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## Palaeoecological Analysis of the Decline in Stromatolite Abundance during the Ordovician Period

Noran Mhm El-Sherif  
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PALAEOECOLOGICAL ANALYSIS OF THE DECLINE  
IN STROMATOLITE ABUNDANCE DURING  
THE ORDOVICIAN PERIOD

A thesis submitted in partial fulfillment of the  
requirements for the degree of  
Master of Science

By

NORAN MHM EL-SHERIF

B.S., Ain Shams University, 1998

2013

Wright State University

WRIGHT STATE UNIVERSITY

GRADUATE SCHOOL

May 20, 2013

I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY Noran MHM El-Sherif ENTITLED Palaeoecological Analysis of the Decline in Stromatolite Abundance During the Ordovician Period BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science.

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## ABSTRACT

El-Sherif, Noran MHM. M.S. Department of Earth and Environmental Sciences, Wright State University, 2013. Palaeoecological Analysis of the Decline in Stromatolite Abundance During the Ordovician Period.

A stromatolite is a laminated benthic microbial deposit. Its uniqueness arises from being present since the Precambrian to the present. Stromatolites recorded a peak time during the Mesoproterozoic, subsequently they witnessed abrupt rises and falls in abundance with the steepest decline in the Ordovician period, from which it never recovered from. There is no consensus yet regarding the reasons behind the decline of stromatolites. Thus the decline of these microbial deposits remains an enigma. Additionally, a literature gap exists regarding the reasons that specifically led to the Ordovician decline. Accordingly, the focus of this literature-based MSc. thesis is to find the reasons that led to the stromatolites decline in the Ordovician – using abiotic and biotic palaeoecological tools – an approach that has not been implemented before in the study of stromatolites. The conclusions are that abiotic factors such as calcium carbonate ocean saturation were likely responsible for much of the decline. However, present-day distributions in harsh environments and negative relationships between stromatolites and metazoan radiations indicate a role for biotic factors.

## TABLE OF CONTENTS

CHAPTER I: STROMATOLITE BACKGROUND .....	1
CHAPTER II: CARBONATES AND SUPERCONTINENT CYCLE BRIEFINGS .....	10
CHAPTER III: MESOPROTEROZOIC & ORDOVICAN PALAEOECOLOGY .....	16
CHAPTER IV: DISCUSSION .....	32
CHAPTER V: CONCLUSION .....	37
CHAPTER VI: REFERENCES .....	44

## LIST OF FIGURES

1. Stromatolite diversity and abundance versus CO <sub>2</sub> variation .....	4
2. Glacio-epochs and supercontinent assembly and break up .....	15
3. Rodinia's assembly during the Mesoproterozoic .....	19
4. Arrangement of supercontinents and continents throughout the Phanerozoic .....	20
5. Mountain building throughout the Phanerozoic .....	21
6. Stromatolite diversity .....	34
7. Carbon excursion .....	40
8. Sea level change .....	40
9. Phanerozoic shelves .....	42

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## **DEDICATION**

My dear parents, you will always be after every successful step I take in my life

# **PALAEOECOLOGICAL ANALYSIS OF THE DECLINE IN STROMATOLITE ABUNDANCE DURING THE ORDOVICIAN PERIOD**

## **CHAPTER I: STROMATOLITE BACKGROUND**

A stromatolite is a laminated benthic microbial deposit (Kalkowsky 1908; Riding 1991a). The organisms that create these structures and their general form have persisted relatively unchanged for over a billion years; creating a long and persistent record of the sedimentary structures. Stromatolites abundance peaked time during the Mesoproterozoic (from 1600 to 1000 Ma<sup>1</sup>), after which they incurred abrupt rises and falls, with the steepest decline in the Ordovician Period (from 495 to 443 Ma), from which it never recovered. A number of researchers have hypothesized the reasons behind the decline of stromatolites (e.g. Riding, 2011; Mata and Bottjer, 2012), but a consensus has not yet been reached. Thus, the decline of these structures remains an enigma to be solved. Additionally, a literature gap exists regarding the reasons that specifically led to the Ordovician decline. Accordingly, the focus of this literature-based MSc. thesis is to examine the reasons that led to the decline of stromatolites' in the Ordovician – through evaluation of the abiotic and biotic paleoecological conditions (e.g. oceanography and community ecology) of that time – an approach that has not been previously implemented in the study of stromatolites.

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<sup>1</sup> Ma (megaannum) is a unit of time equal to one million years.

The term *stromatolite* was coined by Kalkowsky in 1908, yet to the present day there has been no widely accepted definition of what exactly constitutes a stromatolite (and what does not) due to stromatolites having varied characteristics such as both biogenic and abiogenic origins. Stromatolites are layered, mineral structures formed mainly in shallow water by microbial biofilms. These biofilms trap sedimentary materials and bind them together, producing layers that gradually accrete, forming a diversity of three-dimensional structures.

In addition to microbial grain trapping and binding, stromatolites can also be formed by microbial precipitation, and inorganic precipitation (McNamara and Awramik, 1992) of minerals such as carbonates.

The microbial communities that form stromatolites are dominantly composed of photosynthetic cyanobacteria, together with small eukaryotic algae (including brown, green and red algae) (Golubic 1976; Riding, 1991c). The sedimentary layers are composed of fine silt (7.8  $\mu\text{m}$ ) or clay-size (0.06 - 2.0  $\mu\text{m}$ ) sediment or, more rarely, sand-size (62.5  $\mu\text{m}$  - 1.68 mm) sediment (Boggs 2006; Riding, 2012).

Stromatolitic bedding ranges from nearly flat laminations to hemispherical forms in which the laminae are crinkled or deformed. Laminations are generally less than 1 mm thick and are caused by concentrations of fine calcium carbonate minerals, fine organic matter, and detrital clay and silt. Stromatolites composed of quartz grains have also been reported (Davis, 1968). The lamination structure forms because fine sediment is trapped in the very tiny filaments of microbial mats, which are relatively cohesive, active benthic surfaces upon which

microorganisms, metabolize, grow, and reproduce (Awramik et al., 1976). Once a thin layer of sediment covers the mat, the microbial filaments grow up and around sediment grains to form a new mat that traps another thin layer of sediment. This successive growth of mats produces the laminated structure. The shapes of the hemispheres are due to water energy and scouring effects in the depositional environment.

Currently, stromatolites form mainly in the shallow subtidal, intertidal, and supratidal zones of the oceans, and have been noted in lacustrine environments. Because cyanobacteria carry out photosynthesis, stromatolites are restricted to water depths and environments where there is enough light for photosynthesis. Furthermore, stromatolite-forming microbial mats are usually found in extreme environments characterized by hypersaline conditions, increased alkalinity, low nutrient levels, and high or low temperature habitats. It has been assumed that this restriction to harsh environments is to avoid grazers and/or competitors (e.g., Fisher 1965; Schubert & Bottjer, 1992). Most ancient stromatolite fossils occur in limestones (carbonate sediments); however, stromatolites have also been reported in siliciclastic sediments (Riding, 2011).

Stromatolites are considered the only record of life that were widespread and abundant in the Mesoproterozoic. Since this apex, stromatolites have declined throughout the remaining part of Earth's history with episodes of short-lived revival such as during the Cambrian (Zhuravlev, 1996) that do not match their prime time. Fisher (1965) determined that their steepest decline commenced in the Ordovician. Yet they never fully disappeared and have been able to survive to the modern world. Stromatolites currently inhabit environmentally severe regions such as Shark Bay in Western Australia, which hosts the most studied modern examples (Riding, 2000).

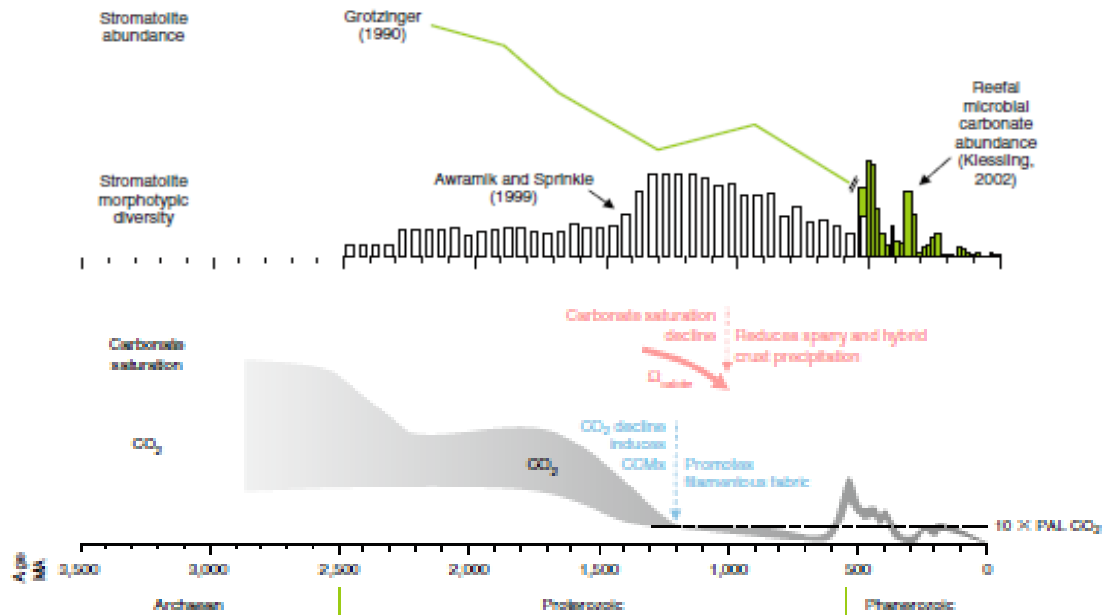


FIG 1: Stromatolite Diversity and Abundance versus CO<sub>2</sub> variation, after Riding, 2011.

