The Jurassic extinction events and its relation to CO_2 levels in the atmosphere: a case study on Early Jurassic fossil leaves

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Abstract: The Mesozoic was a so-called “hothouse” time period in Earth’s history, with high concentrations of atmospheric CO_2 and elevated temperatures, but the exact climate evolution is not fully known for the entire interval. The Early Jurassic for instance is believed to have been a warm period, flanked by two episodes of extremely high CO_2, coinciding with environmental degradation and mass extinctions: the Triassic-Jurassic (200 Ma) and the early Toarcian (183 Ma) mass extinction events. Mass extinctions are often related to variations in climate conditions, which in turn are linked to the global CO_2 concentration, and it is therefore important to understand the levels of CO_2 before, during and after such events. Here, atmospheric CO_2 levels were reconstructed for the late Pliesbachian (*ca.*185 Ma), an Early Jurassic time period that is not well understood in terms of climate. The stomatal proxy method of palaeo-CO_2 reconstructions was applied, using fossil leaves derived from the Clarence-Moreton Basin in eastern Australia. The stomatal proxy relies on the inverse relationship between the density of plant leaf stomata and atmospheric CO_2 concentrations. The ten exceptionally well-preserved fossil leaves derived from the araucarian conifer species *Allocladus helgei*. Two different methods of calibrations, using the nearest living equivalent species *Athrotaxis cupressoides,* were applied to the stomatal data and CO_2 concentrations in the range 600 – 750 ppm were found. These values are high compared to present day CO_2 concentration (396 ppm in May 2012), but are lower than values usually cited for this period, as interpolated between CO_2 concentrations known from the flanking mass extinction events of 1000 – 2000 ppm. The results found here therefore indicate that the Pliensbachian was a cooler period than previously assumed, but that it was still a “hothouse” warm period with higher global temperatures than today.

Keywords: Australian; Early Jurassic; Pliensbachian; Conifers; Stomatal proxy; palaeo-CO_2

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Jurassiska massutdöende-event och dess relation till atmosfärens CO_2 -halter: en fallstudie baserad på fossila jurassiska blad

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Sammanfattning: Mesozoikum anses ha utgjort en ”växthusperiod” i Jordens historia med avsevärt höga koldioxidhalter i atmosfären samt förhöjda temperaturer, men det återstår många frågor att besvara angående klimatutvecklingen för hela detta intervall. Tidig jura karaktäriseras till exempel av ett varmt klimat, och föregås och efterföljs av två kortare perioder med väldigt höga CO_2 halter, som sammanfaller med försämrade miljöförhållanden och massutdöenden. Två massutdöenden kopplas till denna period; trias–jura massutdöendet (200 Ma) samt massutdöendet som inträffade under tidig toarc (183 Ma). Massutdöenden relateras ofta till klimatförändringar som i sin tur återspeglas i de globala CO_2 -halterna. På grund av detta förhållande mellan temperatur och koldioxidhalt i atmosfären är det viktigt för oss att veta hur CO_2 varierat under en längre period, före och efter dessa nämnda event. I denna studie har CO_2 halter rekonstruerats för sen Pliensbach (c. 185 Ma), tidsintervall under tidig jura där det saknas kunskap angående klimatet. Stomataproxy-metoden användes för paleo-CO_2-rekonstruktioner, med hjälp av fossila blad insamlade från Clarence- Moreton bassängen i östra Australien. Stomataproxy-metoden använder sig av det faktum att det föreligger ett omvänt förhållande mellan bladens stomatadensitet och atmosfärens CO_2-halter. De 10 välbevarade bladfossilen härstammar från barrträdet *Allocladus helgei*. Två olika beräkningsmetoder har applicerats på närmaste levande släkting (NLE) *Athrotaxis cupressoides*. Resultaten från beräkningarna visade CO_2-halter i intervallet 600-700 ppm. Dessa halter är höga jämfört med dagens CO_2-halter (~400 ppm i maj -2013), men däremot lägre än CO_2-halter dokumenterade i andra arbeten baserad på interpolering av CO_2-halter omfattande massutdöendeintervallen där värden på 1000-2000 ppm uppvisats. Därmed tyder dessa resultat på att Pliensbach var en kallare period än man tidigare ansett, men klassas dock fortfarande som en ”växthusperiod” med förhöjda halter av CO_2 och högre temperatur jämfört med idag.

Nyckelord: Koldioxidhalt, klimat, Australien, tidig Jura, Marburg subgroup, *Allocladus helgei*, stomata index, CO_2

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1. Introduction

During the Jurassic, as in the rest of the geological past, climate changes had a great influence on life. CO_2 levels have shown to be one of the main contributors to climate changes through radiative forcing (van Hoof,ThomasB./http://www.esrl.noaa.gov/gmd/about/climate.html) and therefore it is relevant to reconstruct CO_2 levels of the past. There are several methods employed and reconstructing ancient levels of CO_2 and include among others the study of the distribution of stomatal pores on fossil leaves (Royer, 2008) by using proxies based on stomatal analyses: e.g. the Stomatal Ratio (SR) method and linear regression transfer function method (Steinthorsdottir et al., 2011; Chaloner and McElwain, 1997). The stomatal method used for palaeo- CO_2 reconstructions is constructed based on the inverse relationship between stomata index (SI) and atmospheric CO_2 (Woodward, 1987, Steinthorsdottir et al., 2011). The stomatal proxy allows for CO_2 reconstruction in deep time (Royer, 2008).

In this study I have applied the stomatal proxy method analysing 10 well-preserved leaves of the Early Jurassic conifer *Allocladus helgei* from the Inverleigh quarry in the Clarence-Moreton Basin (eastern Australia, Figs. 1-2) in order to calibrate the atmospheric CO_2 concentration at the time. These conifers were preserved in floodbasin siltstones of the Marburg Subgroup Inverleigh Quarry during Early Jurassic (Jansson et al., 2008a,b).

The aim of this study was to learn the methods of preparations and how to process the material before calculating the actual stomata index (SI) and further how to correlate the stomata density (SD) in leaves with the past CO_2 levels. The stomata density on leaves is normally directly related to atmospheric CO_2 values and therefore reacts with a decrease in stomata density when CO_2 levels increase (McElwain and Chaloner, 1995, Steinthorsdottir et al., 2011, Woodward, 1987). In general the stomata index (SI) is assumed to be a good proxy when it comes to climate related issues and CO_2 levels, partly because it is stable and gives more reliable results compared to stomata density (SD).

