INFLUENCE OF PALEOGEOGRAPHY, CLIMATE AND EVOLUTION ON CRETACEOUS VEGETATION BIOMES

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ABSTRACT

The Cretaceous Period was a time of extreme greenhouse warmth and a time of major global events. Hence, the Cretaceous represents an interesting geologic time to study a biota that lived under a very different evolutionary context and climate dynamics compared to the present. This thesis examines the geographic patterns of plant biomes based on a global quantitative analysis of palaeobotanical evidence. The distribution, ecology, and composition of Cretaceous floras are assessed through the analysis of databases built from information found in museums, collections, electronic resources and literature published since the 1800s. Biogeographic analyses of Cretaceous woods reveal that araucarioid and podocarpoid conifers were globally codominant in equatorial regions during Early Cretaceous times while cupressoid conifers were most common in mid-latitude. The analysis of pinoid wood reveals these conifers were mainly distributed at high latitudes and exclusively restricted to the Northern Hemisphere since the Cretaceous. Spatial analysis suggests that the loss of conifer forests was linked to the rise of co-occurring angiosperms, which spread and dominated high latitudes until the Late Cretaceous, somewhat latter than indicated by palynological studies. Biogeographic analyses of Cheirolepid conifers show a significant spatial correlation between the distribution of arid climate-sensitive sediments (evaporites and calcrete) and cheirolepid occurrences during the Early Cretaceous. In contrast, Late Cretaceous cheirolepids show a stronger correlation with sediments that indicate humid tropical environments (coal, kaolinite, and bauxite). This finding adds evidence to the fact that the presence of cheirolepid fossil does not exclusively indicate arid environments as previously thought. Biogeographic analyses of Cretaceous plants improve the knowledge of Cretaceous vegetation biomes and allow to investigate possible macroevolutionary patterns over extended spatiotemporal scales, offering a valuable quantitative comparison to integrate with computer climate models proposed for the Cretaceous. Furthermore, two putative Cretaceous woods were examined to clarify their age, provenance and affinity. Results show the valuable use of biogeography, taphonomy, wood anatomy and morphometrics as an essential tool for taxonomic revision of Cretaceous fossil material. An extensive taxonomic re-examination of problematic fossil samples is recommended in order to improve data quality to develop more accurate biome reconstructions.

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CHAPTER 1: THESIS RATIONALE

1.1. SUBJECT OF THESIS

This thesis investigates the influence of paleogeography, climate and evolution on Cretaceous vegetation biomes. Current understanding about the geographic distribution of Cretaceous vegetation is still limited and most hypotheses are either based on climate model reconstructions (e.g. DeConto et al., 2000; Otto-Bliesner and Upchurch, 1997) or information from specific localities (e.g. Cantrill and Poole, 2005; Mendes et al., 2010a) rather than on a global survey of palaeobotanical evidence (e.g. Chumakov et al., 1995). However, the task of completing a global scale study including all kinds of fossil plant material is unpractical for obvious difficulties, such as funding. Thus, in this thesis, the two major datasets obtained, one dealing with fossil wood (Appendix 1), and the other with the record of cheirolepid conifers (Appendix 3), are limited to the collection and analysis of literature available on the internet and information from museums. Unfortunately, this means that a significant amount of relevant studies has not been included in this thesis due to research published in journals of difficult access or not available in electronic media. Literature in other languages, for example, Russian or Chinese was obtained from review papers and not always from the original source.

Among the diversity of fossil plant material, fossil wood represents an especially good subject of study because it comprises a record of arborescent vegetation and therefore allows analysis of canopy-forming trees. Although fossil wood, under fluvial or oceanic conditions, may be transported very long distances (Blokhina, 2004), most fossil wood occurrences have experienced limited transport (up to a few tens of kilometres) from the site of growth (Philippe et al., 2008) and therefore comprise a geographic faithful picture of ancient forest distribution. In addition, preservation of anatomical characters allows identification of general groupings of ancient trees

(Philippe et al., 2003), and tree-rings offer insights into tree growth rates (Creber and Chaloner, 1984a,b; Creber and Francis, 1999; Falcon-Lang, 2005). The present work synthesizes knowledge of Cretaceous woods collected over the last 150 years to address some of the following questions such as 1) How well sampled are Cretaceous rocks? 2) What is the relative abundance of different types of Cretaceous wood, and how have they changed through time? 3) Are biogeographic patterns evident that can be related to climate and physiognomy? 4) What can we learn about the timing and rate of angiosperm diversification and its impact on other forest trees? 5) Was forest productivity elevated in the Cretaceous greenhouse?

The second dataset comprising remains (palynoflora and megaflora, i.e., wood, shoots, leaves, fertile remains) of cheirolepid conifers was developed to understand the evolution, extinction, and ecological tolerances of this extinct family of conifers. This enigmatic and diverse group of plants has long been considered indicative of hot, dry environments (e.g. Vakhrameev, 1970; Kunzmann et al., 2006) as well as costal depositional environments (e.g. Gomez et al., 2002; Upchurch and Doyle, 1981). This study assesses 1) the abundance, decline, and extinction of cheirolepids through the Cretaceous, 2) the geographic correlation between the distribution of cheirolepid conifers and climate-sensitive sediments (such as calcretes and evaporites), and 3) the distribution of cheirolepid conifers in the context of proposed palaeoclimatic reconstructions, to elucidate more about the paleoecology of this extinct conifer family.

A final study in this thesis emerged out of the fossil wood analysis. In the course of checking the ‘quality’ of the literature of fossil woods, I developed an interest in some controversial fossil wood samples comprising putative dipterocarps, whose identity, age and provenance seemed uncertain. Extensive biogeographic, anatomical, and quantitative analyses were employed to help clarify the age, provenance and affinity of these samples, improving the veracity of the fossil record, and solving some longrunning palaeontological disputes. In the discussion, I stress the important of critically reviewing the fossil record, in this way, if global scale evolutionary and biogeographic studies are to be meaningful. For example, some studies based on the Palaeobiological Database (which has been developed on an ad hoc basis, without proper critical review in some cases) are questionable because datasets have not been fully checked.

In the discussion, the new findings of this thesis are examined in relation to previous studies dealing with the evolution and biogeography of Cretaceous floras to augment knowledge of this key time interval in the evolution of plants and the Earth System. In doing so, I stress the importance of fossil plant biogeography as the ultimate proxy (as Humboldt, 1805, 1806 noted) for the calibration of computer climate models.

1.2. AIMS AND OBJECTIVES

1.2.1. Aims

- To evaluate the abundance and distribution of Cretaceous woods at a global scale.
- To assess the abundance and distribution of the main groups of arborescent plants to describe major shifts in vegetation composition during the Cretaceous.
- To estimate biome productivity by comparing Cretaceous tree-rings to recent tree-ring measurements.
- Describe the biogeography of cheirolepid conifers and assess possible distribution differences between pollen, meso- and megafossils of this family at a global scale.
- Test the hypothesis of cheirolepid conifers as an indicator of aridity by analysing occurrences versus climate-sensitive sediment distribution at a global scale.
- Identification of the sample RGM 232138 from Naturalis, Leiden, The Netherlands to clarify the age, provenance and taxonomic affinity of this sample.

