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Honors Thesis

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Department: Geology

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Abstract

The purpose of this study is to examine the biodiversity patterns of a group of fossil organisms called chitinozoans. Chitinozoans are organic-walled, planktonic microfossils that first appear in the Early Ordovician Period (488 million years ago) and diversify rapidly through the Paleozoic Era. The Ordovician Period was a time of great global climate change, and by studying this group of fossil plankton, we hope to better understand how modern plankton, which are the base of the marine food chain, might respond to climate change. We used a method called constrained optimization (CONOP9) to construct a composite range chart of 152 chitinozoan species from 65 Ordovician drill cores and outcrops from the paleo-continent Gondwana. Our results show that chitinozoan biodiversity increases throughout the Early and Middle Ordovician, peaks in the middle part of the Late Ordovician and declines thereafter. These results differ from biodiversity estimates derived from more traditional species counting methods.

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Table of Contents

Introduction

Climate change is a serious problem facing our world today. One of the biggest questions involving climate change is the issue of how it will impact our current biodiversity. Specifically, how it will impact the complex food chain that exists today, and the base of the food chain, which is marine plankton. Investigating past climate change and its relationship to biodiversity in Earth history can provide insights into this issue, because dramatic climate changes were common in Earth history. One time interval that experienced climate fluctuation was the Ordovician Period.

The Ordovician Period lasted from about 488 to 443 million years ago. During the Ordovician, the continental configuration was much different than it is it today. There were several main continents: Laurentia, Baltica, Avalon, Siberia, and Gondwana, and a number of smaller paleo-plates. Gondwana was the largest of the continents, and was located mostly in the southern hemisphere (Figure 1). It consisted of Africa, Antarctica, India, parts of South America, and parts of Australia.
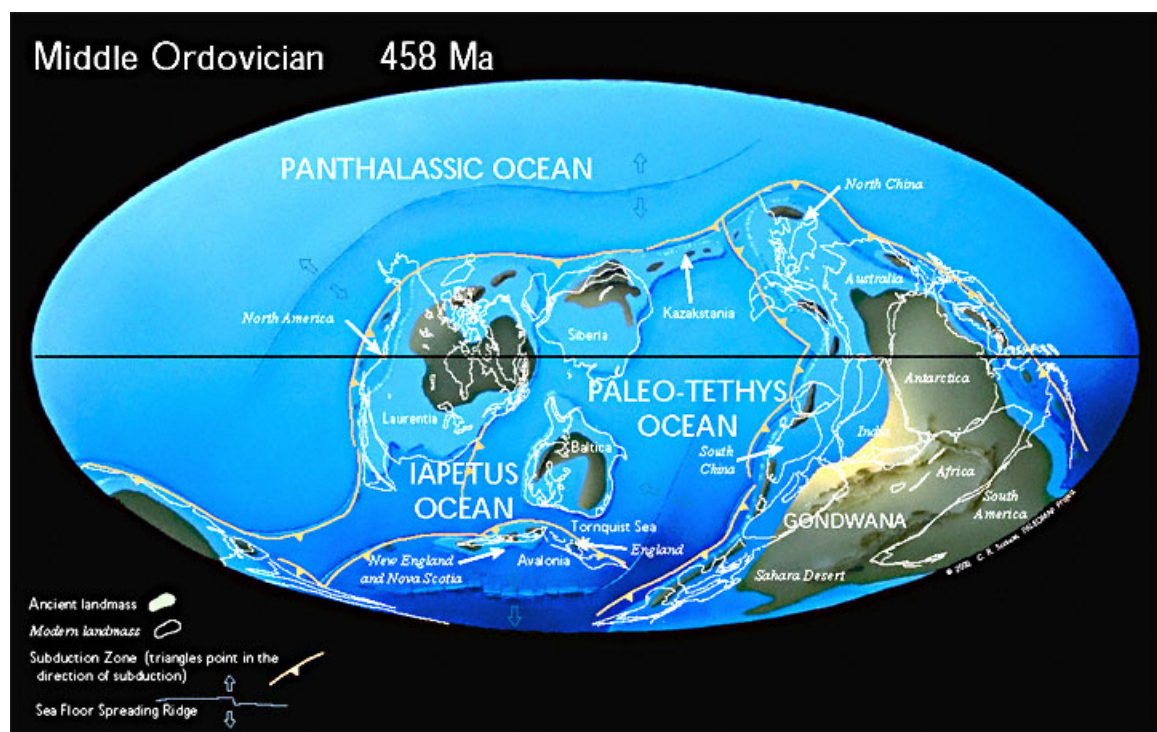
Figure 1: The Earth during the Middle Ordovician. Notice the position of Gondwana in the Southern Hemisphere, and the lack of glaciers. From Cooper and Sadler, 2012.

The Ordovician was a time of dramatic climate change, starting with a "hot house" Earth (an interval of time when the Earth had no continental ice sheets), cooling throughout the Late Ordovician, and then ending with an extensive southern hemisphere glaciation (Cooper and Sadler, 2012). The Earth was so warm during the Lower to Middle Ordovician that there were no glaciers, and the continents were flooded with shallow epicontinental (epeiric) seas (Figure 1). However, as the Earth cooled and a large Gondwanan ice sheet formed, sea levels dropped and these epeiric seas disappeared. The dramatic climate change, which apparently occurred in multiple episodes (Webby, 2004) throughout the latest Ordovician, makes the Ordovician an excellent deep time analogue for modern day climate change.

