Global and Regional Chitinozoan Biodiversity Dynamics in the Ordovician: Relationships to Sea-Level, Carbon Cycling and Tectonics

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Global and Regional Chitinozoan Biodiversity Dynamics in the Ordovician: Relationships to Sea-Level, Carbon Cycling and Tectonics

Honors Thesis
Jordan Watson
Department: Geology
Advisor: Daniel Goldman, Ph.D.
April 2016
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Abstract

Fossil species provide extensive information about the past history of life on Earth. This thesis focuses on the global and regional biodiversity dynamics of the extinct fossil group Chitinozoa, and analyzes the impact and influences of sea-level, global carbon cycling and tectonics on their biodiversity. Biodiversity curves were generated from three different paleo-continents, Laurentia, Baltica, and Gondwana using the automated graphic correlation computer program CONOP9. Traditional methods of biodiversity analysis count fossil taxa in individual intervals of geologic time. The results of these methods are highly dependent upon interval length and the relationship of taxon range to interval boundaries. CONOP9 utilizes an interval free approach to biodiversity analysis. Chitinozoan stratigraphic range data from fossil species collected on several ancient continents (Baltica, Laurentia, and Gondwana) were also combined and analyzed to compare the regional and global biodiversity plots. These biodiversity patterns were then compared to existing sea-level and carbon isotope excursion curves to examine the relationship between environmental change and Chitinozoan biodiversity. The three major carbon isotope excursions of the Ordovician, the MDICE, GICE, and HICE all occur during periods of reduced global chitinozoans biodiversity. Additionally, sea level to some extent appears to be related to chitinozoan biodiversity with reduced biodiversity during periods of sea level decrease and increasing biodiversity during periods of higher sea level.
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Introduction

The Earth is teeming with a rich and diverse assortment of biological life, which is both affected by and responding to extremely dynamic geologic processes. Geologic processes such as plate tectonics, climate change, sea level rise and fall, and biogeochemical cycles all impact the evolutionary dynamics of Earth’s biota. These geologic processes may also influence the biodiversity of species, and understanding the past relationship between Earth and life may help us predict the effects that modern climate change may have on Earth’s biota. Climate change is a critical problem facing the world today and understanding the way species may respond to global change is imperative in mitigating the possible consequences of these changes.

A previous geological time period that could be used as a deep time analog for modern climate change is the Ordovician Period. The Ordovician Period was a time interval of rapid and cyclical climate change between 488 and 443 million years ago. During the Ordovician global paleogeography was extremely different from the current configuration of the tectonic plates (Figure 1). The Earth was comprised of three main paleo-continents Laurentia, Gondwana, and Baltica, and many smaller plates. For modern day reference, Laurentia was of the progenitor of North America, Gondwana comprised Africa, Antarctica, India, and parts of Australia and South America. Baltica consisted of Scandinavia and the Baltic states (PALEOMAP Project 2007).
Figure 1: Map of the continents positions during the Middle Ordovician with modern day outlines (PALEOMAP Project 2007)
For much of the Early and Middle Ordovician Earth’s climate was extremely warm. This long Hot House period resulted in extensive melting of much of the glacial ice around the Earth and the polar ice caps. Consequently, sea level rose, flooding the continents with extensive warm, shallow epicontinental seas. The warm, shallow, well-oxygenated character of these seas provided an excellent habitat for marine life during this time period (Cooper and Sadler, 2012). The suitable conditions for marine life during this time period resulted in one the greatest periods of biodiversification in Earth history referred to as the “Great Ordovician Biodiversification Event” (Webby, 2004). Towards the end of the Ordovician Period climate cooled significantly and precipitated one of the largest mass extinctions in Earth history (Figure 2). The mass extinction event at the end of the Ordovician Period was likely the result of tectonic activity and associated climate change, which resulted in global cooling and associated southern hemisphere glaciation on the continent of Gondwana. This resulted in an overall fall in sea level and the loss of habitat due to the disappearing of the epicontinental seas (Cooper and Sadler, 2012). The extremes of climate change during this time interval provide a good representation of what might be expected from modern climate change.