- Demonstrate the value of biogeographic, anatomical and taxonomic analyses as quantitative tools to determine the age and provenance of the controversial *Woburnia porosa* Stopes, thereby providing some ‘cleaning’ for the fossil wood database.

1.2.2. Objectives

- Create an inventory of all Cretaceous fossil woods published in the literature and housed in major museum collections by developing a palaeobotanical database.
- Analyse the distribution and biogeographic patterns of Cretaceous woods using GIS tools to plot occurrences in palaeogeographic maps of four different time intervals.
- Build a collection of tree-ring measurements from samples in paleontological collections and the literature to compare Cretaceous and present plant growth characteristics and their variation along the latitudinal gradient.
- Produce a database of the fossil record of the extinct conifer family Cheirolepidiaceae.
- Produce a biogeographic spatial analysis of *Classopollis* and other (meso) macrofossils of Cheirolepidiaceae conifers with the help of GIS tools
- Identification of the sample RGM 232138 found in the Naturalis collection, Leiden, The Netherlands by anatomical comparison with wood of extant families housed in Leiden and Kew Gardens collections.
- Perform a quantitative analysis (PCA and CA) of anatomical characters in extant families and similar fossil woods to establish the systematic affinity of RGM 232138.

- Perform a biogeographic analysis of extant wood and other fossils samples with similar anatomical characters to constrain probable age and provenance.

1.3. THESIS OUTLINE

This thesis investigates Cretaceous vegetation at a global scale.

Chapter 2 reviews the origin of the biome concept and explains the importance of the study of ancient life and the different methods used for its investigation.

Chapter 3 places the present work in context by providing a brief description of the world in Cretaceous times, including major events in the evolution of life and the dynamics of the Earth System during that period.

Chapter 4 comprises a global analysis of the Cretaceous fossil wood record investigating two newly collected datasets. The first database documents occurrences to address forest evolution and biogeography (n = 2238). The second dataset (n = 284) is composed of measurements of growth rings in fossil wood and is used as a proxy to assess biome productivity.

Chapter 5 focuses on the biogeographic analysis of the Cheirolepidiaceae to test the hypothesis that these plants are important indicators of aridity and water stressed environments. A database (n = 475) of the geographic distribution of cheirolepidiaceous fossils is compared with the presence of climate-sensitive sediments to test in detail their correlation using a spatial analysis of fossil-sediment occurrences.

Chapter 6 consists of a systematic study of two dipterocarp fossil woods of supposed Cretaceous age. Wood anatomy, biogeography, taphonomy and quantitative comparative analyses are used to clarify age, affinity and provenance of both samples, one of them previously considered as the oldest (much disputed) evidence of angiosperm wood.

Chapter 7 examines the effects of palaeogeographic events, climatic variations and evolution of angiosperms on Cretaceous biomes originally dominated by gymnosperms. This chapter also elaborates on the palaeoclimatic significance of Cheirolepidiaceae conifers and their use as palaeoclimatic indicators. Finally, weaknesses and possible biases of biome reconstructions at a global scale are also discussed critically.

Chapter 8 reiterates the main conclusions of the thesis and briefly discusses possible future projects, including way to improve the use of the new data used here.

CHAPTER 2: THE BIOME CONCEPT AND BIOME STUDIES

2.1. EXTANT BIOMES

2.1.1. The concept of Biome and ecotones

The first modern attempt to classify vegetation in relation to the environment can be traced to the beginning of the 19th century, to Alexander von Humboldt (1805, 1806) who made extensive surveys in South America and described vegetation types depending on the environment they occupied. Later in 1838 (and 1872) Griesebach proposed the term “formation” as a physiognomic unit replacing Humboldt's original "association". The term "formation" became widely accepted as a physiognomic unit and was extensively used by Clements (Clements, 1902; Weaver and Clements, 1929) who adopted the term to designate geographical regions of the same climax vegetation (Grabherr and Kojima, 1993). The concept of formation was subsequently combined with a zoogeographical notion and gave rise to the concept and term, “biome” (Clements and Shelford, 1939).

More recently, the term *biome* has been used to describe a recognizable complex biotic community of a given region, produced by the interaction of climatic factors, organisms, and substrate (Morris, 1992; Odum, 1971; Spurr and Barnes, 1980). However, the term has also been confused as a synonym for an ecosystem of regional-scale (Tansley, 1935) due to the concept of *ecosystems* being regarded as a cause-effect relation between environment and organisms (McIntosh, 1985). Other authors (i.e. Bailey 1998; Helms, 1998) make use of the term *biome* in a broader sense including abiotic factors such as habitat and other physical factors (e.g. substrate and soil), however, this contradicts the original definition of *biome* (*sensu* Clements and Shelford, 1939) which only considers biotic elements.

Furthermore, the concept of *ecotone* was implemented to refer to the zone between two types of formations where a change in vegetation is clearly observed (Clements, 1902; Lloyd et al., 2000). The ecotone could be defined by qualitative and quantitative features, for example, the sharpness of vegetation transition, species composition and richness, change in physiognomy, and the presence of exotic species (Walker et al., 2003). Abrupt boundaries between formations occur mainly where there are sharp environmental changes caused by geomorphologic features such as large canyons and rocky substrate formed in volcanic events (Wilson and Agnew, 1992; Auerbach and Shmida, 1993). In the context of climate change, ecotones regained interest because environmental changes are usually first perceived at ecotones (Allen and Breshears, 1998; Kupfer and Cairns, 1996; Neilson, 1991).

The term *biome* used throughout this thesis describes biogeographic regions based plant associations and climatic parameters (temperature and precipitation) in a broad and general sense. The faunal element of the original concept of *biome* (*sensu* Clements and Shelford, 1939) is excluded since the study of Cretaceous fauna at a global scale is not within the remit of this thesis.

2.1.2. Present-day biome classification

In the History of Ecology there have been many classification schemes to describe and characterize the relation of vegetation and environment at a large geographical scale based on the many approaches, methods, and purposes (Mucina, 1997). One of the first modern classifications of climate and perhaps the most comprehensive is Köppen’s climate classification (1936) based on the concept that native vegetation is the best expression of climate. Climate zone boundaries in this scheme are defined by temperature, precipitation and seasonality in relation to vegetation distribution (Kottek et al., 2006).

A more detailed scheme created by Holdridge (1979) defines biomes based on climatic parameters including evapotranspiration and net primary productivity (Fig. 2.1) (Holdridge, 1979). The measurement of evapotranspiration accounts for the movement of water from the soil, canopy interception, and waterbodies to the atmosphere (Swank and Douglass, 1973). Holdridge's scheme was later simplified by Whittaker (1970) who based his classification only on precipitation and temperature. He describes the gradient in temperature present at different altitudes and latitudes and subsequently summed the effects to get an overall temperature and moisture gradients (Whittaker, 1970). This analysis allows a qualitative expression of the relationship between of types of vegetation and climatic parameters on a worldwide scale (Whittaker, 1970).