In addition to this climate change, the Ordovician also has an interesting biological history. It includes one of the greatest evolutionary radiations recorded in the fossil record, called the Great Ordovician Biodiversificaiton Event (Webby, 2004), and one of the Earth's greatest mass extinctions at its end (Figure 2). Some possible reasons for this great radiation are the presence of many epicontinental seas that provided a suitable habitat for marine organisms, and strong magnetic and tectonic activity (Cooper and Sadler, 2012). This huge increase in marine biodiversity culminated with a mass extinction in the Late Ordovician (specifically during the Hirnantian Stage). It is estimated that 85% of the species on Earth became extinct (Sheehan, 2001). As noted above, this mass extinction event co-occurs with an overall cooling of the Earth and a sea-level decrease associated with glaciation. Glacial features preserved today suggest

that the glacier on Gondwana was more than 6000 km long (Sheehan, 2001). These important biodiversification and extinction events make the Ordovician an interesting time interval in which to examine the relationship between Earth processes and life.
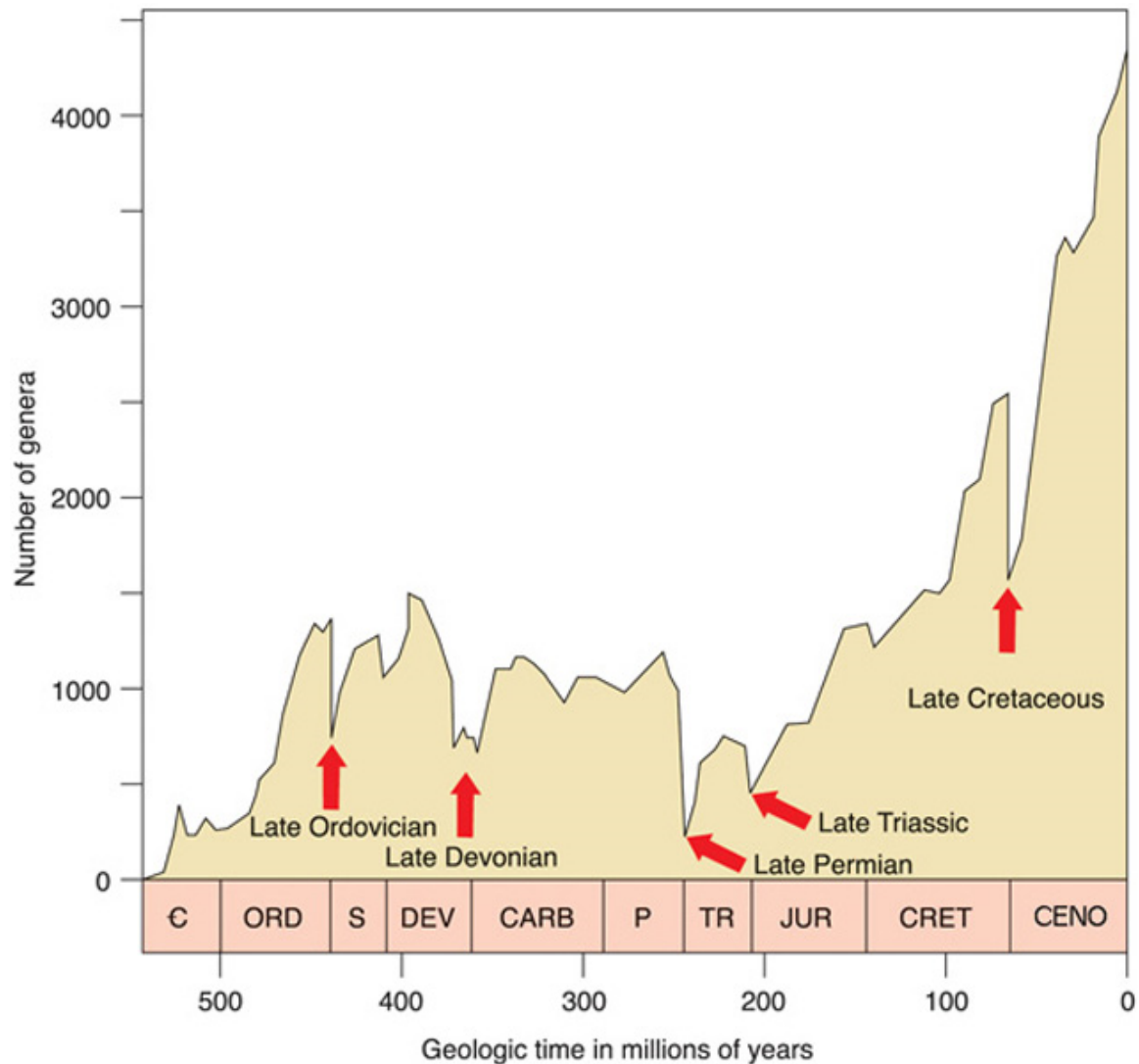
Figure 2: Major Extinction Events in Earth History. The sharp increase at the beginning of the Ordovician indicates the Great Ordovician Biodiversification Event. The decrease at the end of the Ordovician marks the mass extinction, coinciding with the climate deterioration. From: geol.umd.edu.

One group of organisms that evolved and flourished throughout the Ordovician is the chitinozoa. Chitinozoans are organic-walled microfossils that have an unknown

taxonomic affinity (Paris, 1990). They tend to be flask or beaker-shaped with a hollow

interior and variable exterior ornamentation (Figure 3). The origin and taxonomic affinity

of chitinozoans is unclear, but recovery of chains and clusters of linked chitinozoans have

led some workers (e.g., Paris and Nõlvak, 1999) to suggest that chitinozoans may

represent the fossilized eggs of soft-bodied Paleozoic metazoans such as ancient
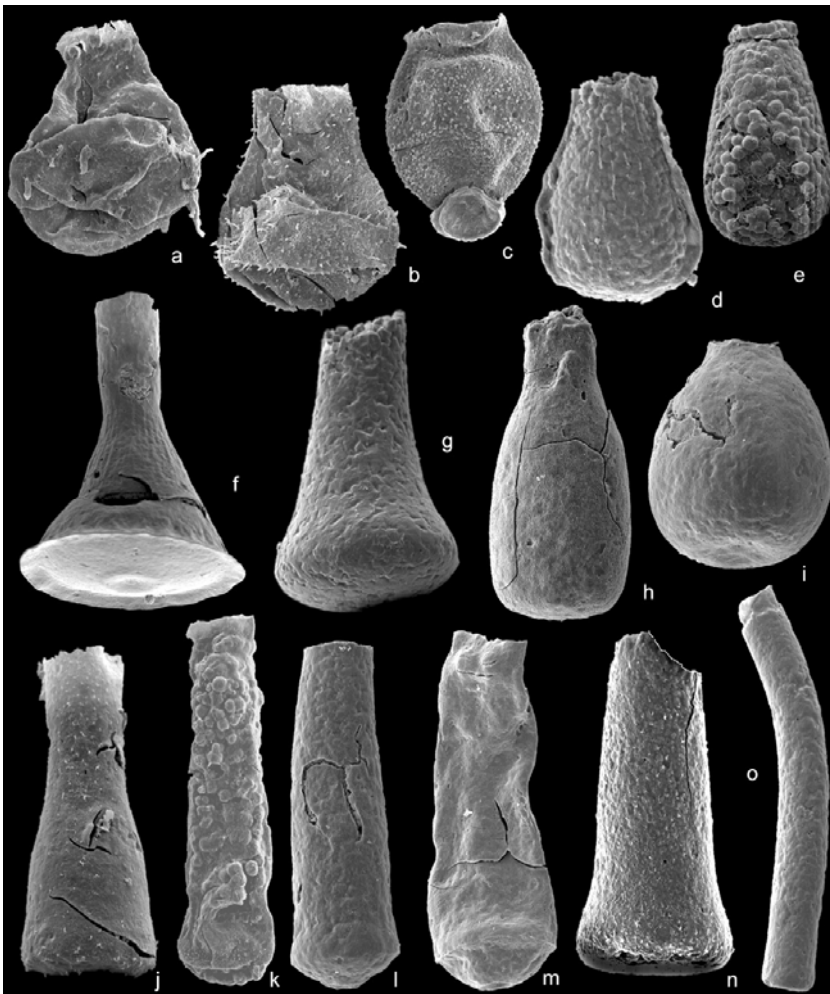
arthropods or gastropods.