Throughout their evolutionary history (Fig. 1), stromatolites have undergone dramatic changes in terms of their microfabric (e.g., microbial species and sediment type), macrofabric (e.g. lamination quality) and external shape (e.g. branched and columnar forms); all of which could easily be traced to their ever-changing ecology. Both the changing character and abundance of stromatolites has been linked to various factors, including: (1) paleobiology/geobiology: eukaryote grazing and habitat competition; (2) oceanography – e.g. variations in sea water chemistry, particularly carbonate minerals supersaturation (Riding, 1991b), as well as tidal effects; (3) atmosphere – e.g., temperature and oxygen levels (Riding, 2000); (4)

biogeochemistry – e.g., dissolved phosphate levels (Merz-Preiß, 2000); and (5) sedimentology – e.g. periods of unusual abundance of ooids and marine cements (Riding, 2000).

The first factor, eukaryotic grazing and habitat competition, has received much emphasis due to the apparent inverse relationship between stromatolite abundance and the rise in dominance of eukaryotes. It has been argued that the first and sharpest decline of stromatolites during the Late Proterozoic was related to the metazoan radiation (Awramik, 1971). It has also been noted that during the Phanerozoic, the brief reductions of metazoan life as an aftermath of mass extinctions prompted a short-lived prosperity among stromatolites (Schubert & Bottjer, 1992). Fossils from this burst of diversity have been nicknamed as “disaster forms.” Shortly after the mass extinction, metazoan life gradually prospered and stromatolites declined. Yet, Riding (1997) advocated that such mass extinction events were accompanied by increases in temperature and seawater carbonate mineral saturation, which favor microbial carbonate formation, irrespective of interactions with eukaryotic organisms.

Riding (2000) concluded that both these arguments (eukaryotic grazing and competition, and seawater carbonate saturation) could be applied to the biotically stressful environments that stromatolites currently inhabit such as in Shark Bay (Western Australia) and Lee Stocking Island (The Bahamas). These environments are noted for their hypersaline lagoons, desiccated tidal flats, and highly mobile sediments, which are conditions that discourage eukaryote competition (Awramik, 1971). Concurrently, these same environments are characterized by enhancing carbonate precipitation through sweeping waves, cementation promoted by currents and desiccated intertidal flats, all of which favor rapid lithification of stromatolites (Riding, 1997).

Since stromatolites are framebuilders, Grotzinger (1989) considered them as legitimate components of reefs, but with increasing reefal biodiversity over time they became subsumed within such complex reef structures (Riding, 2011). Thus, in Fig. 1, it is legitimate to compare the available Grotzinger (1990) and Awramik & Sprinkle (1999) stromatolite graphs with Kiessling (2002) reefal “microbial” carbonates graph.

### **Ordovician Life, Tectonics and Climate**

The Ordovician Period is the second period in the Paleozoic Era. It was preceded by the Cambrian Period and succeeded by the Silurian Period. It is radioisotopically dated from 495Ma to 443Ma (Fortey, 2005). The Ordovician Period was marked by a major marine diversification known as the Great Ordovician Biodiversification Event (GOBE). Organisms that appeared during the Cambrian (e.g., bivalve mollusks and gastropods) became much more diverse and widespread, while other organisms appeared and diversified for the first time (e.g., corals and bryozoans). There was an increase in the complexity of trace fossils and bioturbation through the period, with younger Ordovician organisms burrowing deeper in the sediment (Fortey, 2005). Could these sources of bioerosion have resulted in disturbance of stromatolite structures, eventually leading to their decline?

Geography changed continually during the Ordovician, due to mountain-building and volcanic events, and waning oceans (Fortey, 2005). Until the Middle Ordovician there was an overall transgression; in fact, sea levels during this time were the highest with respect to the entire Palaeozoic Era (Haq and Schutter, 2008). Much of the Ordovician had generally warm conditions (e.g., Frakes et al., 1992) that lasted until the Late Ordovician.

The Gondwana continent, (which was the largest continent at the time and comprised Africa, South Europe, South America, the Indian and Arabian Peninsulas, Antarctica, and Australia) drifted towards the South Pole throughout the period. By the Late Ordovician, Gondwana had gradually undergone extensive glaciation, the effects of which extended well beyond the continent. Oceanic water became tied up in the icesheet, resulting in a general marine regression. Climatic cooling forced the tropical carbonate belt to become extremely restricted, which affected the many organisms adapted to warm, carbonate-rich environments. Much of this biota either died out like stromatolites pushed into small refugia (Fortey, 2005).

Overall, the Ordovician–Silurian extinction event drove about 85% of marine species to disappearance (Munnecke et al., 2010 after Sheehan, 2001). It is worthy to note that Riding (2005) deduced that despite the reduction in metazoan diversity in the aftermath of the Ordovician–Silurian mass extinction, stromatolites did not increase. His reasoning was that due to low global temperatures, seawater carbonate saturation was too low to promote the formation of stromatolites.

## **OBJECTIVES AND SIGNIFICANCE**

As noted above there exist a number of studies examining the decline of stromatolites throughout the geological record. Yet, so far, only a handful of papers have discussed stromatolites in the Ordovician Period, and none have discussed explicitly the decline of the stromatolites in the Ordovician. Thus the ultimate aim of this research is to explore the question: why stromatolites declined in the Ordovician?



To answer this question, one would need to understand the ecological conditions and changes during the Ordovician. Additionally, in order to highlight the palaeoecology of the Ordovician, it is contrasted with the opposing picture during the Mesoproterozoic time, when the abundance of stromatolites was at its peak.

## **METHODS**

This literature-based research is focused on a review of stromatolites, their abundance and ecology during the Ordovician Period, and the reasons for their decline using ecological tools through the following goals:

- I. **Review and summarize existing literature on stromatolites** particularly during the Ordovician. This mainly covers the following topics:
  - a. formation, structure and habitat conditions (e.g. nutritional resources and tidal energy),
  - b. variability in abundance through geologic history, and
  - c. evaluation of why stromatolites declined precipitously during the Ordovician Period.
  
- II. **Conduct a thorough characterization of the global paleoecology** of the Mesoproterozoic (highest peak) and the Ordovician (steepest decline).

One must note that the ecological information regarding the Mesoproterozoic time – when stromatolites' abundance was at its peak – is comparatively limited with respect

to that of the Ordovician time. Accordingly, when needed this study will take a wider picture and consider the Precambrian supereon as a whole instead (which includes the Mesoproterozoic era).

### **III. Determine the effect of Ordovician paleoecology on stromatolites**

Synthesize and consequently analyze conclusions from the previous two steps to develop an informed scenario and hypotheses concerning the conditions that led to the decline of stromatolites in the Ordovician in comparison to the conditions that led to the stromatolites' peak in the Mesoproterozoic.

For example, this research will examine how preservation potential was influenced by the changed habitat conditions that occurred during the two contrasting periods. Were microbial communities able to proliferate during the Ordovician, but surrounding conditions did not favor lithification and thus preservation, or did microbial community abundance decline during the Ordovician and led to a scarcity of lithified – and thus preserved – stromatolites?

## **CHAPTER II: CARBONATES AND SUPERCONTINENT CYCLE BRIEFING**

### **BRIEFING1: CARBON AND THE CARBONATES CYCLE**

As mentioned earlier, this research will focus on carbonate-formed stromatolites. Thus in order to understand the significant role that carbonates play in stromatolites' sustainment and ultimately preservation, it is imperative to have a good understanding of the sources of carbonates and the factors that oscillate such sources.

Carbonates ( $\text{CaCO}_3$ ) are mainly composed of the elements calcium, carbon and oxygen. The main player in carbonate formation is carbon, whose long-term cycle will be the focus of this briefing. The calcium and oxygen cycles will be covered implicitly within this briefing, or explicitly throughout the following chapters when necessary.