Walter's system in contrast with both Whittaker's and Holdridge's schemes, takes into account the seasonality of temperature and precipitation (Walter and Box, 1976). This system proposes 9 major biomes: Equatorial, Tropical, Subtropical, Mediterranean, Warm Temperate, Nemoral, Continental, Boreal, and Polar, each further subdivided into communities (Walter and Box, 1976). The boundaries of each biome correlates to the conditions of moisture and temperature stress, which strongly determine the vegetation that defines the region (Walter and Box, 1976). Later on, Bailey (1976, 1998) developed a similar classification system based on climate patterns, which he divided into seven domains (polar, humid temperate, dry, humid, and humid tropical). However, both Walter's and Bailey's schemes are not very frequently used today.

In recent years, the World Wide Fund for Nature (WWF) assembled a team of biologists to develop an ecological land classification system for identifying priority areas for conservation (Olson et al., 2001). This is the most used classification to prioritize conservation areas (Loyola et al., 2007). Although the use of the WWF biome system has been considered to be unreliable to define the conservation of certain ecoregions (Londoño-Murcia et al., 2010), its simplicity offers a practical frame of reference for broad biogeographic comparisons between modern and ancient biomes and therefore used for comparison purposes in this thesis.

2.1.3. Modern biomes according to the WWF biome system

Tropical and Subtropical biomes	Mean Annual Temperature	Mean Annual PPT
Tropical and subtropical grasslands, savannahs, and shrublands	Summer 25 – 30 °C Winter 20 – 25 °C	500 – 1300 mm
Tropical and subtropical moist broadleaf forest (rainforest)	MAT ~20 °C	2500 – 4500 mm
Tropical and subtropical dry forest	Summer 23 °C Winter 27 °C	300 – 400 mm
Mangrove	Summer 30 °C Winter 16 °C	>2000 mm
Temperate Biomes		
Temperate grasslands, savannahs, and shrublands	Summer 40 °C Winter - 40 °C	250 – 500 mm
Temperate broadleaf and mixed forest	Summer 15 °C Winter 3 °C	600 – 1500 mm
Dry Biomes		
Arid desert	Summer 40 – 50 °C Winter 18 °C	0 – 20 mm
Semiarid desert	Summer 21 – 38°C Winter 10 °C	20 – 40 mm
Mediterranean vegetation	Summer 31 °C Winter 16 °C	~500 mm
Xeric shrublands (Dry Steppe)	Summer 37 °C Winter 0 °C	~250 mm
Polar and Mountain biomes		
Polar Tundra	Summer 3 – 12 °C Winter -28 – -50 °C	150 – 250 mm
Alpine Tundra (Montane Forest)	Summer 10 °C Winter < 0 °C	300 – 400 mm
Taiga	Summer ~18 °C Winter < 0°C	200 – 750 mm

Table 2.1. Temperature and precipitation of present biomes (summarized from Olson et al., 2001) see map in Figure 2.2.

2.1.3.1. Vegetation biome composition for WWF Scheme

Biome	**Representative plant genera**
Polar Tundra	*Abies, Alnus, Alopecurus, Arctophila, Betula, Cassiope, Carex, Cetraria, Cladina, Dryas, Eriophorum, Latix, Ledum, Picea, Pyrola, Salix, Saxifraga,* and *Vaccinium*
Alpine Tundra	*Anemone, Calliergon, Cladonia, Ledum, Oxyria, Silene, Salix, Saxifraga,* and *Trisetum*
Taiga	*Abies, Arctostaphylos, Betula, Juncus, Juniperus, Pecia, Picea, Pinus, Polemonium, Populus, Pseudotsuga,* and *Rubus*
Arid desert	*Ambrosia, Carnegiea, Cercidium, Dalea, Echinocereus, Encelia, Ferocactus, Fouquieria, Opuntia, Olneya,* and *Yucca*
Semiarid desert	*Acacia, Cassia, Encelia, Franseria, Krameria, Larrea, Prosopis,* and *Ziziphus*
Mediterranean vegetation	*Arbutus, Buxus, Callistemon, Cistus, Clematis, Dalbergia, Dalea, Euphorbia, Fraxinus, Juniperus, Larrea, Olea, Pinus, Pistachia, Punica, Quercus, Salvia,* and *Tipuana*
Xeric shrublands (Dry Steppe)	*Acanthothamnus, Artemisia, Baccharis, Calliandra, Cercocarpus, Chrysactinia, Cordylanthus, Cytisus, Mammillaria, Morkillia, Olea, Protea, Quercus, Simmondsia,* and *Ziziphus*
Temperate grasslands, savannahs, and shrublands (Steppe)	*Bouteloua, Brickellia, Buchloe, Cenchrus, Digitaria, Distichlis, Eragrostis, Flaveria, Malvstrum, Vervesina, Vigueria,* and *Waltheria*
Temperate broadleaf and mixed forest	*Abies*, *Acer*, *Araucaria, Betula*, *Carpinus, Comarostaphylis*, *Eucalyptus, Fagus*, *Juglans, Nothofagus*, *Picea*, *Pinus*, *Podocarpus, Quercus*, and *Taxus*
Mangrove	*Aegialitis, Aegiceras, Avicennia, Bruguiera*, *Ceriops, Conocarpus, Laguncularia, Nypa,* and *Rhizophora*
Tropical and subtropical grasslands, savannahs, and shrublands	*Acacia, Andropogon, Aristida, Carpobrotus*, *Erioneuron, Hilaria, Larrea, Lycurus, Muhlenbergia, Senecio*, and *Vellereophyton*
Tropical and subtropical moist broadleaf forest (Rainforest)	*Annona*, *Bambusa, Bougainvillea, Cattleya*, *Cedrela, Ceiba, Chondrodendron, Cocos, Coffea, Croton, Eugenia, Ficus, Hevea, Lepidocaryum, Musa, Manilkara, Protium, Swietenia, Syzygium,* and *Tabebuia*
Tropical and subtropical dry forest	*Beaucarnea, Bursera, Ceiba, Cercidium, Cyrtocarpa, Euphorbia, Haematoxylon, Ipomea, Lysiloma, Leucaena, Lonchocarpus, Pseudosmodingium,* and *Yucca*

Table 2.2. Endemic plant genera in present biomes (Billings, 1968; Murphy and Lugo, 1986; Rzedowski, 1975).

2.1.4. Impact of Palaeogeography, Climate and Evolution on modern biomes

Changes in the geographic landscape such as continental drift, local tectonic events, erosion, and volcanism constantly shape and create land configurations giving origin to new seaways, basins and mountain ridges (Whittaker and Fernandez-Palacios, 2006); therefore, palaeobiogeography plays an important role in the evolution of continental plants communities (Philippe et al., 2006). Furthermore, geographic features have significant effects on the global climate by modifying ocean and wind currents, rainfall, drainage, altitude and latitude of certain region (Boelhouwers et al., 2008). For example, the collision of India into Asia gave birth to the Himalayas, which is, partly, responsible for the aridity of Tibet and western China due to the blocking of the moist air currents from the Indian Ocean (Harris, 2006).