Figure 3: Chitinozoans. Chitinozoans exist in many rapidly changing and distinct forms, which is one reason why they are excellent index fossils. From: Vandenbroucke et al., 2005.

Chitinozoans first appear in the Early Ordovician and evolve rapidly through the

Paleozoic (Armstrong & Brasier, 2005). The majority become extinct at the end of the

Devonian Period, although there a few reported (but suspect) occurrences in the Carboniferous and Permian Periods (Armstrong and Brasier, 2005). Chitinozoans are exclusively marine and occur abundantly in a variety of paleoenvironments ranging from carbonate platforms to slope and basinal settings represented by black shales (Paris, 1990). As an abundant part of the Ordovician microfossil record, chitinozoans provide insights on planktonic biodiversity during the Paleozoic.

Along with graptolites and conodonts, chitinozoans are also extremely important lower Paleozoic index fossils. Index fossils are fossil organisms whose key ecological and evolutionary traits make them particularly useful for making correlations between stratigraphic units and placing them in proper sequence in geological time. Some of these traits include a wide geographic distribution, broad environmental tolerance, abundant in fossil record, distinctive morphologic characteristics, and individual species short time duration. The use of fossils to correlate and relatively age date rocks is called biostratigraphy. Biostratigraphy is the oldest application of paleontology, and has been used to build and refine the geologic timescale since the early 1800's.

Faunal assemblages of different units and ages are typically established over many years through many studies, and are a primary means to order and correlate rock units. Since rocks of the same age tend to contain the same fossil species, they can be correlated biostratigraphically. These fossils are then organized into a set of zones, with each zone defined by key index taxa. Zones are often set by an index taxa's first appearance datum, which could occur at a locality either because of evolution or immigration (Prothero, 2004). Biostratigraphers also document an index taxa's last appearance datum, which can be caused by extinction or emigration (Prothero, 2004). Theoretically, biostratigraphical

zones occur in the same order all over the world. However, determining which order is correct can be somewhat difficult. Some important applications of biostratigraphy include finding petroleum deposits, reconstructing ancient continents, and examining the geologic record of global environmental change. Chitinozoan's widespread distribution, abundance, and resistance to weathering processes make them ideal for both local and global stratigraphic correlations (Armstrong & Brasier, 2005).

Research Goals

There were two main goals of this research: to create a stratigraphic correlation model using an automated graphic correlation program CONOP9, and to use that model to better understand the biodiversity patterns of chitinozoans during the Ordovician in the paleo-continent Gondwana. A stratigraphic correlation model constructed from the stratigraphic range data of chitinozoans could provide a more accurate understanding of the full species longevity of chitinozoans in Earth history. This in turn will provide a more precise picture of Ordovician chitinozoan biodiversity. Since the Ordovician serves as a deep time model for modern day climate change, assessing the biodiversity of this time interval could provide insights into the future of modern day biodiversity assemblages.

Methodology

Dataset and Data Collection

In this study, we collected all of our data by using the previously published literature

(Appendix One). My data was collected from 31 published chitinozoan studies from localities in Gondwana. From these studies I collected stratigraphic range (FAD and LAD) and presence/absence data for 152 species of Ordovician chitinozoans. Although I collected complete presence/absence data from every collection horizon throughout the range of a species whenever possible, we were most concerned with locating the first and last appearances of a species. I either manually documented the presence or absence of every species on each horizon within stratigraphic sections using Excel, or used a data collection program called OnlyALad (Sheets et. al., 2014). OnlyALad is a program designed to collect stratigraphic range data from published range charts with the intent of minimizing human input error. It does this by calling up a taxonomic diction dictionary from which taxon names are pasted into an Excel spreadsheet, thereby eliminating taxon spelling errors. In this study, my complete dataset includes 152 species from 65 outcrops and drill cores from the paleo-continent Gondwana. Having detailed presence/absence data from every collection horizon allows for better confidence estimates of the first and last appearances of species in the fossil record.

Measures of Biodiversity

With this data I constructed a more complete stratigraphic range estimate of each species in order to attain a precise assessment of chitinozoan biodiversity over time. Since the occurrence of taxon range ends (FADs and LADS) at any one section are influenced by sampling and environmental biases, a composite range for each species needs to be constructed (Sadler et. al. 2014). Once that has been accomplished a better understanding of biodiversity through time is possible.

