Spinachitina bulmani* and *Lagenochitina ponceti*.

Biotope IIb: *Pistillachitina pistillifrons*, *Conochitina claviformis*, and *Linochitina mayensis*.

A.3. TWINSPAN group III

Conochitina elegans, *Cyathochitina kuckersiana*, *Belonechitina capitata*, *Conochitina lepida* and *Desmochitina cocca*.

A.4. TWINSPAN group IV

Biotope IVa: *Belonechitina wesenbergensis brevis*, *Belonechitina micracantha*, *Belonechitina seriespinosa*, *Calpichitina lata*, *Conochitina tribulosa*, *Belonechitina wesenbergensis*, and *Belonechitina robusta*.

Biotope IVb: *Conochitina homoclaviformis*, *Eisenackitina* ?*rhenana*, and *Eisenackitina inconspicua*.

Biotope IVc: *Belonechitina vulgaris*, *Conochitina parviventer*, *Belonechitina brittanica*, *Cyathochitina* sp.1, and *Conochitina* aff. *homoclaviformis sensu* Vandenbroucke (2008), *Conochitina chydaea*.

A.5. Excluded from the analyses

Species that have a ‘taxonomical weight’ of ‘one’ have not been included in the analyses. These species are: *Rhabdochitina turgida*, *Rhabdochitina usitata*, *Cyathochitina calix*, *Desmochitina minor*, *Rhabdochitina magna*, *Belonechitina robusta primitiva*, *Rhabdochitina parallela* nom. nud., *Rhabdochitina gracilis*, *Euconochitina conulus*, *Euconochitina communis*, *Rhabdochitina gallica*, and *Desmochitina typica*.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2009.11.026.

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