Calcium ions are naturally abundant in sea-water and are one of the highest concentrations of all ionic species in the ocean (Ridgwella, 2005).

The short-term cycle of carbon ranges from days to tens of thousands of years (Berner, 2004), while the thesis topic will be reliant on a longer-span geological time scale. The long-term carbon cycle is affected and affects many critical paleoecological forces as discussed below.

It must be noted that the long-term carbon cycle encompasses various aspects of the short-term carbon cycle but adds to it the transition of carbon from and to rocks over a span of millions of years that may influence atmospheric  $\text{CO}_2$  (Berner, 2004). Such a long-term effect on atmospheric  $\text{CO}_2$  may drastically affect the climate such as changing Earth's global climate from

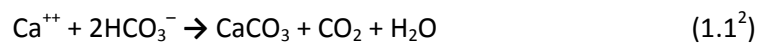
a greenhouse to an icehouse environment (or vice versa) that could prompt a mass extinction event.

According to Berner, 2004 the long-term carbon cycle is divided into two subcycles, as follows:

#### Silicate-carbonate subcycle

Atmospheric CO<sub>2</sub> is captured by land either through rain or plant photosynthesis<sup>2</sup>. The carbonic acid within the rain will react with the minerals of both exposed and subsurface rocks (especially calcium- and magnesium-containing silicate minerals<sup>3</sup>) to produce calcium and bicarbonate ions. These ions are carried by rivers to the sea and are precipitated, mostly biogenically – particularly – in the Phanerozoic) as calcium carbonates, and are subsequently buried in marine sediments.

These reactions are summarized as follows:



To complete the cycle, CO<sub>2</sub> is restored to the atmosphere and oceans through degassing via volcanism, metamorphism, and diagenesis.

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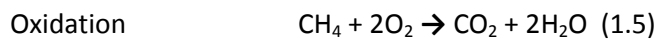
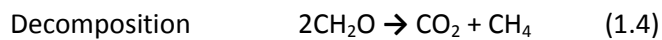
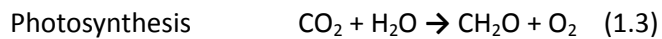
<sup>2</sup> Plants flourished in the Devonian period which occurred after the Ordovician, thus the effect of plants on the long-term cycle of carbon is irrelevant with respect to the thesis topic.

<sup>3</sup> Rocks containing carbonate minerals weather in a time span less than a million year span, thus does not have a long-term net effect on atmospheric CO<sub>2</sub>.

<sup>4</sup> Ebelmen-Urey reaction

#### A- Organic subcycle

After the death of organisms (especially photosynthetic organisms), their organic material maybe incorporated into sediments that may lithify into sedimentary rocks. Upon the decomposition of these organic-containing rocks  $\text{CH}_4$  (methane) is released, which once oxidated will convert to  $\text{CO}_2$  (carbon dioxide), as summarized below.



Such processes directly affect the carbon and  $\text{CO}_2$  global budgets.

#### **BRIEFING2: THE SUPERCONTINENT CYCLE AND ITS OROGENIES**

The assembly of supercontinents results in the peripheral subduction of large volumes of oceanic lithosphere that moves down into the deep mantle, affecting the mantle flow fields (Tackley, 2012). It is speculated that such a process generates upwelling superplumes beneath the supercontinent, which eventually contributes to its breakup and voluminous volcanism and thus a flux of  $\text{CO}_2$  drastically affecting the global climate. Anderson (1982), on the other hand observed that since continental lithosphere is both thick and has a radioisotope-enriched crust, it should act as a thermal insulator to mantle heat flow. Worsley et al. (1984) further argued that supercontinents would become epeirogenically uplifted as heat accumulates beneath the

largely stationary supercontinent, ultimately manifesting as hotspot activity contributing to fragmentation. Both opinions are considered valid and could work simultaneously. Overall, whether assembly or fragmentation, such processes may have catastrophic effects caused by changes in global climate; including the extinction of many types of organisms.

### ASSEMBLY

When continents assemble into large land masses, promoted by double-sided oceanic lithosphere subduction, introversion (closure of interior oceans formed by the previous supercontinent breakup), and extroversion (closure of the exterior ocean), may occur. The newly-formed supercontinent is epeirogenically uplifted as heat accumulates beneath it, which lowers the sea level. Concomitantly, collisional orogenesis are formed. Enhanced weathering and erosional rates occur because of the formation of these mountain belts as well as the overall increased large areas of subaerially exposed continental crust (increased surface area). The weathering process would consume more CO<sub>2</sub> from the atmosphere, which is eventually transferred by erosion through riverine inputs into the oceans. With sea level at its lowest elevation, the production and preservation of terrestrial deposits should be enhanced while that of marine sediments is diminished. As a result, the sequestering of isotopically light carbon in non-marine and organic-rich sediments could be expected to produce a record of low  $\delta^{13}\text{C}$  in the reciprocal marine platform reservoir. The enhanced CO<sub>2</sub> sequestration also leads to cooler climates. This, along with the increased albedo caused by the high land/ocean ratio, would ultimately result in widespread glaciation and at times possibly “Snowball Earth” conditions.

Increased weathering and erosion, including glacial erosion (Follmi, 1995), would also lead to the release of an enormous flux of nutrients into the oceans and more intense ocean circulation, and thus nutrient upwelling and eventually marine productivity and phosphate deposition. This raises O<sub>2</sub> production through enhanced photosynthesis which eventually triggers an explosion of marine life. On the other hand, massive extinctions would be expected to accompany the loss of shallow marine habitat, as well as life that cannot be sustained in cold climates.

#### RIFTING

The crustal extension and the opening of new interior, (Murphy and Nance, 2003) ocean basins, coupled with subsidence of the dispersing continental fragments associated with supercontinent breakup should raise sea level to a maximum elevation. Actively-eroding escarpments along new rift margins contribute sediments to the new rift basins, and marine transgressions would increase the rate of burial of organic and carbonate carbon on stable continental shelves increasing the values of  $\delta^{13}\text{C}$ . An increase in length of the ocean ridge system would also promote mantle degassing and release of CO<sub>2</sub> into the atmosphere (Condie, 2001), and as continental drowning develops – i.e. less weathering and erosion – atmospheric CO<sub>2</sub> levels buildup generating warmer climates, such as in the Mesoproterozoic (Fig. 1).

Increased shallow marine regions would highly promote life in this region. Furthermore, Santosh (2010b) speculated that the breakup of supercontinents and the development of hydrothermal systems in rifts enriched in nutrients might have served as the primary building blocks of the skeleton of early modern life forms.

These rift basins restrict oceanic circulation promoting anoxic conditions in the deeper parts of the basins. Additionally, there is also a likely relationship between superplumes, supercontinent breakup and mass extinction. Upwelling plumes that break supercontinents apart generate large igneous provinces that may, in turn, affect climate by producing large-scale volcanism and plume-induced “winters” with catastrophic effects on the atmosphere and life.

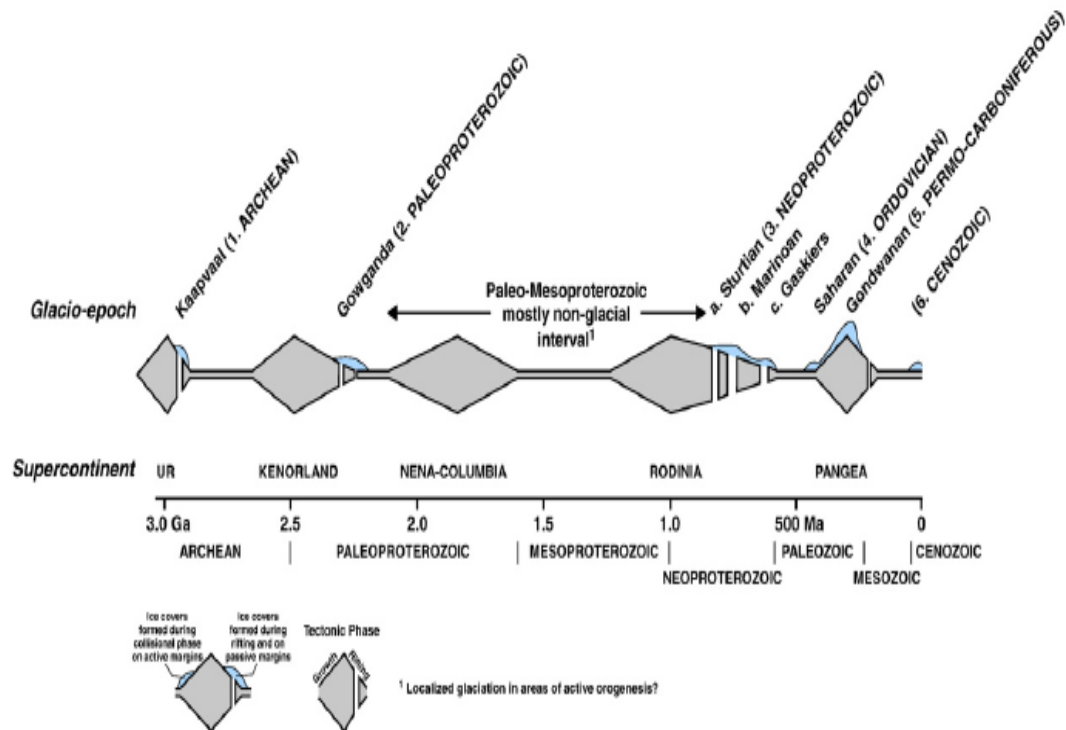


FIG. 2: Glacio-epochs and supercontinent assembly and break up, after Eyles, 2008