Accurately measuring biodiversity in the fossil record can also be difficult. There are four basic ways a species can exist within a time interval (Figure 4). A species can exist throughout the entire time interval, originate before the time interval and become extinct during the interval, originate within the time interval and become extinct afterwards, or a species can originate and go extinct within the time interval. These four ways influence biodiversity calculations (Cooper in Webby, 2004).
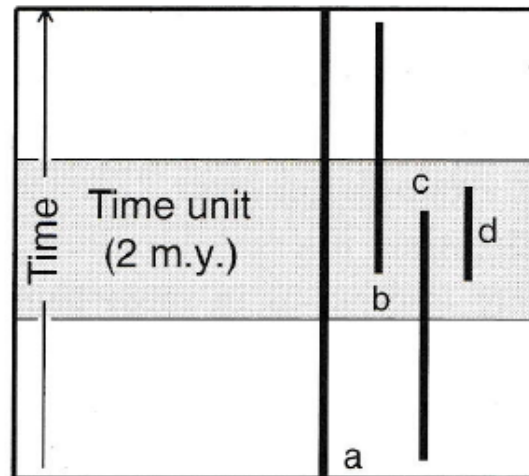
Total diversity $(d_{tot}) = 4$
Species/m.y. $(d_i)\ \ = 2$
Normalized diversity
$(d_{norm})\ \ \ \ \ \ \ \ \ = 2.5$

FIGURE 4.1. The four ways in which a species can be present in a time interval; a, range through; b, originate within the interval and range beyond it; c, range into the interval and terminate within it; d, confined to the time interval. The three measures of diversity for the time interval are shown.

Figure 4: From Cooper in Webby, 2004.

There are several different methods of measuring biodiversity. One is simply counting

the number of species that occur within a time interval. However, this method is highly dependent on the size of the time interval, and tends to overestimate the mean standing diversity of taxa (Copper in Webby, 2004). A more accurate method is to count the number of species and divide by the duration of the time interval in which they occur. This results in a species per million years count (assuming an interval measured in millions of years). This accounts for the size of the time interval, and hence makes for a more precise method of calculating biodiversity than a simple total count.

One final method is called normalized diversity. Normalized diversity assigns a point system to each species, depending on how well described their range is in the time interval (Cooper in Webby, 2004). Of these three methods normalized diversity tends to best estimate mean standing diversity at point in geologic time. While all of these methods have their faults and merits, this study uses computer algorithm to eliminate intervals altogether and provide an estimate of true mean standing diversity – the biodiversity of a taxon group at any one moment in time..

As noted above, in order to obtain a better measure of mean standing diversity, we first had to construct a composite stratigraphic range chart from the biostratigraphic range data of all the species that occur in the various sections. We used the stratigraphic correlation program CONOP9 (Sadler and Cooper, 2008) to produce this composite stratigraphic range chart.

CONOP9 is an automated graphic correlation program that is multi-dimensional; it uses observations from many sections simultaneously (Sadler et. al. in Harries, 2003). As input data, CONOP uses all of the stratigraphic range data from all of the species in all of the individual sections (the first and last appearance of each species at each section), and

using an annealing algorithm produces a correlation model and composite range chart for the studied sections and species, respectively. Depending on the number of sections and taxa, this type of correlation exercise can have billions of solutions. CONOP9 uses a set of rules to eliminate impossible solutions and choose a most probable one. Any time one of the rules is broken, the solution incurs a penalty. In searching for the best solution, CONOP9 will pick the solution that incurs the least amount of penalties (Sadler and Cooper, 2008, Kooser, 2002). The user can set various parameters that determine how CONOP9 is allowed to search for this best solution.

In addition to assigning penalties CONOP9 eliminates impossible sequences, or sequences that cannot exist in nature (Sadler et. al. in Harries, 2003). For example, this computer program would eliminate solutions that include last appearances before first appearances. CONOP9 also maintains all observed taxon co-existences and tries to minimize unobserved co-existences. Finally, CONOP9 operates under the parsimonious tenet; that is, the simplest solution is the correct one. Because of this, CONOP9 searches for the best of the possible solutions by choosing a model that requires the minimum net adjustment of observed ranges and having the fewest unobserved co-existences.

This best solution is the composite stratigraphic section that contains all of our 65 sections and 152 taxa, and has the lowest penalty assignment. In order to use this composite for biodiversity studies, we can simply count the number of species at any single time as a running total of FADs - LADS. This method of calculating biodiversity eliminates some of the problems of counting biodiversity. For example, a total count of biodiversity is dependent on the size of the interval (the larger the interval, the greater the biodiversity). However, an interval-free method eliminates this bias. We believe this to

be the best way to obtain an accurate measure of mean standing diversity (Sadler et. al. in

Harries, 2003).

Results

Correlation Model

The correlation model produced by CONOP9 shows that the data is sparse in some

sections and time intervals (Figure 5). For example, there are few FADs and LADs in

much of section RH14 (as shown by the lack of dark gray bars), and so the ranges of

species in that section are not well constrained. This is true of many of the longest

sections. The smaller sections, such as section TA are typically better sampled and have

more events. This suggests that some of our locations are not well sampled or contain

only a few long ranging species, and that the correlation of those sections, particularly in

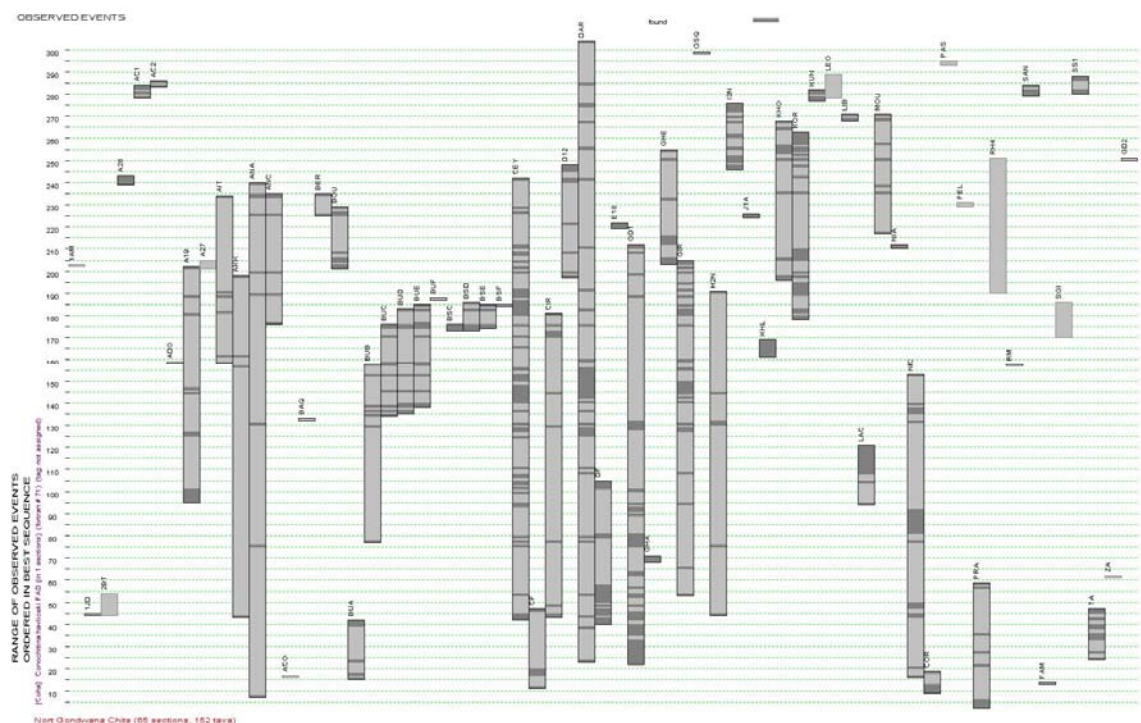the data poor intervals, is imprecise.