Environmental and geographical changes transform biomes because they represent a mechanism for species selection and consequently playing an essential role in the evolution of plant, animal and microbial communities (Shaver and Jonansson, 1999; Luo et al., 2010). Speciation, species replacement and extinctions in biomes are determined by abiotic and biotic factors; geographic (latitude, elevation) and environmental (temperature and precipitation) create abiotic barriers or bridges that affect migration, reproduction, competition and productivity; biotic factors include mutation, pollination, and disease (Chiotti and Lavender, 2007; Craw et al., 1999; Willis, 2009).

Evolutionary changes result in new adaptations that can fully transform biome ecology, for example, during the Late Cretaceous grasses developed new characters that allowed them to adjust to a significant increase in aridity, which permitted grasslands to spread globally and become one of the Earth’s dominant biomes during the Late Neogene (Strömberg, 2011; Woodward et al., 2004).

2.2. RECONSTRUCTION OF ANCIENT BIOMES

2.2.1. Past biomes

Past biomes comprise fossil evidence of fauna, flora and microorganisms (e.g. fungi and bacteria) that lived in a certain region in a specific period of Earth's history, thus the fossil record represents a glimpse of ecosystems that lived under certain evolutionary, climatic, atmospheric, and geographic circumstances (Selden and Nudds, 2005). Paleontological studies include vertebrates (e.g. Brusatte et al., 2010), invertebrates (e.g. Nicholls and Russell, 1990), micropaleontology (foraminifera, conodots, diatoms and dinoflagellates) (e.g. Cronin, 1999), fungi (Garcia Massini et al., 2012) and plants (e.g. Uhl, 2006). The study of fossil land plants is very extensive and comprehends all eras from their origins in the Ordovician to Quaternary floras; palaeobotany includes the study of fossil vegetative (leaves, wood and shoots), and reproductive organs (cones, flowers and seeds), and the study of pollen and spores by palynology as an adjoined discipline (Taylor et al., 2009).

The reconstruction of ancient biomes, however, is not reduced to the study of fossil material but it also involves other disciplines (e.g. taphonomy, sedimentology, geochemistry) that focus on the study of depositional environments. For example, the study of isotopes is used to estimate past temperatures and precipitation from certain types of rocks (Haxeltine et al., 1996; Neilson, 1995). Sedimentology studies the processes of deposition and analyses climate-sensitive sediments to interpret the locality where fossils are found, and placed in a larger regional geological context (Widdowson, 2007). The integration of both fossils and depositional environment studies expand our knowledge of biome composition, productivity, diversity, evolution, and palaeoclimate.

2.2.2. The importance of ancient biome reconstructions

In recent years climate change has awakened the interest of scientists to assess its patterns, results, and consequences for the Earth's ecosystems (Walther et al., 2002). In order to investigate this, climate models are used to simulate possible long-term vegetation changes due for example to CO_2-induced global warming (Sykes et al., 1996). However, the only way to test these models is to compare geological evidence of ancient climate (e.g. lithological and paleontological) with results modelled for past epochs (Herman, 2009). Biome reconstructions incorporate information obtained from palaeontological evidence and results from climate model simulations to improve our knowledge of how vegetation may change in the future (Herman, 2009; Saltzman et al., 2008). The study of palaeoclimate records of geologic time periods characterized by extreme global warmth such as the Cretaceous and the Paleocene–Eocene Thermal Maximum (PETM) are important for a better understanding of the Earth's climate system operating in an exceptionally warm mode (Forster et al., 2007). Therefore information obtained from the reconstruction of ancient biomes is not only relevant to paleontology, but also to other related subjects such as the management and conservation of biological diversity in a changing climate (Willis and Bhagwat, 2010).

Paleontological data produced by biome reconstruction also provide a time frame reference for molecular biology and phylogeny by making it possible to constrain the time of first appearance of certain morphological characters, which help to answer questions about rates of molecular evolution and systematic classification (Magallón, 2004).

2.2.3. Previous attempts to reconstruct past biomes

The literature on biome reconstruction is large and the following are just some representative examples to show different approaches and results offered by these types of studies. Previous work on biome reconstruction includes the integration of floral and lithological data to determine climatic zones for the Permian (Gibbs et al., 2002; Rees et al., 2002). The importance of this series of studies is the use of floral data for interpreting climate-sensitive sediments in detail and the quantitative approach of Permian vegetation to calibrate climate model simulations. Using this approach they concluded that there was an important loss of equatorial 'rainforests' during the Permian while temperate regions were heavily-vegetated and the equatorial region was only seasonally wet, indicating a latitudinal temperature gradient less severe than at present (Rees et al., 2002).

Further biome reconstructions include research of Jurassic–Early Cretaceous vegetation of Gondwana developed by Philippe et al. (2004) who made a detailed analysis of fossil wood that distinguished five climatic zones (summer wet, desert, winter wet, warm temperate, and cool temperate) based on species associations and abundances. The flora of Gondwana that once was regarded as relatively uniform and provided a new understanding on the distribution of Late Jurassic climatic zones in the southern hemisphere that helps to explain the evolutionary changes that occurred later in the mid-Cretaceous (Philippe et al., 2004).

Furthermore, Spicer et al., (1993) assess the Cretaceous global phytogeography and estimate temperature base on fossil plants to develop a climate signal to evaluate the ecological radiation of angiosperms. They conclude plant productivity was concentrated at mid and high latitudes, represented by temperate open forests dominated by conifers, ferns, cycadophytes, pteridosperms and sphenophytes at mid latitudes and polar cool temperate conifer rain forest in high-latitude coastal areas. Low-latitude vegetation was xeromorphic and tropical ever-wet vegetation.

A global biome reconstruction for the Middle Pliocene was developed by Salzmann et al. (2008) based on a comparison of model simulations and palaeobotanical data. The fossil compilation of more that 200 localities indicate a general warmer and moister climate that shifted temperate vegetation northwards and tropical vegetation expanded reaching desert regions.

Chumakov et al. (1995) developed a reconstruction of Cretaceous biomes based in climate sensitive sediments by Chris Scotese and fossil material. Their work offers biome distribution maps for the Berriasian, Aptian, Albian, Senomanian, Santonian, and Maastrichtian. Biomes described in this publication are the northern and southern high-latitude temperate humid belts in polar regions, northern and southern mid-latitude warm humid belts, northern and southern hot arid belts, and an equatorial humid belt. In Berriasian and Aptian maps a tropical–equatorial hot arid belt is proposed, however, recent literature (e.g. Hay and Floegel, 2012) suggest this interpretation is probably a result of absence of fossil evidence.