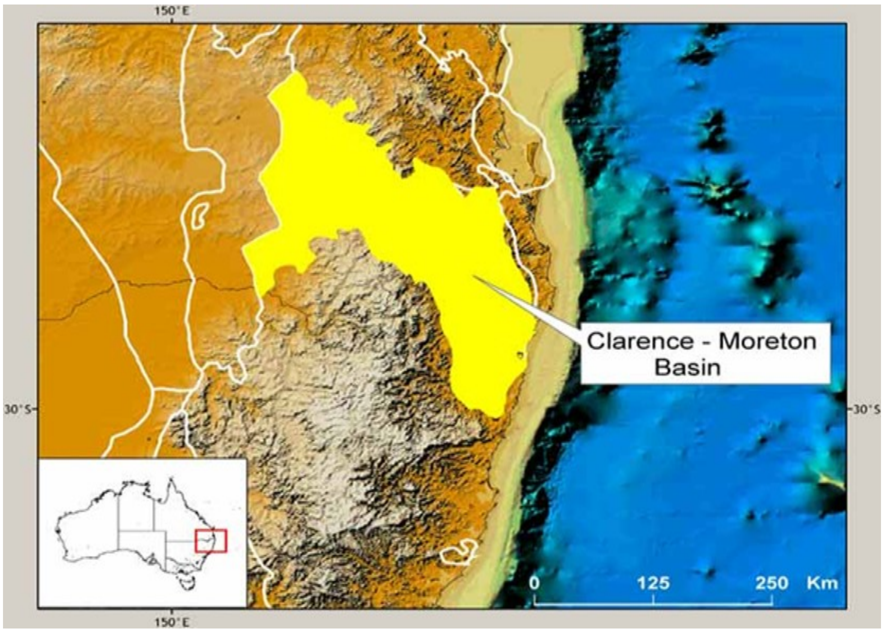

Fig. 1. Map showing the location of the Clarence – Moreton basin from where the plant fossils are derived. (Geoscience Australia: http://www.ga.gov.au/oceans/ea_ofs_ClrMrtn.jsp)

The approach of this study is based on both literature study and laboratory work which have been linked and compared. The climate conditions are infered mainly based on evidences derived from leaf fossils. A nearest living equivalent (NLE) is required when fossil leaves are used as a paleoclimatological tool and the conifer *Brachiophyllum* have been used for this study. CO_2 levels have shown large variations through the geological record and compared to the present values of 395,77 ppm (http://co2now.org/). For example, during the early Jurassic (195 million years ago) the CO_2 levels were close to 1800 ppm (parts per million) according to Beerling and Woodward, (2001) and Berner and Canfield, (1989) and during the very earliest Jurassic the CO_2 values reached their top: 2100 ppm (Steinthorsdottir et al., 2011), which is almost five times higher than the values in present time. Pre-industrial CO_2 levels were counted to 280 ppm, but industrial activity resulted in that the present days levels as by June 2012 reached 395 ppm. These values for Atmospheric CO_2 concentrations were measured at Mauna Loa Observatory.

1.1. Jurassic Climate

Interpretations of Jurassic climate have been based on different proxies, such as composition of vegetation based on fossil plants and stomatal proxy based reconstructions (Woodward, 1987, Steinthorsdottir et al., 2011, McElwain et al., 1999, McElwain et al., 2005, Vajda and Wigforss-Lange, 2009). The climate during early Jurassic was warm, hothouse conditions with no polar ice (Scotese et al., 1999, Price, 1999, Vajda, 2001; Vajda et al., 2013). Indications of more humid conditions in Australia are for example the presence of widespread coals, calcrete nodules, dehydration horizons and lack of evaporites (Hallam, 1984; Johnson, 1995, Jansson et al., 2008a,b), but also arid areas with hot temperatures occurred in some areas (Chandler et al., 1992). Variations in climate during the Mesozoic can be interpreted by sedimentological studies where for example organic carbon rich sediments along continental margins indicate warm and humid conditions (Vajda and Solakius, 1999; Larsson et al., 2000; Vajda and Raine, 2003, 2010; Ocampo et al.

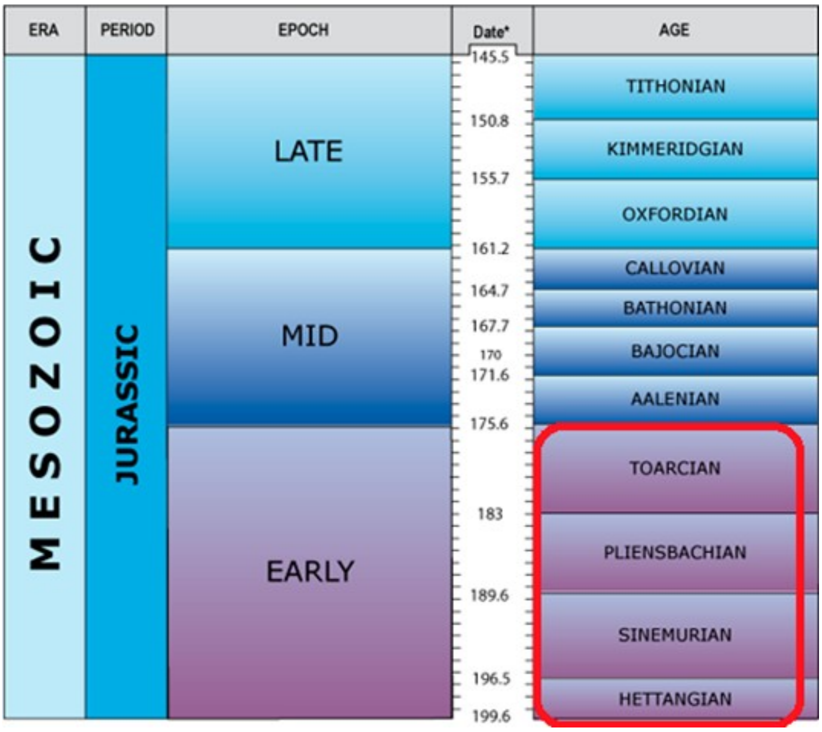

Fig. 2. Timescale showing the Jurassic timeinterval including the Sinemurian from where the fossil leaves of this study (*A. helgei*) origin. Figure borrowed from the British Geological Survey homepage based on '*A Geologic Time Scale 2004*' by F M Gradstein, J G Ogg, A G Smith, el al. (2004), and the International Stratigraphic Chart, 2006 (ICS) with additions.

2006;Negri et al., 2009; Pole and Vajda, 2009; Ruhl et al., 2010).

These black shale-deposits are found among others in Panthalassa and Tethys Ocean (Hallam, 1995; Ruhl et al., 2010). In short terms the Jurassic has been discussed as one of the warmest periods during the Phanerozoic time interval (Mauna Loa observatory).