Figure 5: Correlation Model. Dark grey areas indicate many events (FADs and LADs); light grey areas indicate a lack of events.

Range Chart

CONOP9 provides the composite stratigraphic ranges of each species as part of its output. From this output file, we created a detailed range chart (Figure 6). This range chart is mostly consistent with the accepted order of index taxa and biozones for the Ordovician of Gondwana. However, there are a few range discrepancies. In my range chart, some of the chitinozoan species' LADs appear to range much higher, or their FADs sink much lower than what occurs in nature. For example, in our model *Amoricochitina nigerica* has a FAD that is younger than is generally accepted. Also, *Spinachitina formosa* ranges too high, while *Desmochitina bulla's* range is too low (meaning its first appearance is older than commonly accepted). Finally in my dataset, *Euconochitina brevis,* and *Eremochitina brevis* both had LADs that were too high.

We may be seeing these differences between my range chart produced from CONOP9 and those from more traditional biostratigraphic studies for several different reasons. One factor that could influence these differences is the way the CONOP algorithm assesses range extension penalties. If a LAD at the top of a section or a FAD at the bottom of a section is artificially truncated by the section end, and it does not co-occur with the LAD or FAD of another species in the dataset, CONOP may let this LAD or FAD float or sink unrestrained to the top or bottom of the range chart with no penalty assessment. I was mostly able to manually fix these floating or sinking problems, but it could still cause inconsistences between my range chart and previous studies. Second, it may be that taxon identification errors by the individual study authors could cause

erroneous range extensions. Finally, it is possible that the range chart produced from this study is actually a more accurate picture of species ranges than studies from individual sections. This may be because this study includes a larger area than previous studies, and my range chart was produced using multiple (65) sections as discussed earlier.
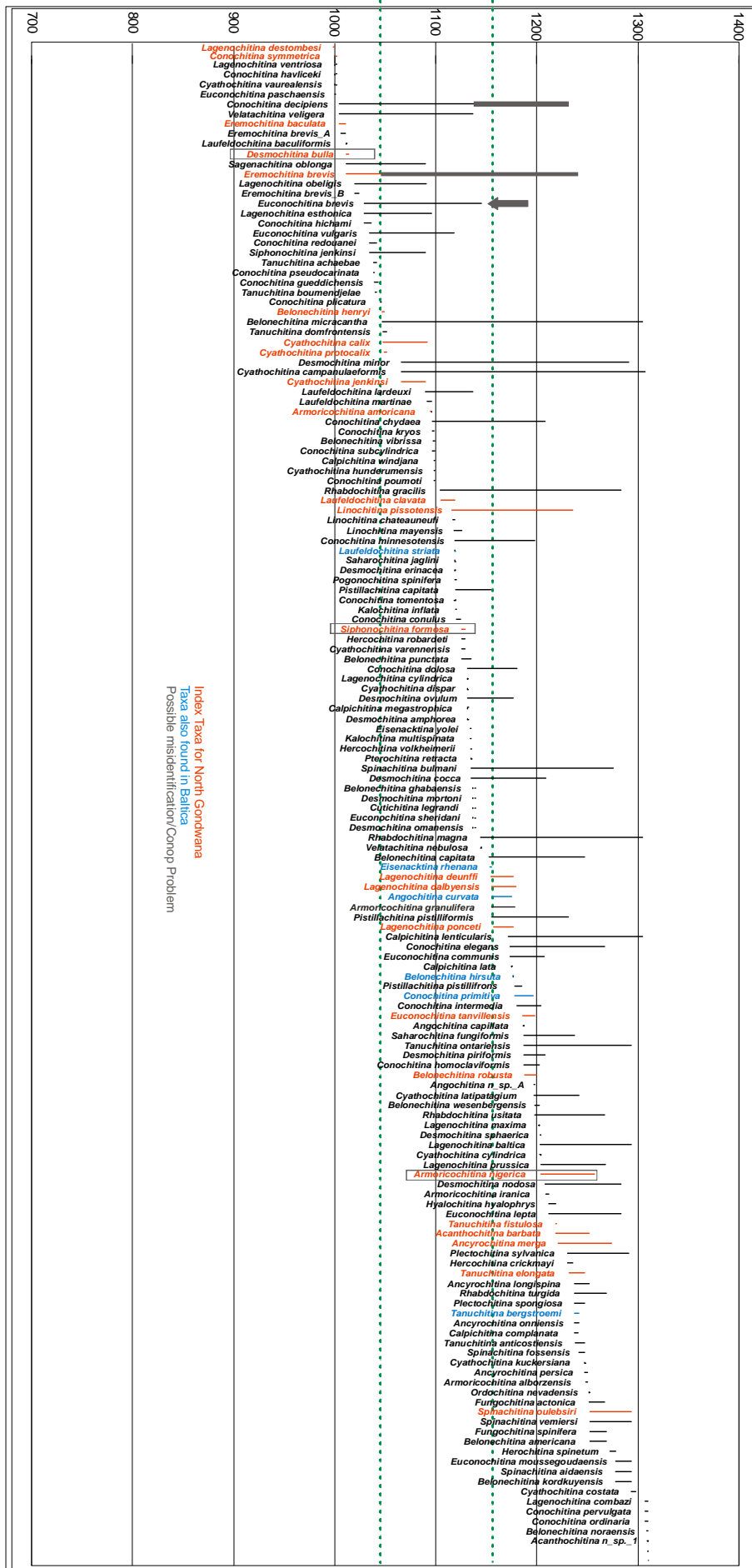
Figure 6: Range Chart. Grey boxes indicate species that may be floating or sinking too high. Grey arrows and bars indicate species whose ranges are known to be too long. The grey bars show the corrected range. The arrow indicates that the species correct range could not be determined.