### CHAPTER III: MESOPROTEROZOIC & ORDOVICIAN PALAEOECOLOGY

To understand why stromatolites abundance declined from the Ordovician (488 Ma – 444 Ma) onwards, it is necessary to understand the palaeoecology of the Ordovician that led to the decline and concomitantly to compare these ecological conditions to that of the opposite scenario, when stromatolites had reached a peak in both abundance and diversity during the Mesoproterozoic Era (1.6 Ga – 1 Ga).

Below is a summary of the major abiotic (lithosphere, atmosphere, hydrosphere, cryosphere) and biotic (biosphere) factors during both the Mesoproterozoic and Ordovician; each followed by an analysis of how such factors affected and maybe were affected by stromatolites (including its constituents).

#### ABIOTIC FACORS – Lithosphere

PRECAMBRIAN	
Archean (4 Ga – 2.5 Ga) & Paleoproterozoic (2.5 Ga – 1.6 Ga)	The early Earth's ocean was at first dominated by island arcs, but through arc-arc collision and accretion, continental crust was assembled into large land masses (Santosh, 2010), later forming almost episodic supercontinents. The supercontinents formed during the Archean were Ur (3.0 Ga) and

	<p>Kenorland (2.5 Ga); the latter fragmented in the early Paleoproterozoic (Condie, 2002; Eyles, 2007 after Rogers and Santosh, 2004).</p> <p>The supercontinent Columbia (or Nuna) supercontinent was assembled 2.1-1.8 Ga.</p>
<p>Mesoproterozoic (1.6 Ga – 1.0 Ga)</p>	<p>The fragmentation of supercontinent Columbia (or Nuna) began about 1.6 Ga ago and continued until about 1.3-1.2 Ga, only to be reassembled again into Meso- to Neoproterozoic Rodinia largely between 1.1-1.0 Ga through the Grenvillian Orogeny collisional events (Rogers and Santosh, 2002; Zhao et al., 2004; Condie, 2002; Zhao et al., 2000 after Dalziel et al., 2000).</p> <p>Rodinia was probably spread from the equator to the polar region at ca. 800 Ma, followed by a rapid ca. 90 degrees rotation that brought the entire supercontinent to a low-latitude position by ca. 750 Ma (Li et al., 2004).</p>
<p>Neoproterozoic (1.0 Ga – 540 Ma)</p>	<p>This era was marked by the continental dispersal of Rodinia (from 750-610 Ma) (Eyles and Januszcak, 2004) and its reorganization into the megacontinent Gondwana during the same period. (Hoffman, 1999).</p>
<p><b>PHANEROZOIC</b></p>	<p><b>With reference to Fig. 4 it appears that the Phanerozoic lithosphere involved lots of mountain building episodes (of varying degrees) and thus less flat land episodes discouraging epeiric seas development.</b></p> <p><b>Mountainous episodes also infer ice ages which would in turn imply a sea level drop. The longest flat land time and thus non-glacial time was in the Cambrian followed by the Triassic and Jurassic. This ties in with the</b></p>

	<b>Phanerozoic sea level in Fig. 5. These flat land, non-glacial, and high sea level times are times that microbial carbonates had flourished in.</b>
Cambrian (540 – 490 Ma)	<p>Gondwana was accreted 600 – 500 Ma and later merged with other continents in 320 Ma to form Pangaea, until breakup between 180 Ma and 100 Ma (Fig. 3) (Veevers, 2005).</p> <p>During the Cambrian, most continents were in tropical latitudes, although the megacontinent of Gondwana extended south to the polar regions (Osborne and Tarling, 1996).</p>
Ordovician (490 – 445 Ma)	<p>During the Early to Middle Ordovician the first major Northern Appalachians orogenic event occurred, coined as the Taconic Orogeny (Staal, 2005).</p> <p>By the Late Ordovician, megacontinent Gondwana had moved towards the South Pole, (e.g. Mata and Bottjer, 2012) and continents Baltica and Siberia started to move northward (Fig. 4) (Herrmann et al., 2004; Veevers, 2005).</p>
Post-Ordovician (445 – Present Ma)	<p>Veevers (2005) states that Pangea was formed in the Carboniferous (320 Ma) and broke apart during the interval between the Jurassic and Cretaceous periods (180 – 100 Ma).</p>