Sedimentological evidences from several places (e.g. England and Germany) indicate a cooler period and more saline waters (regressive trend) in the northwest European shelf-areas during the late Pliensbachian (McArthur et al., 2000; Bailey et al., 2003, van de Schootbrugge et al., 2005), which thereby suggest glacial control on sea level fall (Price, 1999; van de Schootbrugge et al., 2005) and decreasing CO_2 levels. Some groups of Boreal fauna migrated during this cooling period towards southern areas (Smith and Tipper, 1986, van de Schootbrugge et al., 2005) and the Northeastern trade winds changed. But a new warmer period started in the Toarcian and resulted in a decrease of surface water salinity (McArthur et al., 2000, Bailey et al., 2003).

Evidences in general indicate warmer conditions at higher latitudes, meaning lower temperature gradients, and no evidences of ice and bigger diversity of floral groups are found in more polar regions (Hallam, 1985; Hughes, 1973; Jansson et al., 2008b). Lack of land ices would allow the planet to absorb bigger amounts of solar energy and therefore lead to higher temperatures, especially at the higher latitudes. Peat and coal imply high values of precipitation or alternatively little evaporation rates (Hallam, 1984; Parrish, 1988). Theories supporting the theory of arid continental climate are based on the hugeness of the supercontinent and its position in the trade-wind belt, but even if continental aridity occurred at places, the global conditions were not arid. Global precipitation in average were assumed to be higher (by 0.15 mm/day) compared with the present. Monsoonal activity raised the values of rainfall on the continents and overall Pangea experienced very mixed climates during early Jurassic. CO_2 levels affected the continental temperatures (2.3°C warmer) with being six times higher than the values are in present. In general the early Jurassic has shown a global warming of 5 °C to 10 °C and low-latitude regions of western Pangea indicate vast deserts based on eolian sandstones (Fig. 3). Reasons that amplifies the global warming are related to decrease in planetary albedo, which is a result of reduction in sea ice, snow cover, low clouds and last but not least higher values of atmospheric water vapor.

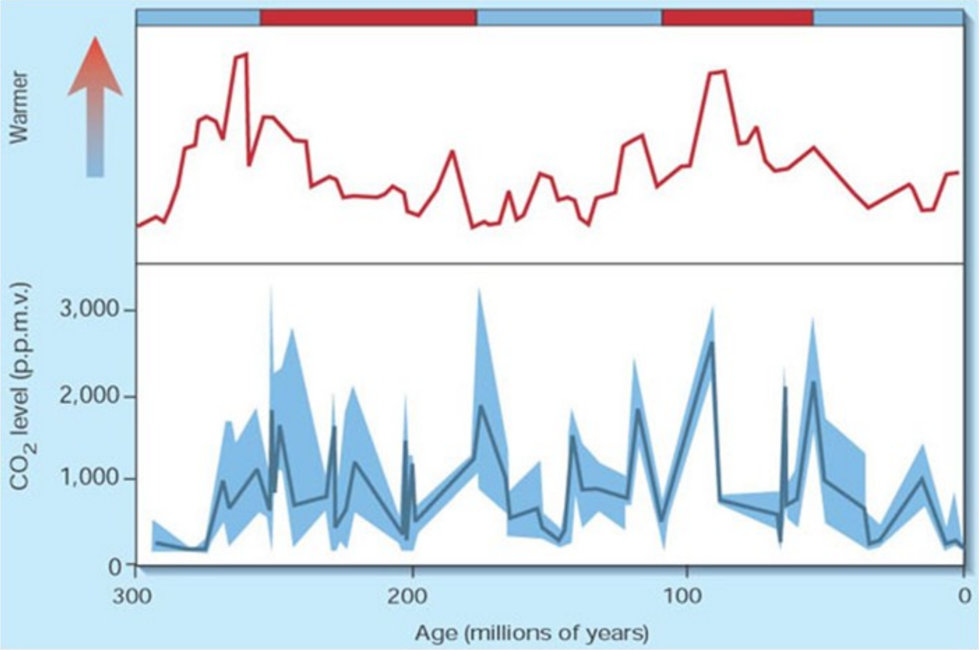

Fig. 3.

Figure illustrating the correlation between temperature and CO_2 levels (from : www.john-daly.com)

1.2. Jurassic World

The early Jurassic covers a time span of nearly 26 million years and is subdivided into Hettangian, Sinemurian, Pliensbachian and Toarcian. This was a period when different species of dinosaurs still dominated the fauna. Dominating Mesozoic plants were among other; ferns, gingkoes and conifers (Vajda, 2001, 2008; Vajda and Wigforss-Lange, 2006; Mehlqvist et al., 2009). In the very early Jurassic the supercontinent Pangea was centered at the equator surrounded by the palaeo-pacific ocean, also known as Panthalassa, and the remaining 56% of the land masses were located in the Northern Hemisphere (Parrish, 1993). Authors have claimed that during the break-up of Pangea a large increase of oxygen took place ending the period of an earlier anoxia and therefore favored some groups of species such as plankton (Quigg et al., 2011). As a result of the break-up of Pangea, sea level started to rise and many new seaways were formed, which resulted in separation of land masses (Hallam et al., 1994) and led to migration of marine faunas and floras (Hallam, 1983; Smith and Tipper, 1986; Smith et al., 1990, Stanley, 1994; Vajda and Turner, 2009). The architecture of the Jurassic world was mainly designed by rifting- processes and sea-level variations (Vajda and Wigforss-Lange, 2009), which are linked to tectonic activities formed by the break-up of Pangea.

Inferring to other authors data (e.g. Hallam, 1999), changes in the global sea level and tectonic activity vary; in general sea-levels have been much higher than in present time, except from a few low-stands that occurred in the Early Jurassic. According to data, the sea-levels were as lowest during the Hettangian (earliest Jurassic) as major regressions had occurred in late Triassic (Hallam, 1992). Sea level variations are often connected to the size of icecaps at the Polar Regions depending on climate conditions and also to formation and destruction of ocean ridges and swells. The Jurassic, global sea-level curve by Hallam (1992) indicate that different processes must have strengthen each other to cause such high sea-levels; tectonic activity seems to be one of the main causes (Hallam, 1988). As a result of higher sea levels a new important seaway opened, the Hispanic corridor (Hallam, 1983; Smith and Tipper, 1986, Smith et al., 1990, Stanley, 1994, van de Schootbrugge et al., 2005) that affected the ocean circulation and created a straight connection between the Tethyan and Paleopacific oceans (Aberhan, 2001; Aberhan, 2002). Another seaway called the Viking corridor opened in late Pliensbachian between Greenland and Norway and created a seaway between the Arctic and Tethys oceans (Westermann, 1993). Circulation changes affected some species, because the new eastward circulation movements through the Hispanic corridor resulted in more humid conditions in eastern parts of the seaway and more arid conditions at the Tethyan side (Aberhan, 2001; Aberhan, 2002, van de Schootbrugge et al., 2005).