Understanding the effects of climate change on biodiversity requires a well-sampled fossil record to avoid the biases commonly associated with biodiversity studies from the fossil record (Cooper, in Webby, 2004). These biases include uneven sampling, poor preservation, and the uncertainties of locating true range ends of fossil taxa.
Figure 2: The 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.
Research Goals:

This research project examines the relationship between Ordovician environmental change and the biodiversity a group of extinct microfossils called Chitinozoans. Chitinozoans are an abundant and well-sampled group of species during the Ordovician. They are organic walled microfossils with unknown taxonomic affinities. They are shaped like tiny flasks and beakers and have various spiked ornamentations on the outside (Figure 3). Their taxonomic affinities are largely unknown, but because clusters of them have been found together some researchers have suggested that they may be the fossilized eggs of Paleozoic gastropods and arthropods (Paris and Nõlvak, 1999).

Chitinozoans existed from the Early Ordovician to the end of the Devonian Period and possibly continued through the Carboniferous and Permian time periods. However, examples of Chitinozoan fossils in post-Devonian rocks are extremely rare and it is not clear exactly how prevalent they were during the Carboniferous and Permian (Armstong and Brasier, 2005). Chitinozoans occur in rocks that represent a variety of marine environments, ranging from deep water basinal shales to carbonate-dominated shelf environments, and were distributed globally across all paleo-continents.

Chitinozoans are extremely useful fossils for a multitude of reasons. Their global distribution, abundance, rapid evolution, and overall biodiversity makes them excellent index fossil for the Ordovician. Index fossils are species whose evolutionary patterns and abundance during their respective time period help to correlate stratigraphic sections to geologic time as well as other stratigraphic units. Thus, chitinozoans are a useful fossil group in which to examine the effects of Ordovician environmental change on marine biodiversity.
Figure 3: Images of Chitinozoans From Butcher et al. 2010
In this study I compiled both regional and global biodiversity curves for Ordovician chitinozoans. In order to construct these curves I first had to produce a set of regional stratigraphic correlation models as well as a global stratigraphic model using the graphic correlation program CONOP9. I compiled individual section data for the paleo continent Laurentia and used existing datasets for Baltica and Gondwana. The datasets were run both individually and together in CONOP9 to produce regional biodiversity curves and a global biodiversity curve. Once this was accomplished, I compared the regional and global biodiversity patterns with each other and with paleoenvironmental proxy data to better understand the relationship of biodiversity to global environmental changes such as sea level rise and fall and carbon cycling.

Methodology

Creating a composite set of species ranges:

The data used and examined in this study was compiled from previous published literature on chitinozoan biostratigraphy. I extracted stratigraphic range data from published literature that detailed chitinozoan occurrences on the paleo-continents of Baltica, Laurentia, and Gondwana. The data that I collected focused on First Appearance Datums (FAD’s) and Last Appearance Datums (LAD’s) data with additional, more detailed presence/absence data for each collection horizon. FADs and LADs are the end points of the stratigraphic ranges of taxa in the fossil record. The total stratigraphic range of a taxon is an approximation of the total duration of that taxon in Earth history, as best as can be estimated from the fossil record.
Accurate calculations of biodiversity without bias through time require good estimates of the stratigraphic ranges of the taxa that are being studied. Sampling, preservational, and ecological biases make it difficult to construct accurate and precise stratigraphic ranges of individual species. In order to avoid these inherent biases composite ranges need to be created from the entire set of LADs and FADs of species from multiple sections (Sadler et al 2014).

Measuring biodiversity as a whole poses a series of complications that need to be acknowledged and accounted for when analyzing biodiversity. There are four distinct ways as species can exist within any set time interval (Figure 4). The species can range through the entire interval. The species can originate before and become extinct during the interval or originate during and become extinct sometime after the interval. Finally, the species range can originate and terminate within the interval (Cooper, in Webby, 2004). Consequently, different methods of counting taxa in a time interval, which take into account the different relationship of their stratigraphic ranges to that interval, yield different biodiversity estimates. Counting taxa in unequal time intervals will likely result in a biodiversity count that is proportional to the length of the interval. Hence, longer time intervals will generally have greater numbers of taxa. Attempts to avoid this include using equal duration time units, which can be difficult to construct, and using normalization techniques that still often result in varying and inflated biodiversity calculations (Cooper, in Webby, 2004). For example, Cooper (in Webby, 2004) suggested giving a full score to range through taxa and half scores to species ranges that begin, end, or are restricted to the time unit in question. Another method, normalized biodiversity, assigns points based on how well the species range is described within the
time interval (Cooper in Webby, 2004). Normalized biodiversity relative to other interval based methods provides the best estimate mean standing diversity in geologic time. A new approach, which avoids counting within intervals completely, is provided by a computational method called Constrained Optimization (CONOP9).