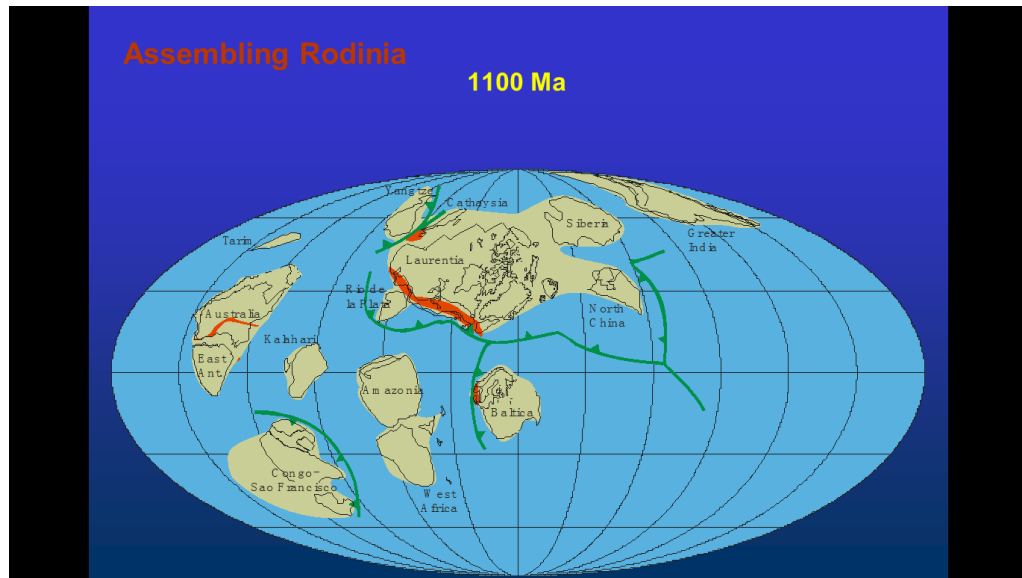


FIG. 3 Rodinia's assembly during the Mesoproterozoic

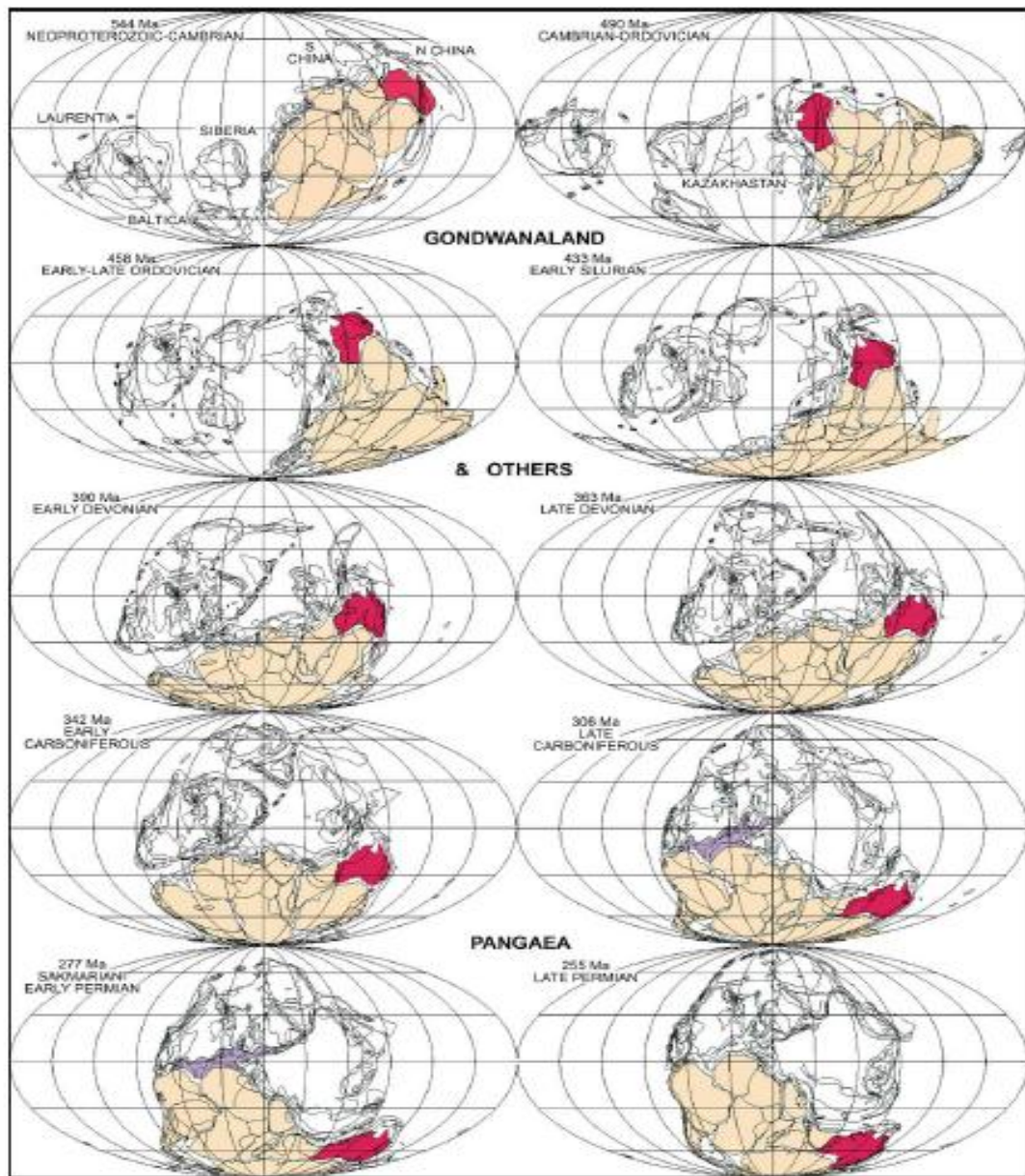


FIG. 4 Arrangement of supercontinents and continents throughout the Phanerozoic

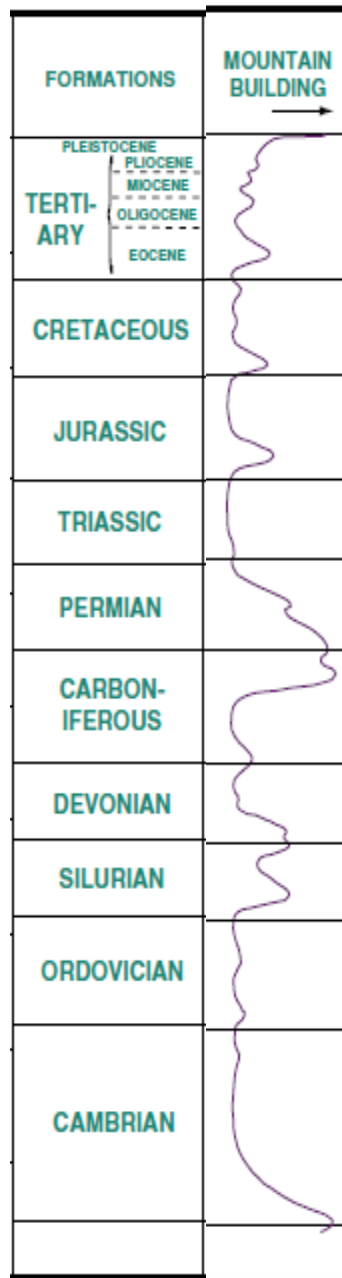


FIG. 5 Mountain building throughout the Phanerozoic

## ABIOTIC FACORS – Atmosphere, Cryosphere and Hydrosphere

PRECAMBRIAN	
<p>Archean (4 Ga – 2.5 Ga) &amp; Paleoproterozoic (2.5 Ga – 1.6 Ga)</p>	<p>After the primordial steam atmosphere had rained out to form an ocean, it is prevailingly viewed that to compensate for the reduced solar luminosity (the young sun paradox) – which would have left the Earth in a global glaciation with no “liquid” water – greenhouse gasses would have dominated the atmosphere particularly CO<sub>2</sub> and water vapor, and also H<sub>2</sub> and N<sub>2</sub> (e.g. Kasting, 1993; Kasting and Siefert, 2002; Shaw, 2008; Kasting, 2013). Later on methane (CH<sub>4</sub>) was introduced by methanogens living in a reduced upper ocean (Kopp et al., 2005 after Pavlov et al., 2000), through the synthesis of CO<sub>2</sub> and H<sub>2</sub>, outweighing the CO<sub>2</sub> abundance temporarily (Kaufman and Xiao, 2003). Ammonia (NH<sub>4</sub>) was also abundantly produced biologically (Kasting, 1993). So far, the Archean’s atmosphere remained anoxic, whereby only anaerobic life could survive.</p> <p>The appearance of “photoautotrophic” cyanobacteria in the Archean (ca. 3.7 – 2.8 Ga) and their ability through time to generate excess oxygen to oxidize the methane-rich atmosphere, transforming it to CO<sub>2</sub> (a less effective greenhouse gas) – a phenomena famously known as the Great Oxygenation Event (GOE), as well as the Oxygen Catastrophe, Oxygen Crisis or Great Oxidation. Kasting (1993) contends that it occurred around 2.0 Ga,</p>

	<p>while Holland (2006) expands it to 2.45 – 1.85 Ga. Surface ocean waters became oxidized and productive, while the methanogens escaped the poisonous effects of oxygen to the still anoxic deep ocean (Arnold, 2004) which was also oxygenated later in the Neoproterozoic (Eriksson, 2012). To summarize, Sheldon (2006) notes that the atmospheric CO<sub>2</sub> was “fairly constant and elevated” during the Paleoproterozoic (2.5 to 1.8 Ga ago), and Holland (2006) notes that the photosynthetic oxygen pump led to a drastic reduction in the concentration of CO<sub>2</sub>.</p> <p>The overthrow of the hot greenhouse atmosphere rich in CH<sub>4</sub> and CO<sub>2</sub> into a cooler rich O<sub>2</sub> atmosphere triggered off a planetary-scale glaciation (snowball Earth), in the Paleoproterozoic era (e.g. Kasting and Siefert, 2002; Kopp et al., 2005).</p> <p>Finally, the Archean and Paleoproterozoic oceans were likely greatly oversaturated with respect to calcium carbonate (calcite and aragonite), which would have facilitated the precipitation of large reefs even without biological participation (Kopp et al., 2005). The ocean saturation then took on a decline mode throughout the rest of the Proterozoic and the Phanerozoic (Grotzinger, 1989).</p>
<p>Mesoproterozoic (1.6 Ga – 1.0 Ga)</p>	<p>The Mesoproterozoic Era was unique among the other Proterozoic Eras in being a nonglacial period and thus lacking any snowball events (Hoffman and Schrag, 2002). A sharp decline in atmospheric CO<sub>2</sub> was recorded (Fig. 1;</p>



	Sheldon, 2006; Kah and Riding, 2007). Atmospheric oxygen levels were almost stable; surface oceans were mildly oxygenated; while deep oceans remained anoxic or were mildly oxygenated (Holland, 2006; Arnold et al., 2004). Holland (2006) contends that the period 1.85 to 0.85 Ga as the the 'boring billion.'
Neoproterozoic (1.0 Ga – 540 Ma)	With most of Rodinia's extensive land area at the equator both atmospheric CO <sub>2</sub> drawdown and global albedo increased, which, along with waning plume volcanism led to low-latitude glaciation (Li et al., 2004). Holland (2006) mentions that perhaps the largest three ice ages visited the Earth (after Hoffman & Schrag 2002; Hoffman in press) during this Era. Such snowball events have been related by other workers to the second major increase in photosynthetic oxygen coined as the Neoproterozoic Oxygenation Event (NOE) (Eriksson et al., 2012; Holland, 2006). The shallow oceans followed the rise in atmospheric oxygen, but the deep oceans remained anoxic, particularly during the intense Neoproterozoic ice ages (Holland, 2006). Kasting (1993) suggests that the decline of CO <sub>2</sub> and other greenhouse gases counterbalanced the effect of the brightening sun. Canfield et al. (2007) propose that during the Late-Neoproterozoic after (580 Ma) deep-ocean oxygenation was initiated.
<b>PHANEROZOIC</b>	<b>Atmospheric oxygen levels in the Phanerozoic were significantly higher than that of the Precambrian, reaching maximum value during the</b>