Tectonical evidences show a consistent pattern of rifting that started in the Sinemurian and continued being active during the Pliensbachian (Rasmussen et al., 1998), which is related to the break- up of Pangea event. In the upper Pliensbachian to the lower Toarcian is a marked regression throughout the Tethyan seaway (Cobianchi and Picotti, 2001), and it agrees with sea level curves made by Haq et al. (Haq et al., 1987). Also manganiferous limestones and ironstones indicate regression around the Tethys and northwestern seaways (Taylor, 1998).

Plant productivity and diversity reached their top at the mid-latitudes (Rees et al., 2000). Lower latitudes were dominated by conifers and bennettites characterized by small leaves, and polar areas were dominated by conifers with larger leaves: for example ginkophytes and seed-ferns (Rees et al., 2000; Vajda et al., 2013).

High-diversity palynofloras that dominated earlier got exchanged during the Early Jurassic and conifer groups called Cheirolepidaceous became dominating instead (Jansson et al., 2008a,b).

2. Mass Extinctions

2.1. Triassic-Jurassic Mass Extinction

Stomatal frequency analyses have been extensively used as a proxy for climatological interpretations on sediments spanning the Triassic-Jurassic boundary as a tool to reveal the causes behind this major extinction event (McElwain, 2005; Steinthorsdottir, 2011). For example cuticle fragments derived from sediments across the T-J boundary from several sections on Greenland have revealed stongly increased paleo CO_2 levels at the T-J boundary (Stenthorsdottir, 2011). Although this study is not focussed on the Triassic-Jurassic boundary interval, it serves as an example on how to apply the stomatal frequency analyses.

Two mass extinctions occurred during the Early Jurassic and had effects on the floral assemblages, namely the Triassic-Jurassic (200Ma) and the Toarcian (183Ma) extinctions (Hallam, 1998; Palfy et al., 2001; Akikuni et al., 2010; Sha et al., 2011 Vajda et al., 2013). Mass extinctions are commonly related to variations in climate conditions that in turn are linked to global CO_2 levels and therefore important factors indicating changes. The Triassic-Jurassic boundary event occurred nearly 200 million years ago representing a big mass extinction in fauna and also a big turnover in flora (Ruhl et al., 2010; Mander et al., 2010; McElwain et al., 2007). This event-boundary is characterized by two negative carbon isotope excursions (McElwain et al., 2007; Hesselbo et al., 2002b, Ruhl et al., 2010). Investigators claim that it has been one of the five largest extinctions through Phanerozoic time (Sepkoski, 1981; Deenen et al., 2010) and this event has clearly left its′ traces; such as big changes in groups of species dominating during and after the extinction-event (Sepkoski, 1981; Kiessling et al., 2007; Deenen et al., 2010; Steinthorsdottir et al., 2011; McElwain et al., 2007).

Data from the T-J boundary indicate enormous genus losses; over 23% and 50% in both marine and continental realms (McElwain et al., 2007; Raup and Sepkoski, 1982; Sepkoski, 1994; Ruhl et al., 2010) and varied losses of marine families and widespread extinction of e.g.: ammonites (Newell 1963), bivalves (McRoberts and Newton 1995), radiolarians (Tipper et al. 1994) and coral reefs (Kiessling 2001, 2005).

Depending on location the rates of extinction vary. Extremely high rates are found in Triassic-Jurassic assemblages in parts of Sweden and Greenland where over 80% of terrestrial plant species (McElwain et al., 2007; McElwain et al., 1999), and almost half of the terrestrial vertebrate families in North America got extinct (McElwain et al., 2007; Olsen et al., 1987). According to some investigations, the continental plants suffered the most (Burgoyne et al., 2005) with very big losses and turnovers; even up to 95% got affected in the North Atlantic region (Beerling and Berner, 2002). There are several hypotheses concerning the extinction for example indicating that the event was related to an asteroid impact at the T-J boundary (Olsen et al., 2002; McElwain et al., 2007), or linked to changes in environmental conditions due to releases of methane and global warming (Palfy et al., 2001; McElwain et al., 2007). There are evidences that imply increased CO_2 concentrations in the atmosphere; e.g. the double negative δ13C excursion (Palfy et al., 2001; Hesselbo et al., 2002a, McElwain et al., 2007; Ruhl et al., 2010) and changes in stomatal density (SD) (Steinthorsdottir et al., 2011). The carbon isotope excursion is seen both in inorganic and organic carbon and may have led to strong perturbation of the global carbon cycle (McElwain et al., 2007; Palfy et al., 2001; Ruhl et al., 2010). Disturbances of the global carbon cycle could be related to the onset of Central Atlantic Magmatic Province volcanics (CAMP) as because the onset of volcanic activity and CAMP deposition are very close to match the carbon isotope excursion in time, but yet there are no reliable facts about timing and duration of the CAMP eruptions (McElwain et al., 2007; Whiteside et al., 2007, Marzoli et al., 2004, Ruhl et al., 2010).

2.2. Toarcian Mass Extinction

The second mass extinction was the Toarcian Mass Extinction that took place in the early Jurassic, about 183-181.2 million years ago (Little and Benton, 1995; Hallam, 1986, Hallam, 1987; Palfy and Smith, 2000a; Gomez et al., 2008,;Dera et al., 2010; Cecca and Macchioni, 2004; Gomez and Goy, 2011). This event is documented in the carbon isotope record by a distinct negative carbon isotope excursion and other evidences documented by geochemica, sedimentological and paleontological methods are: changes in hydrological cycle and biota (Cecca and Macchioni, 2004, Gomez et al., 2008), high rates of organic burial, increased temperatures, losses of marine species and formation of black shales indicating anoxic conditions (Jimenez et al., 1996, Beerling et al., 2002).

This event mostly affected terrestrial species; it provides a turnover of conifer families in both Northern and Southern hemisphere floras (Helby et al., 1987). Major climate changes resulted in a rapid warming during the early Toarcian. What activated this event is not known, but very likely it is connected to big releases of greenhouse gases that may be related to the Karoo- Ferrar eruptions (Palfy and Smith, 2000; Hesselbo et al., 2000). The reason to why studies so clearly suggest that these extinction events are related to pulses of CO_2 induced environmental changes is among others: enhanced nutrient input, productivity driven anoxia and rises in seawater temperatures (Gomez et al., 2008).