Vakhrameev (1991) published a vast amount of Cretaceous plant research that previously only available in Russian. He summarises and makes accessible valuable data on the USSR, China and Japan floras dividing the continents into regions (i.e. Siberian-Canadian, Euro-Sinian) and provinces showing the palaeolatitudinal climatic arrangement of Cretaceous floras. Although palaeoclimatic interpretations are considered nowadays outmoded, Vakhrameev’s work fills an important gap of knowledge on the biogeography of Russian fossil floras (Francis, 1993).

2.2.3.1. Limitations and weaknesses of past biome studies

Although biome reconstruction has proved to offer interesting results, they have also weaknesses in their attempt to describe the interactions between vegetation and climate due to the nature of the fossil record itself, which is incomplete and fragmented (Foote and Sepkoski, 1999). Paleontological evidence is often subjected to sampling biases, fossil misidentification and age uncertainties and therefore its quality may depend on the approach, discernment and type of analyses applied to fossils (Benton and Storrs, 1994).

One of the main limitations in palaeobotany is the absence of a method to analyse all of the available fossil plant data due to limited availability of resources for research (Rees et al., 2000). The low resolution of spatial models and paleontological evidence coverage is also one of the key challenges in biome reconstructions (Salzmann et al., 2008).

The use of leaf morphology, stomata density and other environmental proxies to calculate climatic parameters also have disadvantages; for example, seasonality and productivity inferred from growth rings in fossil wood (e.g., Creber and Chaloner, 1985; Francis, 1986; Spicer and Parrish, 1990) has been proved to be consistent for Tertiary and Quaternary studies, however, these proxies tend to be less reliable for pre-Tertiary studies (Wheeler and Baas, 1993).

Although the use of computer climate models in biome reconstructions offers important information on past climates, they tend to have disadvantages because they represent simplifications of the real world (Spicer et al., 2008). For example, major discrepancies between temperatures suggested by computer models and fossil evidence at high-latitudes, where models predict low temperatures far beyond the tolerance limits indicated by fossil plants (Rees et al., 2000). Other important things to consider are the various uncertainties in delimiting biomes using climate parameters, as well as uncertainties in model physics and/or geological boundary conditions between biomes (Salzmann et al., 2008).

2.2.4. Cretaceous vegetation biomes

During the Early Cretaceous, the world maybe divided into three main floral provinces, the Arctic, the Equatorial and the Antarctic province (McLoughlin, 2001; Vakhrameev, 1991), also referred in palynological literature as Boreal, West Africa–South America, and Gondwana provinces (Herngreen and Chlonova, 1981).

The dominant components of the Early Cretaceous Arctic Province include ferns, cycads, ginkgoes, Pinaceae and Taxodiaceae (Cupressaceae) conifers present in localities such as Canada (e.g. Falcon-Lang et al., 2003; Harland et al., 2007) Alaska (e.g. Parrish and Spicer, 1988), and Asia (e.g. Takahashi and Suzuki, 2003; Wang et al., 2007).

The Equatorial Province was characterized by the presence of dry vegetation such as cycads, Cheirolepidiaceae and Cupressaceae conifers (Doyle et al., 1982; Vakhrameev, 1991). Important localities in this province include the Potomac Group (e.g. Herendeen, 1991; Srinivasan, 1995), and the European Wealden facies (e.g. Gerards et al., 2007; Watson and Alvin, 1996). Palynology suggests the absence of rainforests from these regions during the latest Jurassic–Early Cretaceous, while semi-arid floras dominated tropical Africa and South America (Rees et al., 2000). However, new palynological observations suggest that the vegetation of Gondwana was more humid than previously thought (Mejia-Velasquez et al., 2012).

The Antarctic Province was dominated by ferns, podocarpaceous, araucarian, minor taxodiaceous/cupressaceous conifers and other extinct gymnosperms taxa (Cantrill and Poole, 2005; Hill and Brodribb, 1999). Studies on Early Cretaceous floras from the Southern Hemisphere include the Otway Basin in Australia (e.g. Cantrill, 1992; Hill, 1995), the Antarctic Peninsula (e.g. Cesari, 2006; Falcon-Lang and Cantrill, 2001; Torres et al., 1997), and Patagonia (e.g. Del Fueyo and Archangelsky, 2002; Tidwell and Wright, 2003).

Subsequently, during the Late Cretaceous the number of modern angiosperm families increased rapidly in floras of North America (Crane and Herendeen, 1996; Graham, 1993). In Cenomanian–Santonian times there was a progressive replacement of previous plant communities until the mid to Late Cretaceous when angiosperms became important both in terms of diversity and abundance (Cantrill and Poole, 2005). By the Campanian–Maastrichtian the extinction of earlier forms allowed the appearance and diversification of modern angiosperm families (Friis et al., 2011; Heimhofer et al., 2005), probably facilitated by the warming trend towards the Late Cretaceous due to increased atmospheric CO_2 levels (Berner, 1990).

Fossil leaves from the Arctic region at 82°N suggest a MAT of ~6 ºC (Spicer and Herman, 2010), which is consistent with several occurrences of fossil reptiles (e.g. Brinkman and Tarduno, 2005) and high ocean temperatures (Jenkyns et al., 2004). Late Cretaceous floras from the northern hemisphere include Siberia (Moiseeva, 2013; Spicer et al., 2008), Canada (Falcon-Lang et al., 2004), Wyoming (Wing et al., 1993), Texas (e.g. Estrada-Ruiz et al., 2012; Wheeler et al., 1994), and Europe (e.g. Falcon-Lang et al., 2001; Gomez et al., 2002; Iamandei and Iamandei, 2004).

The fossil record in the Southern Hemisphere shows that during the Late Cretaceous latitudes of 65º S were dominated commonly by forests that grew in a warm seasonal environment (Francis, 1999; Hathway et al., 1998). Equally, Late Cretaceous floras from the Southern Hemisphere, indicate forest composition in the Antarctic region went from being dominated by ferns, conifers and cycads during the Early Cretaceous, to progressively become dominated by angiosperms from the mid-Cretaceous onwards (Eklund, 2003). The evidence of this vegetation shift has also been observed in floras from the Antarctic Peninsula (e.g. Cantrill and Poole, 2002; Falcon-Lang et al., 2001; Falcon-Lang and Cantrill, 2000, 2001; Poole and Cantrill, 2006).

Palynological evidence and regional reviews have yielded valuable information on the different vegetation provinces and their evolution throughout the Cretaceous (e.g. Chumakov et al., 1995; McLoughlin, 2001; Vakhrameev, 1991). However, until now there have been no attempts of documenting the palaeobotanical record at a global scale to test and corroborate our current knowledge of Cretaceous biomes.