	<p><b>Carboniferous (359 - 299 Ma) before returning to its present value (Holland, 2006). The shallow oceans were probably oxygenated throughout the Phanerozoic, while the deep oceans fluctuated widely, perhaps on rather geologically short time-scales (Holland, 2006).</b></p> <p><b>With reference to Fig. 1, it can be inferred from the CO<sub>2</sub> decline that the Phanerozoic was overall cooler than that of the Phanerozoic climate.</b></p> <p><b>Fig. 1, a CO<sub>2</sub> drop was recorded from the period ca. 400 - 300 Ma, representing almost all of the Devonian and the entire Carboniferous periods - two periods are characterized by an explosion of botanical life.</b></p>
Cambrian (540 – 490 Ma)	<p>The late Proterozoic to Cambrian interval witnessed the change from a saturated 'aragonite sea' to a 'calcite sea', corresponding to a change from 'icehouse' to 'greenhouse' climatic conditions.</p> <p>Hughes and Heim (2005) suggest that the rapid seafloor spreading associated with the breakup of Pannotia caused a global sea-level rise, and increased global volcanism. Their reasoning is based on the absence of evidence of persistent glaciation. Additionally, it can be inferred that the increased global volcanism would entail a substantial increase in atmospheric CO<sub>2</sub> – a Phanerozoic peak that was never regained since then.</p> <p>By the end of the Cambrian CO<sub>2</sub> started its eventual decline (Fig. 1).</p> <p>In the late Cambrian the Sauk Transgression – a shallow sea – covered large continental areas. Consequently, most Cambrian formations contain</p>

	significant amounts of carbonate rock (Osborne and Tarling, 1996).
Ordovician (490 – 445 Ma)	<p>Munnecke et al. (2010) state that driven by an extended greenhouse climate from the Cambrian, extensive, epicontinental seas developed in this period (after Algeo and Sessler, 1995; Pratt and Holmden, 2008). Sea levels were possibly the highest of the entire Phanerozoic Eon (after Hallam, 1992; Miller et al., 2005; Haq and Schutter, 2008).</p> <p>The southward drifting of Gondwana assumedly led to the Late Ordovician Gondwana glaciation (Herrmann, 2004).</p> <p>Munnecke et al. (2010) note a decrease in Ordovician temperatures (after Trotter et al., 2008), and that cooler waters may have been more welcoming for marine life (after Trotter et al., 2008). Or that increased calcium carbonate saturation aided the precipitation of the heavier skeletons of the Palaeozoic benthos (after Pruss et al., 2010).</p> <p>With reference to Fig.1 , the CO<sub>2</sub> decline was enhanced by the Gondwana glaciation.</p>
Post-Ordovician (445 – Present Ma)	<p>The climate of the Silurian started cold but soon global temperature switched; as deduced from carbonate build-ups and bioherms indicating warmer waters (Cocks, 2005).</p> <p>The Devonian rise of large vascular land plants ‘perturbed the long-term carbon cycle’ by accelerating the silicate rocks weathering by their roots, and also removing atmospheric CO<sub>2</sub> via photosynthesis, and producing O<sub>2</sub>,</p>

	<p>aided by the increased burial of organic matter in sediments (Berner, 2004).</p> <p>Atmospheric CO<sub>2</sub> was further depleted (Fig. 1) and O<sub>2</sub> was significantly increased due to a major radiation in vascular land plants particularly seed plants in the Early Carboniferous (Scott, 2005).</p>
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### BIOTIC FACORS – Biosphere

PRECAMBRIAN	
Archean (4 Ga – 2.5 Ga) & Paleoproterozoic (2.5 Ga – 1.6 Ga)	<p>Stromatolites' recorded history begins in the Archean ca. 3.45 Ga, and is considered of biogenic origin (Riding, 2011 after Hofmann et al., 1999; Allwood et al., 2006).</p> <p>Late Palaeoproterozoic and Early Mesoproterozoic rocks provide evidence for a moderate diversity of eukaryotic organisms (Knoll, 2006).</p>
Mesoproterozoic (1.6 Ga – 1.0 Ga)	<p>Stromatolites diversified widely (e.g Grotzinger, 1990) during most of this era, but towards the end they commenced a long-term decline. Eukaryotes diversity increased during the late Mesoproterozoic (Anbar and Knoll, 2002 after Porter and Knoll, 2000).</p>
Neoproterozoic (1.0 Ga – 540 Ma)	<p>Near the Precambrian-Cambrian boundary ca. 575 Ma the Ediacara biota – shallow and littoral marine (Allaby, 2008) soft-bodied metazoa (organisms and colonies) – arose shortly after the last glaciation of the era, suggesting a causal link between their appearance and the NOE that further oxygenated</p>

	<p>the atmosphere and changed the deep ocean to an oxic state (Canfield et al., 2007; Canfield et al., 2007 after Narbonne and Gehling, 2003 and Bowring et al., 2002).</p> <p>The Ediacaran “soft-bodied” life abruptly disappeared concurrent with the Cambrian explosion of “skeletal” life (Canfield et al., 2007 after Narbonne, 2005 and Knoll et al., 2006).</p> <p>Eriksson et al. (2012) notes that the Ediacaran–Cambrian transition was marked by an increase in bioturbation intensity (after Droser and Bottjer, 1988) – a “substrate revolution” (after Bottjer et al., 2000) – that dramatically reduced the thickness and distribution of once ubiquitous microbial facies and mats (after Garrett, 1970; Hagadorn and Bottjer, 1997).</p> <p>McMenamin (2005) states that towards the end of the period, the seafloor mat seal began to break down, perturbing the global carbon budget (e.g., buried carbon was put immediately back into circulation). Simultaneously, a tremendous flux of mineral nutrients went to the oceans resulting from the final breakup of supercontinent Rodinia and formation of megacontinent Gondwana.</p> <p>Stromatolites continued their long-term decline. Concurrently, the burrowing and lamination-disturbing activities led the stromatolites’ concentric lamination to give way to a clotted, thrombolitic texture (McMenamin, 2005).</p>
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	<p>Eriksson et al. (2012) also note that metazoans biomineralization (after Erwin et al., 2011) marked a widespread appearance of skeletonized taxa during this transition, that could be sourced from the flux of minerals caused by the breakup of Rodinia.</p>
<p><b>PHANEROZOIC</b></p>	<p><b>The biosphere in the Phanerozoic proliferated at unprecedented rates. Simultaneously, a multitude of extinctions occurred, and notably five mass extinctions; namely end-Ordovician, Late Devonian, end-Permian, end-Triassic, and end-Cretaceous.</b></p> <p><b>According to Riding (2011), Schubert and Bottjer (1992, 1995) note that if metazoans are able to outcompete (e.g. by overgrowth) microbial carbonates then temporary reduction in metazoa through mass extinctions should permit temporary increase in microbial carbonates. Thus, they dubbed the post mid-Permian extinction stromatolites as “post-mass extinction disaster forms.” Another resurgence was recorded after the Devonian extinction. However, they did not globally increase following the end-Ordovician, end-Triassic, and end-Cretaceous mass extinctions (Riding, 2006).</b></p>
<p>Cambrian (540 – 490 Ma)</p>	<p>Known for the “Cambrian Explosion,” this period witnessed the diversification of abundant metazoan life that Earth never witnessed before. The Cambrian fauna were overridingly marine dwelling in the shallow seas of the continental margins. No freshwater or land organisms had yet</p>

	<p>appeared. Nevertheless, there are traces of plants bearing strong resemblance to modern types of seaweed (Osborne and Tarling, 1996).</p> <p>During the Cambrian, microbial reefs demonstrated the highest resurgence in the Phanerozoic.</p>
Ordovician (490 – 445 Ma)	<p>Munnecke et al. (2010) report that this period recorded one of the two most significant radiation events in the history of marine life, coined as the Great Ordovician Biodiversification Event – resembling a massive rise in marine biodiversity (after Sepkoski, 1981) and biocomplexity (after Droser and Sheehan, 1997). Such an event can be directly related to the extensive, epicontinental seas developed during this period.</p> <p>By the Late Ordovician the second biggest mass extinction in the Phanerozoic occurred eradicating 85% of marine life (Munnecke et al., 2010). It has been suggested that due to the absence of extraterrestrial evidence, the Late Ordovician glaciation could have been the cause of the extinction. (Herrmann et al., 2004).</p> <p>Fisher (1965) determined that stromatolites steepest decline commenced after the Mid-Ordovician.</p>
Post-Ordovician (445 – Present Ma)	<p>Cocks (2005) notes that the Silurian marine realm recorded abundance and diversity of the invertebrates (including benthos).</p> <p>The biological invasion (flora and fauna) of land began with modest</p>