Biodiversity

The biodiversity curve produced by CONOP's interval free method shows some interesting trends (Figure 7). Our chart shows a general upward trend throughout most of the Lower and Middle Ordovician, with a spike in the Sandbian (early Late Ordovician). Biodiversity is generally higher in the Upper Ordovician than in the Lower or Middle Ordovician. However, this could be due the greater amount of data that we have from the Upper Ordovician. Our highest peak is in the early Hirnantian, or latest Ordovician. After this high, biodiversity drops dramatically, coincident with the Late Ordovician climate crash and mass extinction event. A simple origination and extinction rate shows that origination increases rapidly throughout the Lower Ordovician and steadily decreases throughout the Middle Ordovician. Extinction is much higher than origination during the late Upper Ordovician.
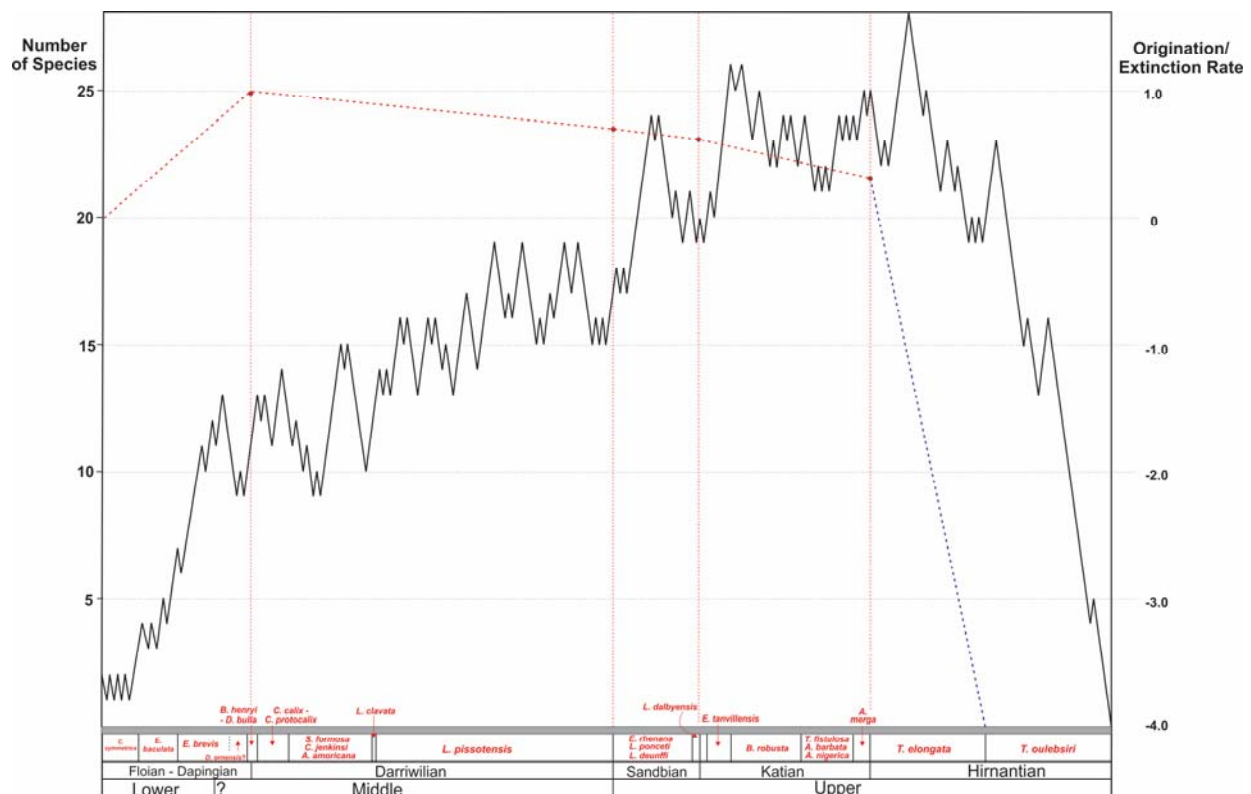
Figure 7: The Biodiversity Chart calculated though CONOP9 using an interval-free method.

Discussion

Comparison with Previous Studies

These results have some interesting differences with previously calculated biodiversity trends for Ordovician chitinozoans (Grahn and Paris, 2010; Paris et al. in Webby, 2004). Grahn and Paris (2010) use balanced total diversity (a measure similar to normalized diversity) to calculate biodiversity. The high peak on this curve is in the late Middle Ordovician (Figure 8). Paris et. al. in Webby (2004) uses mean number of species per million years to calculate their biodiversity curve (Figure 8). Interestingly, their trend seems to mirror ours more than the balanced total diversity calculation. The mean number of species per million years has a high in the Upper Ordovician, like the CONOP interval-free biodiversity. Both calculations from previous studies, and our interval-free method, show a steady increase in biodiversity throughout the Lower and Middle Ordovician.

One reason for these discrepancies could be that there is more data in the literature for the Middle and Upper Ordovician than for the Lower Ordovician. This produces a bias, where the range chart appears to have more species in the Middle and Upper Ordovician than the Lower Ordovician. In particular, the newer literature that we used (post-2010) was heavily weighted with Hirnantian data. Similarly, because there is less data for the Lower (and Middle) Ordovician, this dataset does not have some index taxa or good zonal control resulting in poorer constraint on taxon ranges. These characteristics of our dataset could be one reason for the differences between our diversity curve and those in

previous studies.

Figure 8: Biodiversity Analysis Comparison. The black line is the CONOP9 interval free diversity curve, which is FAD's minus LAD's. Blue and Green Lines show comparative biodiversity methods.