FIGURES CHAPTER 2

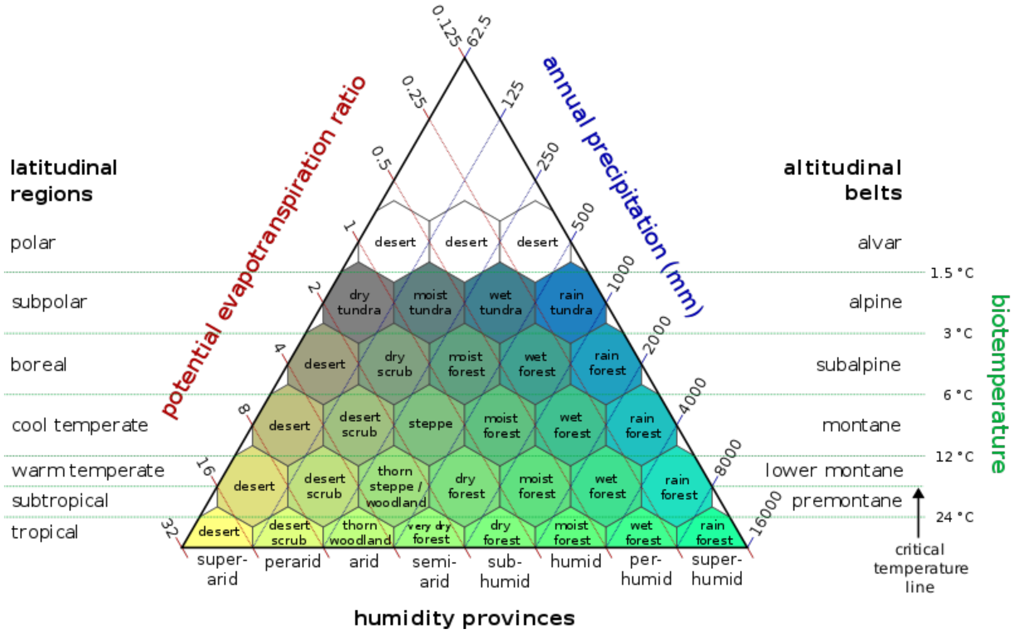


Figure 2.1. Life zone classification scheme (Holdridge, 1979).

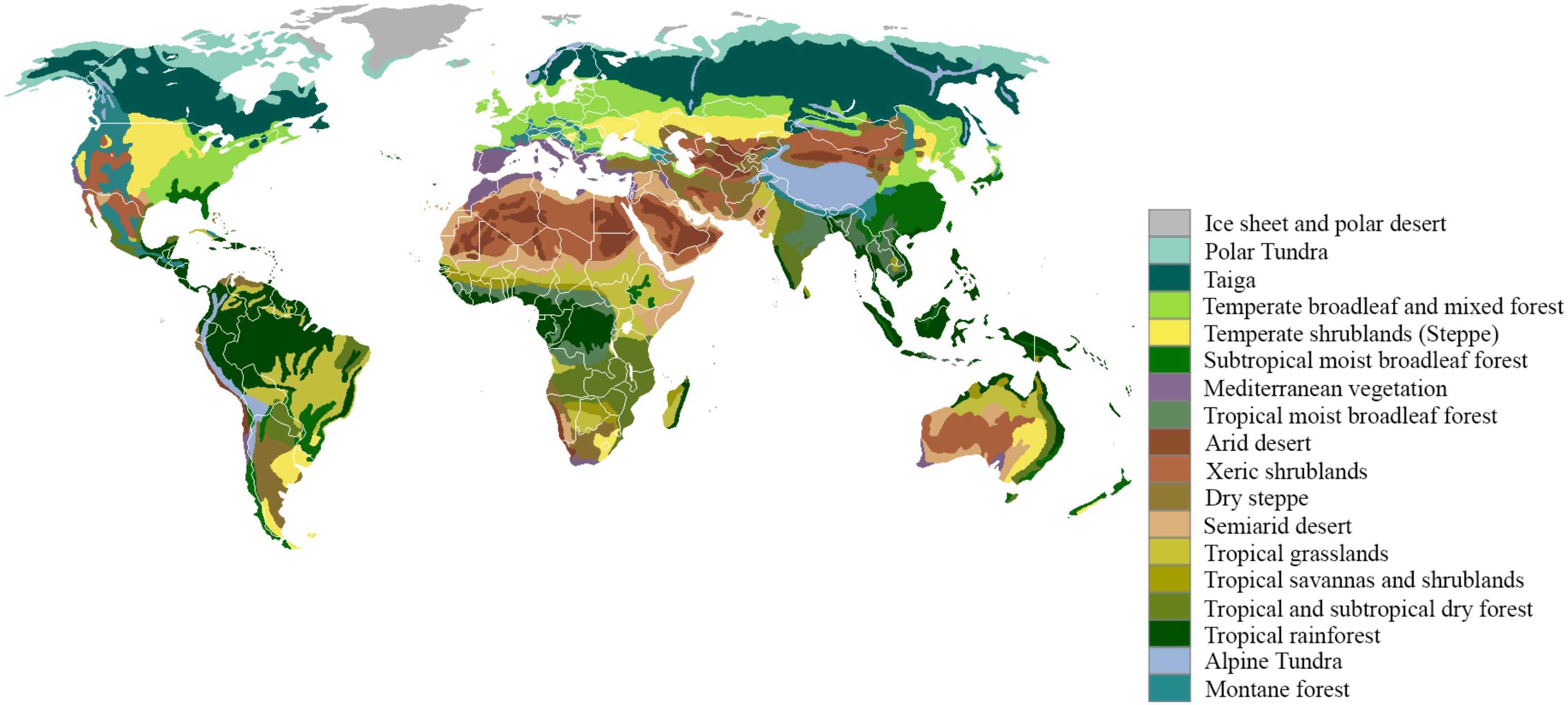


Figure 2.2. Modern biomes according to the World Wide Fund for Nature biome biome system (Olson et al. 2001).

CHAPTER 3: THE CRETACEOUS WORLD

3.1. INTRODUCTION

The purpose of this chapter is to introduce the reader to some of the major events that occurred in the Cretaceous in relation to the global paleogeography, climate and biota. The Cretaceous is the name given to the period of time in Earth's history from 145.0 to 66.0 million years ago (Fig. 3.1), the third and final period of the Mesozoic Era (Walker et al., 2012). Cretaceous is a name derived from the Latin word for chalk, *creta*. Chalk is a common type of sedimentary rock that formed during this period (Hay, 2008). The term Cretaceous was first used in 1822 by d'Omalius d'Halloy, a Belgian geologist who mapped the Paris Basin strata (Muller and Schenck, 1943). Chalk was later correlated with chalks mapped earlier and formally named in the geological map of England and Wales by William Smith (1815). Since its formal definition in the Nineteenth Century, geologists correlated the Cretaceous System with chalks found in Europe and all the other continents (Muller and Schenck, 1943).