CONOP9 is an automatic graphic correlation computer program and unlike traditional biodiversity analyses the program constructs an interval-free biodiversity curve by creating a composite stratigraphic section from all of the taxon FAD’s and LAD’s in multiple individual sections. CONOP9 uses an annealing algorithm to compile a composite stratigraphic section based on input stratigraphic range information. The input data consists of a prepared dataset containing the stratigraphic range data for various taxa from preselected sections. CONOP9 then searches through all the possible sequencing and spacing of range end possibilities (numbers of which can range up into the trillions based on the amount of input data) and chooses the best possible solution (Sadler et al 2003). CONOP9 decides the best solution based on the lowest total penalty occurred in producing the result. Penalty is assigned for every taxon range extension and manipulation.
Figure 4: The four ways that a species can be present in a time interval. a) range through, b) originate in the interval and range beyond it, c) originate before the interval and end within it, d) restricted to the time interval. From Cooper, in Webby, 2004.
The user may also adjust the parameters manually for specific tasks in order to analyze in greater detail a certain result. CONOP9 also prevents impossible occurrences such as an FAD occurring after an LAD. In addition the program also maintains all observed species coexistences and attempts to avoid and minimize any unobserved species co-occurrences. The program operates under a parsimony principle, assuming that the simplest solution is likely the right solution. Thus it attempts to minimize extension of taxon ranges. Instead of using a traditional interval based approach in which the counts of biodiversity are summarized per geologic intervals CONOP9 uses an interval free approach. An interval free instead of using intervals uses a running total of FADs and LADs and compares them to one another in a composite comprehensive composite. Biodiversity curves are then produced from the composite by subtracting running total LADs minus running total FADs. Using CONOP9 to calculate composite taxon ranges and construct a biodiversity curve can provide new insights into both regional and global chitinozoan biodiversity patterns and the effects of geologic cycles on biodiversity.

Data Collection:

In order to minimize human input error the data were extracted from stratigraphic range charts in the published literature using a computer program titled OnlyALAD (Figure 5, Sheets et. al., 2014). This program allows the user to collect stratigraphic range end and presence/absence data for each species from individual collection horizons within its overall stratigraphic range. The program also contains a taxonomic dictionary that contains an extensive compiled list of taxa and is used to prevent spelling errors in
taxon names when compiling data. The data that I used included the data that I compiled from localities on the Laurentian paleo-continent (23 localities, 92 Species) as well as two previous compiled data sets for the paleo-continents Gondwana (62 localities, 152 species) and Baltica (27 localities, 140 species). The resulting integrated data set consisted of a total of 112 different stratigraphic sections and 282 species and allows for a nearly global examination of chitinozoan biostratigraphy and biodiversity, as well as a comparison among different regions (Appendix I).

**Results**

**Correlation Model:**

One of the results of CONOP9 is a correlation model of stratigraphic sections. The correlation model displays the distribution of FADs and LADs within all of the sections over the three paleocontinents Laurentia, Gondwana, and Baltica. The model shows the density of events (FADs and LADs) within the sections - time intervals with light grey areas have few FADs and LADs and intervals with darker grey areas have many events (see Figure 6). These event-rich time intervals within each sections are better constrained with respect to time and their correlation with the global composite. Overall the correlation models indicates some sections are not very well sampled or contain only a few species with long ranges leading to some imprecision in the time placement for some sections.
Figure 5: OnlyALAD computer interface window. The dashed pink lines mark collection horizons and the dotted green line mark individual taxa.
Figure 6: CONOP9 Correlation Chart – The light grey areas are event (FADs and LADs) poor intervals; the dark grey intervals are event rich.
Figure 7: Range Chart of Laurentian Taxa. Taxa highlighted in red are Laurentian index taxa and were used to evaluate the composite.
Details of the Range Chart:

After running a composite CONOP9 provides the composite stratigraphic ranges (FADs and LADs) of each species as part of its output. From this output file a stratigraphic range chart can be created (Figure 7). The range chart mostly matches the accepted order of index taxa and biozones for the region of Laurentia. However, some range discrepancies do exist in the range chart. Some of the chitinozoan species’ LADs appear and range much higher, or their FADs sink much lower than what is the accepted order of taxa. For example, *Belonechitina pirum* has a FAD that is older than what is expected from accepted order of index taxa. Additionally, *Conochitina brevis* occurs much earlier than it should in the range chart. These range chart produced from CONOP9 differs from those constructed in more conventional 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. Second, it may be that taxon identification errors by the individual study authors could cause erroneous range extensions. Finally, some taxa such as *Conochitina brevis* only have one short occurrence in one section in the entire data set. As a result the program is unable to constrain the taxa range due to the limited available data.
**Biodiversity:**