	<p>beginnings of autotrophic microbes to mosses to even trees through the Cambrian to Silurian periods (Berner, 2004; McGhee, 2005). But it was only in the Late Silurian to Early Devonian, that life's invasion of land dramatically accelerated; which included vascular land plants and hence the first forests (McGhee, 2005).</p> <p>The largest development of reefal ecosystems ever occurred in the Devonian, estimated at maximum development to have covered over 5 million km<sup>2</sup> of seafloor (McGhee, 2005). This ties in with a slight rise of microbial reefs (Fig.1).</p> <p>By the end of the Devonian, one of the 'Big Five' mass extinctions occurred, caused by another switch from a hot greenhouse state to a cold icehouse one (McGhee, 2005).</p> <p>The significant Carboniferous oxygen-rich atmosphere caused by a major radiation in vascular land plants may have attributed to the growth of arthropods including insects (Scott, 2005).</p> <p>Carboniferous marine life resulted from extensive tropical shallow-water carbonates during the Mississippian, but soon a major glaciation throughout the tropics followed (Scott, 2005). The second temporarily Phanerozoic peak of microbial reefs (Fig.1) recorded in the Carboniferous can thus be explained by the increase in tropical shallow-water carbonates.</p>
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## CHAPTER IV: DISCUSSION

Grotzinger (1989) noted that there is an “excellent correlation” between inferred paleo-water depth and stromatolite form, whereby shallow-water forms often have lower synoptic relief (after Grotzinger, 1986; Hoffman, 1988; Ricketts and Donaldson, 1988). Riding (2011) elaborated on this view by stating that the stromatolite’s shape is determined by the original synoptic relief, which reflects the surrounding environment’s accretion rate. Low relative accretion rates would typically produce low relief, but would allow stromatolites to “laterally” encrust sediments, thus fostering complex shapes. In contrast, for stromatolites to survive a high relative accretion rate and avoid being smothered they would have to grow vertically producing high relief and simple shapes. He concludes that the Mesoproterozoic stromatolites’ highly conspicuous diversity (of low synoptic relief) and abundance could actually resemble the beginning of its decline due to either: 1) reduction in synsedimentary lithification (resulting from low accretion rates); and/or 2) reduced microbial growth. Riding (2006) noted that “calcified” cyanobacteria was equivocal in both the Paleoproterozoic and the Mesoproterozoic and that the palaeogeographical distribution of calcified cyanobacteria was very limited during the period of ‘Snowball’ glaciations and its aftermath (after Riding, 1994). He also noted that calcified cyanobacteria became widespread and diverse only early during the Cambrian (after Riding & Voronova, 1984). With respect to microbial growth, both the Paleoproterozoic and Neoproterozoic Eras were generally characterized as “Snowball Earth” periods, and as per Quesada and Vincent (2012) based on present-day cryosphere analysis cyanobacteria are able to colonize cold habitats yet their diversity is considered low. Hence, since the Mesoproterozoic was a non-glacial period, it

follows then that cyanobacterial diversity would increase. Accordingly, the “reduced microbial growth” reasoning cannot be supported as discussed above.

With respect to low synsedimentary lithification:

- (i) warm temperatures favor carbonates production, and since the Mesoproterozoic was a non-glacial period, stromatolites would have been able to thrive better in terms of abundance than during the ‘Snowball’ glaciations periods – for a short period.

The supercontinent Columbia started to fragment at the beginning of the Mesoproterozoic Era ca. 1.6 Ga and continued until ca. 1.3 - 1.2 Ga (Zhao et al., 2004). Hence, according to the supercontinent cycle sea level rose and possibly epeiric seas were formed. It is known that shallow water carbonate sedimentation cannot keep up with major sea level rises through glacial melting. Accordingly, for stromatolites to sustain they would have to grow laterally, and thus foster complex shapes and thus diversity – until the Snowball Earth glaciation arrived.

Almost instantly (in geological terms) the Mid-Mesoproterozoic witnessed the formation of the Rodinia supercontinent, largely between 1100 and 1000 Ma yet some infer its amalgamation back to 1300 Ma (Condie, 2002). Consequently, the resulting Grenvillian Orogeny enhanced silicate weathering, which drowned and

inhibited the carbonate factory – that the greenhouse should have entailed – but instead a Snowball Earth glaciation commenced.

Hence, accretion rates were reduced and thus the lithification of the stromatolites began to adopt a declining phase, ultimately, negatively affecting the stromatolites' abundance altogether. With reference to the period 1.3 Ga in Fig. 6, indeed this is the pinnacle point of diversity, and after that the long-term decline was embarked.

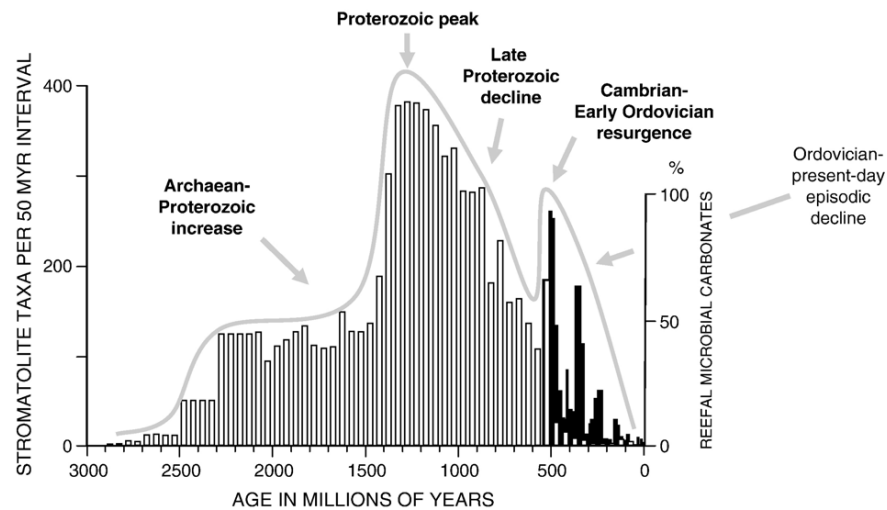


FIG.6 Stromatolite diversity, after Riding, 2007

The following Neoproterozoic Oxygenation Event led to the diversification of mobility and feeding modes amongst late Ediacaran-early Cambrian metazoans (after McIlroy and Logan, 1999; Erwin et al., 2011; Eriksson et al., 2012) and drastically affected the physical and chemical

nature of marine sediments. This entailed an increase in bioturbation intensity (after Droser and Bottjer, 1988); a “substrate revolution” (after Bottjer et al., 2000) that dramatically reduced the thickness and distribution of previously ubiquitous microbial facies and mats (after Garrett, 1970; after Hagadorn and Bottjer, 1997) and thus reduced the occurrence of stromatolites (Eriksson et al., 2012).

The Ediacaran–Cambrian transition also marked a biomineralization revolution whereby the widespread appearance of skeletonized taxa is noted – previously recorded on a much minimal scale. Diversification in biomineralizing organisms was followed by an increase in overall skeletal contribution to shallow-water carbonate facies in the Ordovician, especially by heavily calcified corals, bryozoans, brachiopods, and echinoderms (after Pruss et al., 2010). Subsequently, biomineralizing foraminifera (benthic in the Devonian and planktonic in the Jurassic; after Hart et al., 2002) and coccolithophores (Triassic) significantly affected carbonate facies distribution by transferring carbonate deposition offshore (after Tucker, 1985; after Milliman, 1993; Erba, 2006), which is a location not generally favored by stromatolites.

Three more points remain related to why stromatolites underwent a steep decline after the beginning of the Ordovician:

First was the Taconic Orogeny triggered the aggregation of the supercontinent Pangaea, which prompted the same cycle of enhanced silicate weathering (Kump et al., 1999). Second, the significant event that is still prevalent to the present day was an abyssal CO<sub>2</sub> sink. Wellman (2003), noted that the earliest generally accepted and widespread fossil evidence for land plants comes from microscopic dispersed spores recorded in the mid-Ordovician age. Thus

photosynthesis captured the CO<sub>2</sub> that would have instead assisted in forming the carbonate-forming stromatolites. Third, metazoan organisms continued to expand in abundance and diversity.

## CHAPTER V: CONCLUSION

Previous work has pointed out two main reasons behind the general decline of stromatolites: (1) seawater carbonate saturation; and (2) metazoan competition/grazing.

This present research has taken a more “acute” evaluation of stromatolite decline by comparing the steepest decline in the Ordovician with the highest peak in the Mesoproterozoic. The results favor the former reasoning provided by previous work – but digs further into the reasons that affected each of the two periods under investigation. Yet, it must be noted that the second reason is not totally disregarded, but rather dampened as discussed below.