Fig. 4. Map showing the locatity of Inverleigh Quarry (red ring) from where the studied leaf fossils derive

3. Geological setting

3.1. Sedimentology

The Clarence-Moreton Basin from where the studied fossils derive is located in eastern Australia (location: 28°17′02.87″S 151°58′ 55.64″E), reaching from northern New South Wales to south-eastern Queensland (Fig 4). The Clarence- Moreton basin is divided into three parts: one sedimentary sequence called the Woogaroo Subgroup, the Marburg Subgroup and the "post-Bundamba Group sucession" (O'Brien and Wells, 1994). The Marburg Subgroup succession consists of mature quartzose sandstones and shales, and is the origin for the studied fossil leaves used in the thesis. The sediments hosting the fossil leaves are exposed in the Inverleigh quarry (Day et al., 1983) and of a Sinemurian age. The Gatton Sandstone, which is approximately 500 meters thick, is the dominating part of the Marburg Subgroup-succession (Fig. 5). Beneath the sandstone is the Koukadowie Formation, which is located in the eastern parts of the basin and have a thickness of around 250 meters (O'Brien and Wells, 1994, Goscombe and Coxhead, 1995).

In general mudstones and sandstones are deposited in flood basin lakes, mires and crevasse splays, and when it comes to root traces or traces of burrows it may be connected with exposure, pedogenesis or colonization by vegetation (Jansson et al., 2008b). Above the lowest succession follows a fossil -rich siltstone, which is covered by sandstones and granule-stones.

3.2. Palaeobotany

Some of the most common conifers growing in the Southern Hemisphere during the Mesozoic were the broadleaved conifers *Araucariaceae* and *Podocarpaceae* (Stockey, 1990; McLoughlin and Vajda 2005; Greb et al., 2006; Jansson et al., 2008a,b). Fossil collections from the Sinemurian Walloon Measures of the Clarence-Moreton and Surat basins (Fig. 1) show that these were also prominent in the area from where the plant fossils of this study are derived (Gould, 1980; McLoughlin and Drinnan, 1995). According to data by Jansson et al. (2008b) the conifer *Allocladus helgei* was the dominating conifer in the macroflora at the location of investigation. Fossil leaves in the Inverleigh quarry are found usually in flood basin-shales, and show little fragmentations which indicate that their origins are near the depositional places (Jansson et al., 2008a,b). Apart from the conifer leafs which are the focus in this study, other plant groups present are free-sporing herbaceous plants, e.g. club mosses, horse tails and ferns and seed-bearing plants e.g. *Allocladus, Sagenopteris, Rintoulia.* The ferns and isoetaleans belong most likely to some herbaceous subgroup while the conifers and seed-ferns belong to the shrub- to tree-sized statum (Page, 2002).

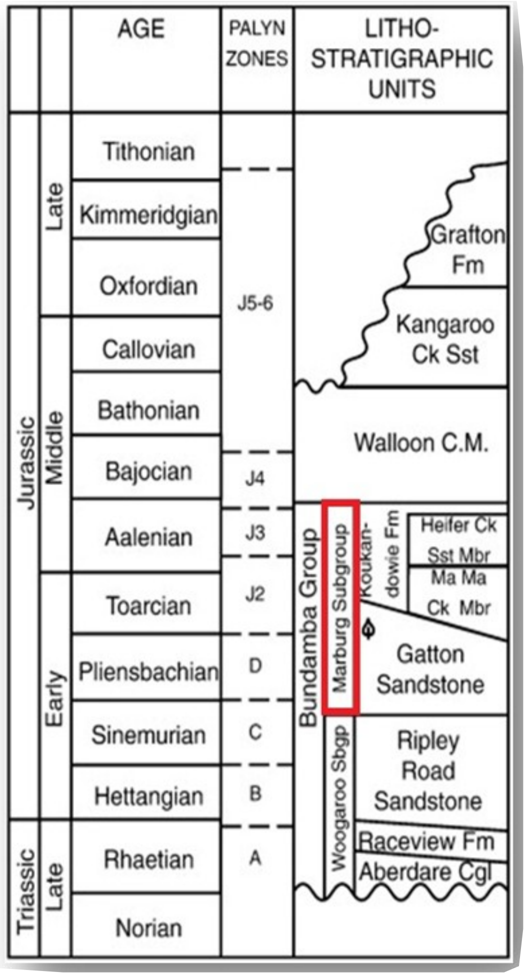

Fig. 5. The Lithostratigrpahic units of the succession in Clarence– Moreton basin in Australia. From Jansson et al., 2008.

Allocladus helgei belongs to conifers, with leaves having dentacles and resemble *Araucarieae*. They have stomata in files, distributed in compounds or single files. The amount of subsidiary cells may vary depending on CO_2 levels (Kouwenberg et al., 2003). *A. helgei* has stomata only on the lower side of the leaf. Each conifer family, genera and species possess unique cuticular features and stomatal patterns, therefore they are very important tools in taxonomical studies (Pole and Douglas, 1999). *A. helgei* has been shown to possess rare cuticular and macromorphological combinations that are not present in other conifer families, which makes it difficult to find its extant relatives (Pole and Douglas, 1999).

A. helgei has significantly longer microdenticles compared to many other groups – which is a much more specific character. The Podocarpaceae have normally stomata in strictly defined long files with two polar and two lateral subsidiary cells, meanwhile the Araucariaceae have files of stomata with four to six subsidiary cells in each complex and are more similar to the structure of *A. helgei*. Araucariaceae may also have stomatal openings and waxy plugs like the *A. helgei* (Fig. 6.) (Jansson et al., 2008a).

4. Stomata

4.1 Stomata & Stomatal Physiology

The stomatal pores are used by plants for gaseous exchange (Woodward, 1987). Plants take up carbon in the form of CO_2 for photosynthesis, while simultaneously expelling O_2 and H_2O via diffusion (Woodward, 1987).

Photosynthesis equation:

$$\underset{\text{Carbon dioxide}}{6CO_2} + \underset{\text{Water}}{6H_2O} \xrightarrow{\text{Light}} \underset{\text{Sugar}}{C_6H_{12}O_6} + \underset{\text{Oxygen}}{6O_2}$$

Stomata show an inverse relationship between stomatal frequency and atmospheric CO_2 concentration levels (Woodward, 1987; Kouwenberg et al., 2003, Steinthorsdottir et al., 2011a). So called guard cells enclose the actual stomatal pore, surrounded by epidermal cells (Kouwenberg et al., 2003; Croxdale, 2000). The guard cells open and close by help of turgor pressure; they function as hydraulic valves and therefore respond to humidity, radiation and temperatures (Sharpe et al., 1987; Taiz and Zeiger, 2006). Plant leaves have species-specific patterns and structures of stomata; which means that stomata may be found on both sides of the leaf or only one side (Evert and Esau, 2006), but the conifers here studied have only stomata on one side as earlier mentioned. The main purpose with stomata and stomatal control has to do with maximized water use efficiency (WUE), which is defined as the ratio of CO_2 obtained for photsynthesis compared to the H_2O lost in transpiration (Woodward, 1987). The stomata adapt the exchange of water vapor and CO_2 according to atmospheric conditions; by opening during specific times and the leaf can also change the number of stomata compared to the number of epidermal cells (Woodward, 1987; Taiz and Zeiger, 2006). Stomatal frequency shows a clear link to atmospheric CO_2 concentrations: Leaf stomata react in most situations with a decrease when CO_2 levels get elevated (Fig. 7) (Kouwenberg et al., 2003; Steinthorsdottir et al., 2011b; Woodward et al., 2002; Woodward, 1987). Drought and irradiance also influence stomatal density (number of stomata/mm2), wheras stomatal index (% of all cells that are stomata) is mainly influence by CO_2 (Woodward, 1987).