The data from each paleogeographic region was run through CONOP9 separately to create separate biodiversity curves for each individual region (Figure 8). The sequence of index taxa in the Baltic region CONOP composite results matched the published chitinozoan zonation with each index taxon falling into the correct stratigraphic position. The Baltic biodiversity curve shows that the period of highest biodiversity occurred during the Darriwilian Global Stage with a slight decrease at its upper boundary with the Sandbian Stage (base of the Upper Ordovician Series). Diversity began to rise again through the Sandbian Stage, but eventually began to decrease as the end of the Sandbian period approached and continued to decrease in the Katian and Hirnantian.

In the Laurentian composite, a few of the index taxa were not in the same sequence as in published data. This is likely due to their rare occurrence in the section data which prevented the program from constraining their ranges and their range ends consequently “floated or sank” in the CONOP composite. The fact that taxa commonly accepted as biostratigraphically useful index taxa are actually uncommon in sections described in the published literature is difficult to explain. The Laurentian biodiversity curves show that the highest chitinozoan biodiversity occurred during the Sandbian Stage with another small spike during the Katian.

The Gondwana biodiversity curve was the most problematic even though it contained the highest amount of section and event data. Our CONOP9 curve did not match well with previously published curves (see Grahn and Paris, 2010; Paris et al.)
2004). Several of the index taxa in this region only occurred in one or two sections creating similar problems to those found in the Laurentian data. However, correcting for these errors shows Gondwanan biodiversity was highest during the Hirnantian.

Comparing the individual biodiversity results together shows several interesting occurrences. The Laurentian peak occurred during a low of Gondwana biodiversity and during the descent of Baltic biodiversity. Additionally, a rise in biodiversity occurred during the boundary of the Katian and Hirnantian in both the Laurentian and Gondwana data, but not the Baltic data. The presence of these patterns could be the result several factors such as more sampling in some regional localities and geologic periods, lithofacies changes, or latitudinal effects. The Gondwanan peak in the Hirnantian could simply be the result of the fact a large portion of the section data is sampled from that time. The preferential sampling could be due to either better conditions for fossil preservation or the focus of researchers on this time period in particular. Additionally, the extensive variation on a regional level suggest that individual regional tectonic and oceanic events have more significant of an impact regionally then global environmental events.
Figure 8: Regional Biodiversity Analysis comparisons. Calculated from CONOP9 interval free diversity curve produced from total FADs minus LADs.
The data from Baltica, Gondwana and Laurentia were put all together in a single data set to construct a global composite. Due to some of the previously mentioned problems with unconstrained taxa, some blocks of index taxa for the individual regions sank or floated within the composite especially within the Gondwana data. Interestingly, these regional index taxa maintained a correct sequence relative to each other, but the zones that they define did not correlate well with other regional zones. Adjusting for these exceptions a global chitinozoan biodiversity curve was produced (Figure 9). The integrated composite has several distinguished features. The curve has several peaks of biodiversity occurring in the Sandbian, Katian, and Hirnian stages and shows a plateau of biodiversity throughout the Darriwilian.

Discussion

The biodiversity curves for each individual region were compared to existing published biodiversity curves (Figure 10). The published biodiversity curves were created using a measure similar to normalized biodiversity called balanced total diversity (BTD). The relative peaks and lows of the Baltic and Laurentia biodiversity matched those found in the published literature (Paris et al. 2004). However, the Gondwana curve did not match the published curved and is missing a peak of biodiversity during the Sandbian that is present in the published curve. This could be the result of a bias created as a result of more data, especially recently, being present for the upper and middle Ordovician particularly the Hirnian e.g. Achab et al. 2011, Abuhmida, F. 2013, Ghavidel-Syooki, M. et. al. 2011, Le Herisse et. al. 2013. However, the other two CONOP9 produced
curves Baltica and Laurentia matched the published curves produced using the more
conventional interval based method of balanced total diversity.