Cyanobacteria heavily rely on atmospheric CO<sub>2</sub> for both photosynthesis and calcification; concurrently stromatolites heavily rely on carbonates for sedimentation. Accordingly, since the main source of carbonates is atmospheric CO<sub>2</sub> (along with Ca), the analysis of both periods entailed a deep understanding of the factors affecting the fluctuations affecting atmospheric CO<sub>2</sub>.

Simply, the carbon budget can be allocated to either sources (mainly volcanism,-metamorphism and diagenesis) or sinks (rocks and marine, animal and plant life). Throughout Earth history there has been a continuous variational interplay between both carbon sources and sinks.

The arguments that support a decline in stromatolite abundance due to seawater carbonate saturation are:

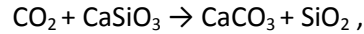
### 1. Mesoproterozoic

Sheldon (2006) noted that atmospheric CO<sub>2</sub> was constant during the period 2.5 to 1.8 Ga ago (Paleoproterozoic); and then dropped significantly between 1.8 and 1.1 Ga ago (mostly Mesoproterozoic). Kah and Riding (2007) also confirmed a decrease in CO<sub>2</sub> during the Mesoproterozoic through cyanobacterial analysis. Accordingly, this backs Riding's (2011) assumption that stromatolites' peak in abundance and diversity was an indicator of the beginning of the decline, because of lower seawater carbonate saturation.

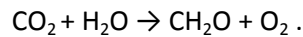
### 2. Cambrian and Ordovician Explosion

During the Precambrian time, competition for CO<sub>2</sub> and accordingly carbonate formation was limited. Besides bacteria, there was hardly any organic life. But with the start of the Ediacaran period the biosphere was totally revolutionized through two waves of intensified developments in life; namely the Cambrian Explosion and the Great Ordovician Biodiversification Event. These radiations of life had the greatest negative impact on stromatolite occurrence. Prior to the Phanerozoic time, CO<sub>2</sub> and accordingly carbon products were arguably monopolized by cyanobacteria and carbonate rocks. With the appearance of multicellular life, the distribution of carbon products was significantly altered. To summarize this point from a chemical reaction perspective, it is as follows:-

During the Precambrian the overwhelming continental geochemistry was related to the following formula:



and the Precambrian atmosphere witnessed the following bacterial photosynthesis:



With the continued increase of  $\text{O}_2$  in the atmosphere, multicellular life proliferated, but instead of forming bacterial organic material based on the previous bacterial photosynthesis, through respiration it locked up more carbon products, and accordingly depleted the carbon budget previously available for stromatolite formation.

### 3. The Ordovician Hirnantian Glaciation Mass Extinction

Glaciations generally result in a sea level drop and thus an exposure of shallow-water continental shelves. This was the case during the Hirnantian glaciation, which was one of the worst extinction events in Earth's history. But what was unique about the End-Ordovician glaciation was that prior to its occurrence there was an unprecedented diversification of marine life. With the exposure of shallow-water continental shelves, 85% of marine life was eradicated. This entailed a sudden astronomical amount of buried organic material. In other words, carbon would be locked up in the organic material for a long time before volcanic outgassing would reemit it out to the atmosphere again in the form of  $\text{CO}_2$ .



Fig.7 shows that the Ordovician  $\delta^{13}\text{C}$  (marine carbonate rocks; representing organic carbon) was at its lowest stage throughout all of the Phanerozoic. This also ties with the lowest sea level (because of the end-Ordovician glaciation) during the Phanerozoic (Fig. 8).

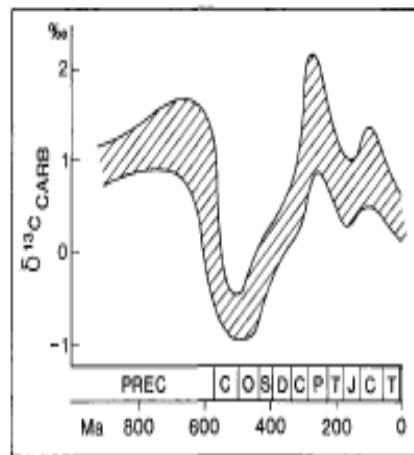


Fig. 9.16 Generalized secular variations of  $\delta^{13}\text{C}$  in marine carbonate rocks. After Veizer et al. (1980).

FIG. 7 Carbon Excursion

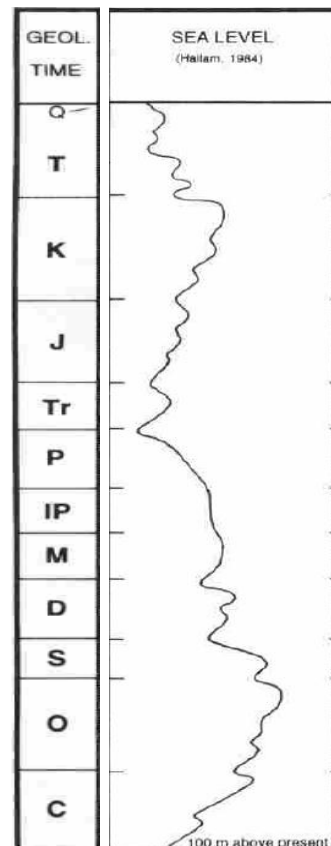


FIG. 8 Sea level change

This point is further backed by the presence of microbialites (microbial carbonates) in Silurian rocks in the Waldron Shale in SE Indiana and their absence in the Ordovician Cincinnati Series in SE Indiana even though they have the rest of the facies identical (Schmidt, 2006).

On the other hand it could be argued that the exposed carbonate shelves would provide more carbonate sources through weathering of these shelves, but, this glaciation occurred mainly in the Southern Hemisphere on the Gondwana Continent – a location that generally receives less sun than the equator and thus doesn't favor carbonate formation.

#### 4. Post Ordovician time

From the first appearance in the Ordovician, through the Silurian until the Devonian plant life increased significantly in abundance and variety acting inversely to the stromatolites abundance and variety. This was another blow to the atmospheric CO<sub>2</sub> budget, as depicted from the CO<sub>2</sub> graph in Fig.1.

#### 5. Carbonate Shelves

Production of carbonates occurs abundantly in warm equatorial regions within a boundary of 30° latitude. According to Walker (2002), carbonate shelves have witnessed a continuous drastic decrease throughout the Phanerozoic as seen in Fig.9. This could be attributed to the general drift of the continents towards both poles vis-à-vis their equatorial concentration during the Precambrian. In other words, the favorable habitat for stromatolites occurrences has in itself undergone a drastic decline, thus pushing stromatolites to stressed locations where temperature is warm enough to allow them to grow and persist.

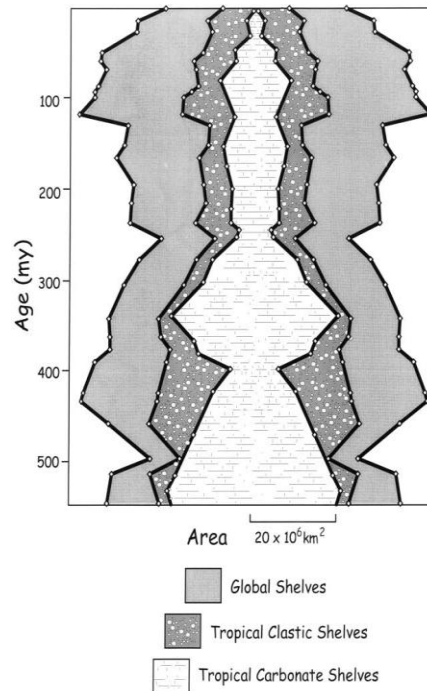


FIG. 9 Phanerozoic Shelves, after Walker 2002

To summarize the conclusions of this research, stromatolites steeply declined in the Ordovician for the following hypotheses:

- 1- A continuous decline in atmospheric  $\text{CO}_2$  since the Mesoproterozoic
- 2- An explosion in multicellular life during the Cambrian and Ordovician that outcompeted and grazed on stromatolites
- 3- The End-Ordovician Mass Extinction that locked organic carbon for a longer period than usual and thus adversely affected the carbon budget availability.

- 4- The appearance of plant life that consumed CO<sub>2</sub> through photosynthesis and locked more organic carbon.
- 5- The decrease of carbonate shelves during the Phanerozoic, which is a favorable environment for stromatolite formation.

#### Suggested Future Research

In order for the above hypotheses to be validated, further data collection is suggested that would support or refute the roles of each of them. In addition to a study of the geomicrobial ecology of microbial mats. Finally, an in-depth palaeoecological analysis of stromatolites' decline during the rest of the Phanerozoic is also suggested for further research.

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