The mechanism behind stomatal opening and closing was unknown for a long time, but recently we learned that plants and animals for instance, use the same enzyme called carbonic anhydrase for detecting CO_2. The carbon anhydrase is an enzyme and a sensor at the same time (Frommer, 2010). Hu et al. (2010) discovered that carbonic anhydrases function in CO_2 sensing in plants.

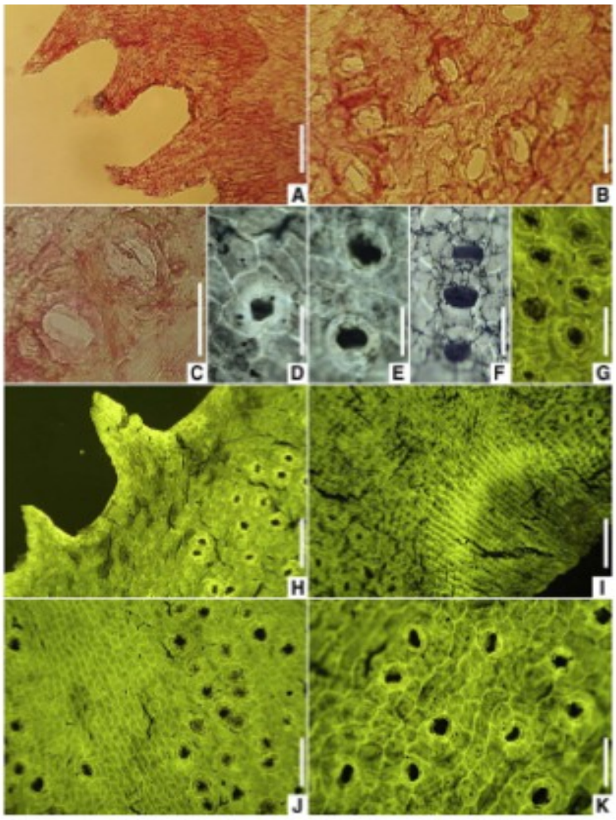

Fig. 6. Cuticular details of *Allocladus helgei* from Jansson et al. 2008

4.2. Stomatal density and stomatal index

The stomatal density is defined as the number of stomata per unit leaf area (mm^2), whereas the stomatal index is the amount of stomata divided by all epidermal cells (normal epidermal + stomata), which will give the percentage of stomata-bearing cells per unit (Steinthorsdottir et al., 2011; Kouwenberg et al., 2003). The reason to why it is preferable to use stomatal index (SI) rather than stomatal density (SD) is among others that stomatal density may reflect other factors than CO_2 changes in the values, such as humidity levels, cell expansion and leaf size (Steinthorsdottir et al., 2011; Kouwenberg et al., 2003, Kurschner, 1997). Whereas it is recognized that stomatal index gives more stable data related on changes in atmospheric CO_2 (McElwain and Chaloner, 1995). One of the purposes with the stomatal frequency is that it can be used as an indicator of palaeo-CO_2 and also as a control on atmospheric data from other modeling and proxy sources (Kouwenberg et al., 2003, Steinthorsdottir et al., 2011b, McElwain and Chaloner, 1995). To keep in mind, not all plants react always to increasing CO_2 with decreasing stomatal frequency, but close to 90% of all studied fossil plants have reacted positively. Also close to 40% of modern plants respond the wanted way, positive correlations between SD/SI and CO_2 are rare (Steinthorsdottir et al., 2011b).

5. Material and Methods

The stomatal proxy method of palaeo- CO_2 reconstruction utilizes the inverse relationship between atmospheric CO_2 concentrations and leaf stomatal density (including expressed as stomatal index, or S.I.) (Woodward, 1987). In order to calibrate CO_2 concentrations using this method, fossil plant S.I. values have to be compared to their modern equivalent. Ideally, the modern equivalent is of the same species or genus – a nearest living relative (NLR). However, it is not always possible to find NLRs for deep-time fossil plants, so a nearest living equivalent (NLE (Chaloner and McElwain, 1995)) is utilized instead in order to compare with the fossil plants. A NLE is a modern plant

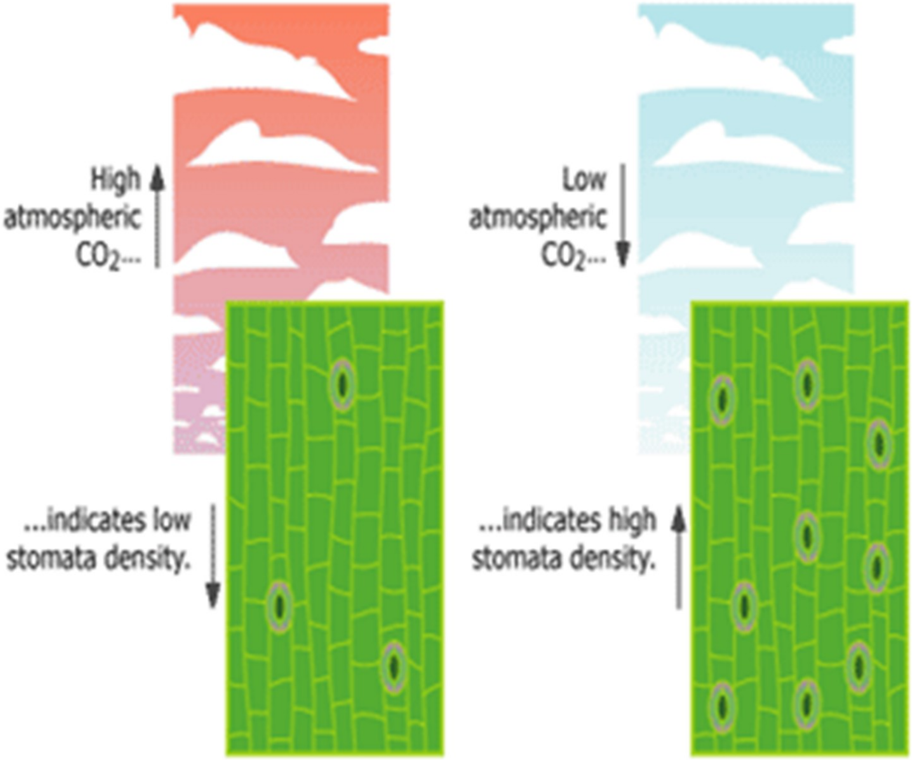

Fig. 7. Figure showing how increases in CO_2 affects the amount of stomata. In leaves.http://evolution.berkeley.edu/evolibrary/search/imagedetail.php?