The integrated global composite biodiversity curve was also compared to a
published global balanced total biodiversity curve and was missing a middle Ordovician
peak in the Darwillian, but had the published subsequent later peaks in the upper
Ordovician (Figure 10). The missing peak that is present in the published curve, but not
in the CONOP9 produced curve is likely the result of the missing peak in the Gondwana
biodiversity curve carrying over into the integrated composite or possibly the prevalence
and dominance of the Baltic and Laurentia data during this time. The heavy amount of
Hirnantian data in Gondwana could have inflated biodiversity in the composite causing
eye peaks to no longer appear. Additionally, most of the Baltic and Laurentian data
occurs in the early and middle Ordovician can could also reduce or obscure the peak in
the middle Ordovician.
Figure 9: Global Biodiversity Pattern comparisons to sea level and carbon isotope excursion curves. The black line is a CONOP9 interval free diversity curve produced from total FADs minus LADs.
Correlation to Sea level and Carbon Stable Isotopic Excursions:

Several environmental factors are correlated strongly with chitinozoan biodiversity on Earth (Achab and Paris 2007). One of the main environmental variables is sea level regression and transgression cycles. Periods of regression result in the erosion of continental shelf removing habitat for marine life including chitinozoans and generally reducing the chance of fossilization. Periods of transgression have the opposite effect. These periods of high sea level provide more habitat for marine life to exist within and would likely result in a spike in biodiversity (Achab and Paris 2007). The results of the integrated composite curve were compared to an existing Ordovician sea level curve with several noticeable features (Figure 9). Many of the highs of sea level occur with highs in biodiversity and many of the lows in sea level occur with lows in biodiversity.

Another environmental variable to compare to the global biodiversity curve is changes in the global carbon cycle as expressed by carbon stable isotopic excursions in rocks and/or organic matter. Even though their exact cause and origin is unclear these changes likely represent significant global environmental events. Photosynthesis in plants favors $^{12}$C sequestration over $^{13}$C in organic matter due to the reduced amount of energy needed in the reaction (Kump and Arthur, 1999).
Figure 10: Normalized diversity curves for the Ordovician chitinozoans from Laurentia, Baltica and northern Gondwana regions, and global curve. The dashed lines represent the available samples per time-slice. (Paris et al. 2004)
The favoring of $^{12}$C over $^{13}$C results in oceanic environments depleted of $^{12}$C. In contrast, organic-rich sediments deposited at the bottom of the ocean contain elevated levels of $^{12}$C due to its concentration in photosynthetic processes and typically this organic material remains isolated and does not quickly return to the environment. However, some periods have uncharacteristically high levels of $^{13}$C in rocks suggesting a spike in plankton productivity, sea level changes or shelf erosion in order to account for the lack of deposited $^{12}$C (Young et al. 2005).

Notable carbon isotopic excursions are the Middle Darriwilian Carbon Isotopic Excursion (MDICE), the Guttenburg Carbon Isotopic Excursion (GICE), and the Hirnantian Carbon Isotopic Excursion (HICE) (see Figure 9). When these major carbon cycling events are compared to the global biodiversity curve several interesting features appear. There is a plateau of global biodiversity that coincides with the MDICE. Additionally, the GICE and HICE appear to co-occur with drops in global chitinozoan biodiversity. Carbon isotopic excursions, even though their exact nature is unknown, reflect significant changes in the marine environments on Earth and the co-occurrence of these events with drops in chitinozoan biodiversity suggest they may have negatively impacted the species.

**Conclusion**

This study’s goal was to examine the biodiversity of chitinozoans on both a regional and global level, using the CONOP9 interval-free approach to avoid biases and
error within traditional biodiversity calculations. The Ordovician Period, due to its strong climatic changes and periods of high biodiversity makes it an excellent deep time analog to modern day climate change. In my analysis of global biodiversity using CONOP9 I found biodiversity increased up to the Katian, decreased slightly and rose again within the Katian, decreased approaching the Hirnantian, increased after the HICE and then decreased towards the end of the Ordovician.

Global biodiversity also appears to have some correlation with sea level and carbon cyclicity. Lows and highs in sea level appear to co-occur with lows and highs in biodiversity respectively, and each of the Carbon Isotopic excursions appear to co-occur with plateaus and/or decreases in global chitinozoan biodiversity. The correlation of these events suggest the idea that marine life is affected by these geologic cycles. This study can help to understand the impact of continuous geologic cycles and climate on the biodiversity of marine life on Earth.
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(Appendix II) Laurentian Data Set CONOP9 Files

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