3.2. PALAEOGEOGRAPHY

At the start of the Cretaceous Period the supercontinent of Pangaea had already split into two smaller continents; Laurasia in the North and Gondwana in the South; these were divided by an equatorial sea known as Tethys (Fig. 3.2). There was a circum-African Seaway extending from the western Tethys “Mediterranean” region through the North and South Atlantic and into the early Indian Ocean (Hay et al., 1999). At the same time (Albian–Cenomanian) the Atlantic Ocean was opening between North America and Europe and between Africa and South America (Fig. 3.3) (Blakey, 2011 date accessed). The rapid expansion of the Atlantic was due to the high seafloor production at the mid-oceanic ridge system, which extended at one of the highest rates ever documented (70–86 mm/a) (Seton et al., 2009). The fast seafloor production altered the volume of the ocean basins and displaced a large volume of seawater causing a significant rise of the sea level (Hallam and Wignall, 1999).

During the Cenomanian–Turonian, the final break-up of Gondwana drove sea level to reach its maximum causing widespread flooding of low altitude areas, forming the great epicontinental seas in North America, northern Africa, and Eurasia (Fig. 3.4) (Hart, 1990; Hay et al., 1999; Philip et al., 1993). After the formation of the Atlantic Ocean, the Tethys was divided into two autonomous parts; the Caribbean basin in the west and the Late Cretaceous Tethys in the east (Zharkov et al., 1998).

Meanwhile in the Pacific Ocean a long episode of rapid growth and reorganization developed subduction zones along the western margin of North and South America causing major volcanic events (Anderson, 1994). Other significant events such as continental rifting and effusive volcanism in the form of mantle hot spots caused extensive flood basalts to develop (e.g. Deccan Traps of India and Parana-Etendeka field) (Courtillot et al., 1986).

By the latest Cretaceous the Atlantic-Indian Ocean was a large complex of basins extending around Africa and connecting with the Pacific now formed by a central deep pelagic zone and other widened abyssal basins (Fig. 3.5) (Hay et al., 1999; Zharkov et al., 1998).

During the Tertiary the breakup of the Pangaea was at its latest phase, as the separation of the last gondwanan fragments such as Antarctica, Australia, Africa, and South America, gave place to the Atlantic as we know it today (Scotese et al., 1989).

3.3. CLIMATE, ATMOSPHERE AND OCEAN CIRCULATION

The Cretaceous was a time of elevated global temperatures (Frakes et al., 1995; Norris et al., 2002; Valdes, 2000; Wilson et al., 2001). Major tectonic events, such as the break-up of Gondwana, and sea level changes resulted in drastic climatic re-organization (Fluteau, et al., 2007).

Elevated temperatures in the Cretaceous ocean is suggested by ∂^{18}O isotope analysis of foraminiferal shells, which indicate an average sea surface temperature of 15–20 °C in the Arctic Ocean during the Albian–Maastrichtian interval and a thermal maximum during the Turonian–Cenomanian (Barron, 1983; Forster et al., 2007; Huber et al., 2002; Norris et al., 2002; Wilson et al., 2002). However, sea-surface temperature reconstructions based on δ^{18}O isotope data observed in foraminifera are subject to uncertainties, for example, ocean salinity variations have a direct effect on the density driven thermohaline ocean circulation (Cooper, 1988; Murtugudde and Busalacchi, 1999) and therefore the reliability of isotope studies is still debated (Schouten et al., 2003). On the other hand, the absence of polar and high-latitude glaciers and ice restricted only to the Antarctic continent (Jenkyns et al., 2004, 2012; Miller et al., 2003) support the high sea-surface temperatures reported by these studies for the Arctic Ocean.

High temperatures during the Cretaceous (Fig. 3.6) also had a major impact on land ice and ice cap volume, causing a significant increase in sea levels (Hart, 1990; Miller et al., 2003; Stoll and Schrag, 1996), which furthermore favoured climate fluctuations (Haq et al., 1987).

In contrast to the previous common belief of warm stable (equable) climates in the Cretaceous, there is faunal and floral evidence of cool-temperate to sub-tropical conditions near to the poles (e.g. Cantrill and Poole, 2005; Falcon-Lang, 2003; Frakes and Francis, 1990). The study of mudstones located in central Australia containing outsized exotic blocks have led to the conclusion that the blocks were emplaced by ice-rafting, implying that high-latitude ice was present at sea level (Frakes and Francis, 1988). This is supported by findings of glendonites, a type of calcite that suggest the presence of periodic sea-ice at high-latitudes (Frances and Frakes, 1988). However, the timing of Cretaceous cooler episodes, which occurred mostly during the Early Cretaceous, is still not well constrained and understood (Steuber et al., 2005).

The Cretaceous palaeobotanical record also supports this scenario of climate variations, showing a 15° poleward shift of tropical vegetation (Fig. 3.7) (Vakhrameev, 1991). Mid-Cretaceous fossil floras at high latitudes indicate mean annual temperatures of 9 °C in Siberia (Herman and Spicer, 1996; Spicer et al., 2002; Vakhrameev, 1991) and 10 °C in Alaska and the Antarctica Peninsula (Barrera et al., 1987; Spicer and Corfield, 1992; Spicer et al., 1987, 1993). Forests growing at high latitudes also had a major impact on surface air temperatures and the hydrologic cycle by providing more efficient energy transport into the interior of the continents via increased precipitation (Hay, 2008). Vegetation and climate at high-latitudes in Cretaceous times had very different dynamics from those we know of tundra in the present (Fluteau, et al., 2007).

The concentration of carbon dioxide in the atmosphere is believed to be a primary determinant of climate (Arrhenius, 1896). During the Cretaceous, atmospheric greenhouse gasses (CO_2 and CH_4) and water vapour content in the atmosphere had very high concentration levels (Hay, 2008). In comparison to our present levels of CO_2 and CH_4, different studies based on stomatal and paleosol proxies, and model results suggest the Cretaceous atmosphere had higher levels of CO_2 and CH_4 (Bice et al., 2006; Haworth et al., 2005; Nordt et al., 2002), however the lack of consensus on the concentration levels is caused by large uncertainties when comparing different studies (Fig. 3.8) . However, higher atmospheric levels of CO_2 and CH_4 would have allowed much greater amounts of heat transport from the equator poleward than in the present time causing warmer climates (Barron, 1983; Ufnar et al., 2004).

The circulation of Cretaceous oceans was also very different from today, with episodes of local anoxia occurring during the earlier Cretaceous and becoming regional to global in extent during the middle of the Cretaceous (Arthur and Schlanger, 1979; Bralower et al., 1994). Global changes in the ocean-climate system are related to ocean crust production, volcanism, hydrothermal activity increase, plankton evolution, sea level changes, and large temperature variations, which consequently triggered ocean circulation changes, water column stratification, nutrient partitioning, carbon cycle disruption, and widespread carbonate deposition (Leckie et al., 2002). The expansion of epicontinental seas was the result of warm climates coupled with poor oxygen water masses caused by poor circulation (Seton et al., 2009).

3.4. CRETACEOUS LIFE

3.4.1. Cretaceous flora

During Cretaceous times, the Earth was dominated by conifers, which formed the framework of most forests. Other diverse elements included ferns, cycads, cycadeoids, and later during the Late Cretaceous, angiosperms. Sphenopsids and lycopsids were relatively insignificant.