species which possesses morphological and/or ecological similarities to the studied fossil plants. For this study, the southern hemisphere conifer *Athrotaxis cupressoides* (S.I. = 11.2%) was chosen as a NLE, based on a similar leaf- and cuticle morphology (see Haworth et al., 2010).

Firstly, S.I. was calculated. The ten most well-preserved fossil *A. helgei* leaves from the Inverleigh quarry were selected and placed on glass slides with the stomatal surface (abaxial side) up, protected by cover slips. The leaves were then photographed at 200x magnification using an epifluorescence microscope (Olympus BX51) with a digital camera (Infinity2). Stomata and epidermal cells were counted using the software program Analyze. The counting areas were framed on the photographs by engraving seven evenly distributed grids of $300 \mu m^2$ across the leaf surfaces (following the methods of Poole and Kürschner, 1997), see Fig. 8 for visualization of the counting procedure. S.I. is the percentage of stomata relative to epidermal cells and was calculated for each leaf with seven grid counts, using the equation of Salisbury (1927):

Stomatal index = number of stomata/ (number of stomata + number of epidermal cells) x100%

Pliensbachian CO_2 concentration levels were then calibrated based on the S.I. values, using 1) the stomatal ratio (SR) method (McElwain and Chaloner, 1997) as well as 2) simple transfer function, based on the experimental responses of *A. cupressoides* to raised levels of CO_2 concentrations (Haworth et al., 2010; Steinthorsdottir et al., 2011).

The first method used is the stomatal ratio method (McElwain and Chaloner, 1995; McElwain, 1998). Atmospheric palaeo-CO_2 levels were calibrated by help of the stomatal ratio (SR) method, with the "Carboniferous standardization", which has been found to work best with Palaeozoic and Mesozoic stomatal indices. The stomatal ratio method is based on the comparison between the ratio of stomatal indices of fossil and the nearest living equivalent, and the ratio between CO_2 concentrations today (preindustrial = 300 ppm) and either modern (1:1) or Carboniferous (1:2) CO_2:

CO_2 (palaeo) = (S.I. NLE/ S.I. fossil) x 600

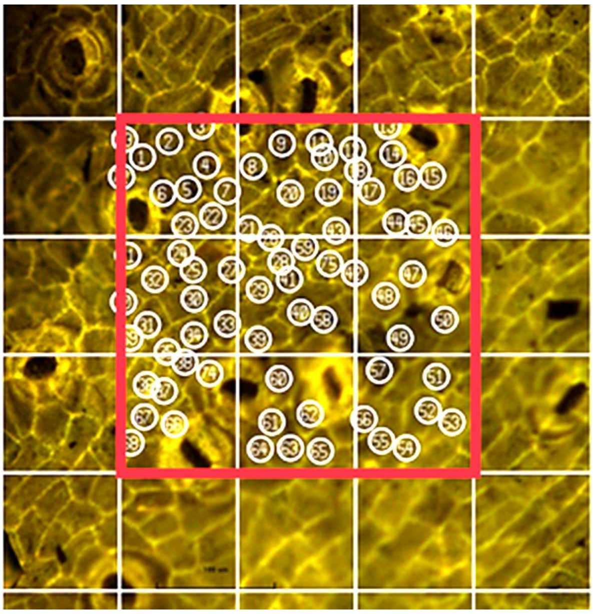

Fig. 8. This figure shows how the stomata and epidermal cells on a part of a leaf. The stomata are the dark pores (holes) and the rectangular features are the epidermal cells. Each white circle represents a count. The results were used for calculating stomata index and density.

The second method, a transfer function, may display more realistically the responses of modern plants (including non-linear response) and is used as addition to the SR method. The regression for *A. cupressoides* is based the experiments of Haworth et al., 2010), and simplified for the low Pliensbachian S.I. values (following the methods of Steinthorsdottir et al., 2011):

CO_2-palaeo= (SI-11.2)/-0.0038

6. Results

The stomata indices of ten fossil *A. helgei* leaves recorded in this study were found to have a fairly narrow distribution of values, with a mean resultant S.I. of 8.9, supported by a running mean analysis (see Fig. 10 and Table 1). The overall spread of stomatal indices was 8.1–9.5%, with the running mean analysis settling on 8.9% after counting four of the leaves (see red curve in Fig. 9, flattening out at leaf nr. 4) and staying at between

8.8–9% for leaves 5–10.

Stomatal indices were next calibrated to CO_2 concentrations, using both a transfer function and the stoamtal ratio method as detailed in section 5 above, in both cases employing *Athrotaxis cupressoides* as NLE, with SI of 11.2% (Haworth et al., 2010). Using the simplified transfer function of Steinthorsdottir et al. ((2011), modified from Haworth et al., 2010), the average CO_2 concentration of *ca*. 600 ppm (597 $^{+/-18.1}$). When using the stomatal ratio method with Carboniferous standardization, the resultant CO_2 concentration was considerably higher, at *ca*. 750 ppm (752.8 $^{+/-5.6}$), see Table 1 for all values indicated with standard errors. The analysis conducted in this study thus indicates Pliensbachian CO_2 concentrations of *ca*. 600 – 750 ppm.