Correlation with Sea Level

One environmental factor that could be influencing the trends in the biodiversity curve is

sea level rise and fall. Sea level fall exposes the shallow marine shelf to erosion and also

reduces the marine habitat area. Thus there is less area for the chitinozoan animal to live

and less rock preserved from which to extract the fossils. Sea level rise produces the

opposite effect. Hence, I expected sea level rises to coincide with increases in

biodiversity, since this would create more habitats for chitinozoans. Conversely, a

decrease in sea level should coincide with decreases in biodiversity because this creates

less habitat for chitinozoans. I compared my biodiversity curve with a sea level curve for

the Ordovician, to see if the curves showed any correlation (Figure 9). During the

Ordovician, sea level rose throughout the Lower Ordovician, plateaued throughout the

Middle Ordovician, and decreased throughout the Upper Ordovician with the glaciation

event (Dronov et. al., 2011). Within those general trends, there are smaller rises and falls.

Many of these sea level rises correlated with an increase in biodiversity, while many of

the sea level fall correlate with a biodiversity decrease. This result is not surprising, but it

does support the validity of the CONOP derived biodiversity curve. Overall, the

correspondence of the biodiversity curve and the sea level curve supports my results.
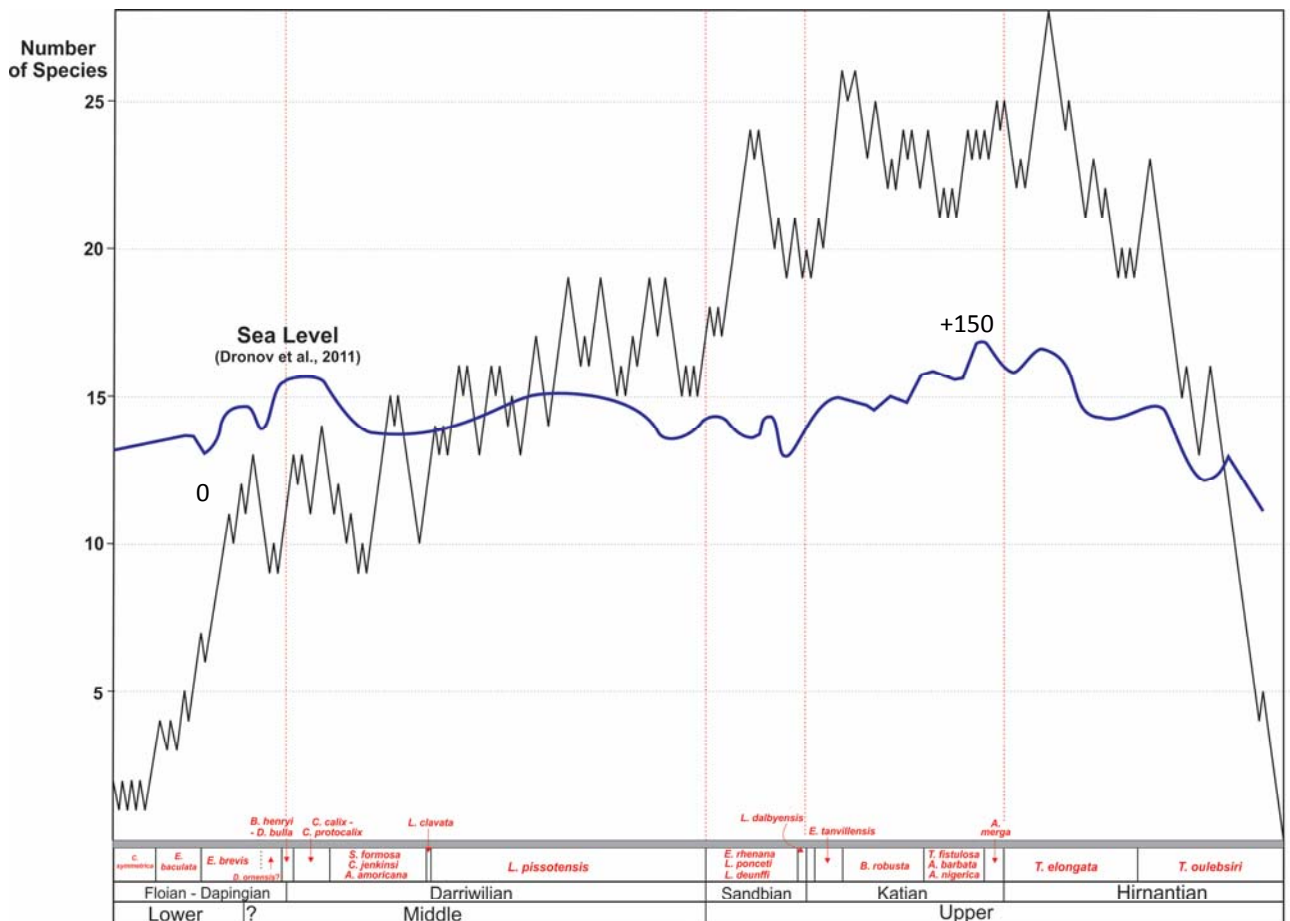
Figure 9: Correlation with Sea Level. The blue line represents sea level changes. Sea level changes throughout the Ordovician, starting rather high and decreases with the global cooling event.

Correlation with Global Carbon Cycle

Another environmental factor I compared to my calculated biodiversity curve was changes in the global carbon cycle recoded as carbon stable isotopic excursions (Figure 10). What events these changes in carbon isotopic ratios are recording are not completely clear, but they are likely recording a major environmental event. Carbon exists in three forms: ^{12}C, ^{13}C, and ^{14}C. About 99% of the Earth's total carbon exists as the stable isotopes ^{12}C or ^{13}C, and of that 99%, only 1% is ^{13}C. Photosynthetic processes tend to sequester Carbon as ^{12}C relative to ^{13}C,(Kump and Arthur, 1999). Because of this, organic carbon tends to have a carbon ratio with more ^{12}C than ^{13}C, and in highly productive waters the environment becomes depleted in ^{12}C relative to ^{13}C . When organic matter is buried in sediments, its carbon isolated and does not rapidly return to the environment. These carbon ratios can be measured and analyzed for the ratio, which is known as $\delta^{13}C$. At certain times in Earth history, the amount of ^{13}C in the sediments is uncharacteristically high. These are known as carbon isotopic excursions and are thought to represent major changes in plankton productivity, sea-level changes, and/or shelf erosion (Young et al., 2005).