7. Discussion & Conclusion

The main aim of this study was to learn the methods involved in utilizing the stomatal proxy method to reconstruct palaeo-CO_2 concentrations, using fossil plant leaf material. I calibrated Pliensbachian (Early Jurassic) atmospheric CO_2 concentrations using the stomatal indices of the fossil conifer *Allocladus helgeii* from a single stratigraphic level of the Inverleigh Quarry, eastern Australia. Using two separate methods of palaeo-CO_2 calibration with the NLE *Athrotaxis cupressoides*, CO_2 concen-

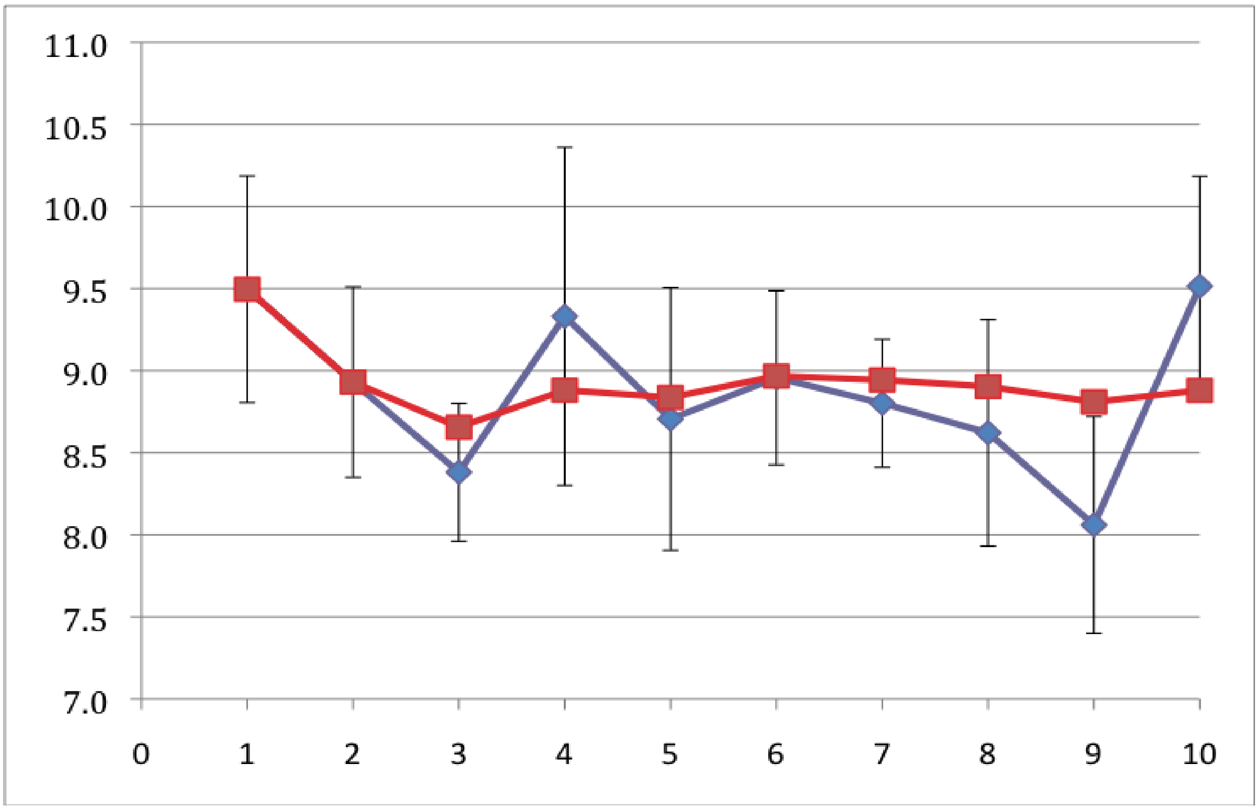

Figure 9. The figure shows the stomatal index for each of the ten analysed fossil leaves of species *A. helgeii* with standard errors (blue curve) as well as the running mean average stomatal index, (red ciurve), settling after four counts at around 8.9%.

Leaf nr.	Stomatal index (SI)	SI standard error per leaf	SI running mean average	CO_2 Transgression	CO_2 Stomatal ratio method
1	9.5	0.69	9.5	448.2	707.6
2	8.9	0.58	8.9	597.1	752.4
3	8.4	0.42	8.7	669.4	776.3
4	9.3	1.03	8.9	610.1	756.6
5	8.7	0.8	8.8	621.6	760.4
6	9.0	0.53	9.0	587.5	749.4
7	8.8	0.39	8.9	593.7	751.3
8	8.6	0.69	8.9	604.3	754.7
9	8.1	0.66	8.8	628.9	762.8
10	9.5	0.67	8.9	610.4	756.7
Mean	**8.9**			**597.1**	**752.8**
St Dev	**0.5**			**57.3**	**17.6**
St Error	**0.1**			**18.1**	**5.6**

Table 1. The table lists the stomatal index for each of the ten *A. helgeii* fossil leaves, with standard error, as well as the mean stomatal index with standard deviation and error, and the running mean average. Concentrations of CO_2 calibrated using a simplified transgression and the stomatal ratio method are listed for each leaf, and as mean contrations were found to be approximately 600 – 700 ppm. This range of concentrations is substantially higher compared to the values of present time (*ca*. 396 ppm in May 2012), as measured at the Mauna Loa Observatory, a research facility in Hawaii (see e.g. http://co2now.org).

However, compared to previously published papers estimating CO_2 concentrations in the Early Jurassic to be generally in the order of 1000 – 2000 ppm (e.g. Royer, 2008; Chandler et al., 1992, Retallack, 2001; Steinthorsdottir et al., 2011, see introduction), the CO_2 concentrations reported here are rather low. This could indicate that Pliensbachian CO_2 concentrations were lower than the Hettangian and Toarcian levels, perhaps reflecting a cooler Jurassic period during the Pliensbachian when the Marburg Group sediments, hosting the *A. helgei* leaf fossils, were deposited. In general during periods with cooler climate and documented absence of ices the CO_2 values have been lower (less than 500 ppm) compared to times with no ice caps when CO_2 levels reached values over 1000 ppm (Royer et al., 2004). Most of the Mesozoic time (65-250 Myr) the CO_2 levels have reached values around 1000- 2000 ppm (Retallack, 2001). Only two periods during the past 300 Ma are characterized with low CO_2 concentrations and both of them are correlated to ice ages (Retallack, 2001). The CO_2 concentration as calibrated here thus indicate a cooler episode in the Early Jurassic, but not sufficiently cool for glaciation. The fossil leaves which the CO_2 concentrations are based upon derive from a single sedimentary level, and more work needs to be done before it can be fully established whether the Pliensbachian was a cool Mesozoic time interval. Should future results support this interpretation, it will be of significant interest to the palaeo-climate research community.

I conclude that I have achieved the goals of my Bachelor thesis research, by learning how to reconstruct atmospheric CO_2 concentrations in the past, using the stomatal indices of fossil plants, together with the appropriate calibration methods. I acquired knowledge about the stomatal proxy method, which relies upon the physiological responses of plants to preserve water, about Mesozoic climate and environment, including mass extinction events, and about the relationship between CO_2 concentrations and climate. In addition, I acquired skills in lab techniques and analysis methods. To summarize, I gained a thorough understanding on how the scientific method and academic research works in practice, and some practice in communicating research results in writing.

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