Three major carbon isotopic excursions occur during the Ordovician: the Middle Darriwilian Carbon Isotopic Excursion (MDICE), the Guttenburg Carbon Isotopic Excursion (GICE), and the Hirnantian (HICE). The MDICE occurs in the Middle Ordovician, and it is the smallest of the three. The MDICE doesn't show a strong

correlation with my biodiversity curve; there is not particularly strong increase or

decrease in biodiversity when it occurs. This may be because it occurs over a long period

of time, and so may not represent as rapid an environmental perturbation as the other

excursions, although this is speculation. Also, the MDICE is not as well studied or

extensively documented as the GICE and the HICE. The GICE and the HICE are known

to record changes in the global carbon cycle. These two carbon isotopic excursions

coincide with a decrease in biodiversity (Figure 10). These results are not unexpected, as

a major change in the environment would most likely result in a local extinction.
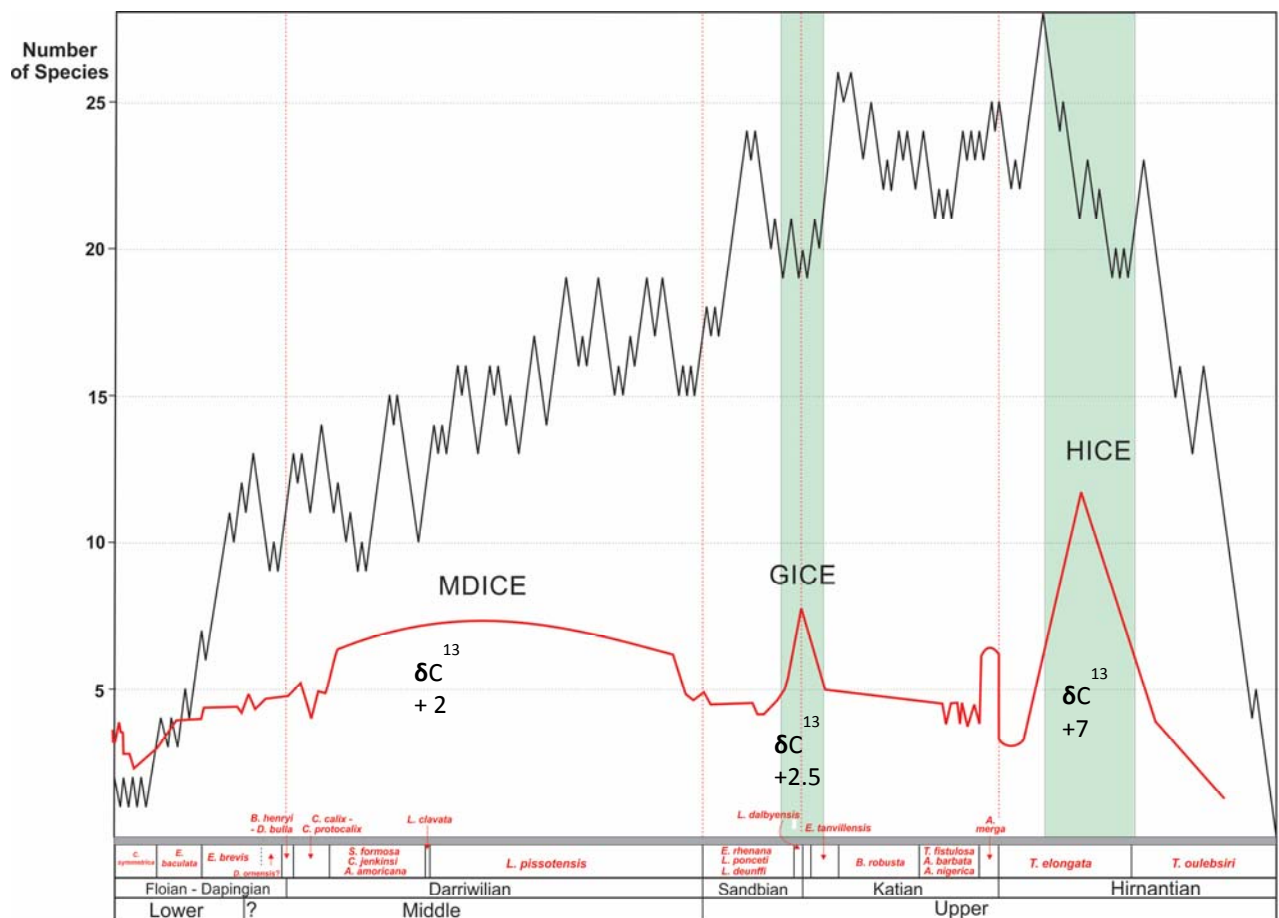

Figure 10: Correlation with Carbon Isotopic Excursion. The relative strength of the excursion is indicated below each excursion. The two excursions highlighted in green are the two that correlate the most with the biodiversity curve.

Future Studies

The results of this study point to some interesting future studies. Expanding the dataset to include other paleo-continents such as Laurentia and Baltica could increase the accuracy of the correlation model and the range charts, especially for the Lower Ordovician. It would also expand the regional biodiversity analysis to global in scope. In addition, comparing the chitinozoan biodiversity curve to the curve for other Ordovician fossils like graptolites and conodonts could provide some insights into the overall biodiversity of the Ordovician, and how environmental change impacted several different groups.

Conclusion

This study sought to examine the biodiversity pattern of chitinozoans in the Ordovician strata of Gondwana, using an interval free method calculated in the automated graphic correlation program CONOP9. Studying biodiversity in this time interval is useful because the Ordovician may serve as a deep time analogue for modern day climate change. Using CONOP9 to measure biodiversity, I found that the diversity of chitinozoans increases steadily throughout the Lower and Middle Ordovician, peaks in the Upper Ordovician, and then decreases rapidly. Previous studies have found a slightly different trend; typically, there is a peak in biodiversity in the Middle Ordovician. These differences can possibly be attributed to the nature of our dataset or the CONOP algorithm, or may better reflect the true diversity pattern of Ordovician chitinozoans in Gondwana.

Our biodiversity pattern appears to have a correlation with environmental changes during the Ordovician. When compared to sea level, the lows in our biodiversity often occur at

the same time as low sea level and the highs in our biodiversity often co-occur with highs in sea level. Also, two of the three carbon isotopic excursions that occurred during the Ordovician also match up with lows in chitinozoan biodiversity. These results are not surprising, but do support a hypothesis that the diversity of marine plankton can be influenced by global environmental changes. This study may help predict how planktonic biodiversity might change in response to modern day climate change.

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