3.4.1.1. Conifers

The origin of conifers goes back to the mid-Carboniferous. The oldest conifer-like plants are the Cordiatales, which originated during the Serpukhovian (Miller, 1977) with true conifers appearing first in the Moscovian (mid-Pennsylvanian). The conifer clades present in the Cretaceous are broadly related to the extant families Araucariceae, Cupressaceae, Pinaceae and Podocarpaceae (Fig. 3.9) (Farjon, 2001; Taylor et al., 2009) as well as some extinct groups such as the Cheirolepidiaceae (Watson, 1983). Some other extant families (Sciadpityaceae, Cephalotaxaceae, Taxaceae) as yet have a poor fossil record and are not addressed here.

Fossils of the Araucariaceae are among the most beautifully preserved, however, they are sparse and rare in the fossil record in most parts of the world (Kershaw and Wagstaff, 2001). There are reports of araucarian fossils from the Paleozoic and the Upper Triassic but their identification is doubtful (Miller, 1977). The greatest diversity and widest distribution of araucarians occurred during the Jurassic and it extended through the Early Cretaceous when they were geographically widespread, and even occurred in the Northern Hemisphere (Hill and Brodribb, 1999). However, since Late Cretaceous times, the family has gradually declined in numbers of taxa and its geographic distribution today is restricted to the Southern Hemisphere (Fig. 3.10A) (Kunzmann, 2007; Stockey, 1982). Cretaceous fossils related to the Araucariaceae commonly found include *Wairarapaia* seeds (Cantrill and Raine, 2006), *Wollemia* cones (Chambers et al., 1998), *Araucariacites* pollen (Pole and Vadja, 2009), *Agathoxylon* wood (Falcon-Lang and Cantrill, 2002), and some types of *Brachyphyllum* foliage (Kunzmann et al., 2004), for example.

The Cupressaceae is the largest and most widely distributed of the extant conifer families and in recent studies it incorporates members of the former family Taxodiaceae

(Fig. 3.10B) (Farjon, 2005). Some features of Cupressaceae can be traced back to fossils of Permian age such as *Pseudovoltzia* (Voltzioideae) (Miller 1977; Miller, 1982; Schweitzer, 1963), but the earliest undisputed evidence dates from the Middle Triassic of Antarctica (Yao et al., 1997). The fossil record of Cupressaceae is divided into five mayor divisions Taiwanioideae, Athrotaxoideae, Sequoioideae, Taxodioideae, and Cupressoideae; these were already present and distributed worldwide by the Early Cretaceous (Taylor et al., 2009). Fossil evidence of Cupressaceae includes *Athrotaxites* foliage (Miller and LaPasha, 1983), *Cunninghamiostrobus* cones (Miller, 1975), *Metasequoia* (Canright, 1972), *Protaxodioxylon* wood (Vozenin-Serra and Diez, 2011), *Elatidopsis* shoots (van der Ham et al., 2001), and *Parataxodium* as a whole plant reconstruction (Arnold and Lowther, 1955).

The Pinaceae is the richest extant conifer family with more than 200 species and 11 genera distributed exclusively in the Northern Hemisphere (Fig. 3.10C) (Eckenwalder 2009; Farjon 1990). The fossil record indicates that most extant genera first appeared in the high-latitude and high-altitude regions of North America during the early Tertiary (LePage, 2003), but they had a rapid radiation and may have first evolved earlier during the Late Jurassic (Rothwell et al., 2012). The earliest unequivocal evidence of this family is a *Picea* cone reported from Early Cretaceous (Valanginian) strata in Canada (Klymiuk and Stockey, 2012). Common fossils related to Pinaceae from Cretaceous sediments include *Pityostrobus, Eathiestrobus* cones (Ohsawa et al., 1992; Rothwell et al., 2012), *Prepinus* foliage (Gandolfo et al., 2001), *Protopiceoxylon,* and *Keteleeria* wood (Blokhina et al., 2006; Harland et al., 2007).

The Podocarpaceae is the second largest extant conifer family in terms of number of genera and presents the greatest amount of morphological diversity. In the present, the family is predominantly distributed in the Southern Hemisphere (Fig. 3.10D), which suggests its evolution and current biogeographic distribution could be strongly related with the breakup of Gondwana (Woltz, 1986). The oldest podocarp remains are compressed leafy twigs and detached pollen and seed cones from the Triassic of South Africa, Australia, Chile, Argentina, Antarctica, and Madagascar (Hill and Brodribb, 1999; Troncoso et al., 2000). Although the podocarps were once believed to have been restricted to Gondwana throughout their geologic history, megafossil evidence, together with scattered Northern Hemisphere reports of pollen, suggest that some of the members of this group may have been more cosmopolitan in their distribution (Taylor et al., 2009). Fossils related to Podocarpaceae include *Squamastrobus* cones (Archangelsky and Del Fueyo, 1989), *Podocarpidites* pollen (Perez Loinaze et al., 2012), *Trisacocladus* pollen cones, seed cones, and leaves (Archangelsky, 1966), and *Protophyllocladoxylon* wood (Wang et al., 2007).

Conifers of Cheirolepidiaceae first appear in the Late Triassic, being a dominant element in equatorial regions throughout the Jurassic and Early Cretaceous vegetation (Barnard, 1973; Vakhrameev, 1978). This family of Mesozoic conifers has a long and complex taxonomical background (Watson, 1982). As previously documented and summarized by Alvin (1982) and Watson (1988), the *Hirmeriella-Cheirolepis* group and frenelopsid conifers were considered to be two unrelated conifer families (Watson, 1988). The relation between these two groups was not discovered until Hlustik and Konzalova (1976) and Alvin (1977) reported cones of *Frenelopsis alata* and *Pseudofrenelopsis parceramosa*, respectively, associated with *Classopollis* pollen *in situ* (Axsmith et al., 2004). These discoveries established the relation between the two groups and Cheirolepidiaceae was recognized as a single family (Watson, 1988).

The maximum diversity and abundance of Cheirolepidiaceae was in the Jurassic-Early Cretaceous (Kunzmann et al., 2006). They were mainly present in southern

Laurasia and northern Gondwana (Batten and MacLennan, 1984; Kunzmann et al., 2006), and they are commonly found at low palaeolatitudes (Alvin, 1982). Evidence of the presence of these conifers at high latitudes is rarely found (e.g. Cantrill and Falcon Lang, 2001; Falcon Lang and Cantrill, 2000). During the rise and subsequent dominance of angiosperms by the Early-Middle Cretaceous, the family declined in abundance (Lupia et al., 1999), and became extinct during the late Maastrichtian (van der Ham et al., 2003). Although pollen has been found in Early Tertiary sediments (Vakhrameev, 1970), it is considered to be reworked (Balme, 1995; Srivastava, 1976).

Some of the most representative macrofossil vegetative and reproductive structures reported are *Cupressinocladus, Frenelopsis, Pseudofrenelopsis,* and *Tomaxellia* (foliage); *Classostrobus* (cones), and *Protocupressinoxylon* (wood), which are found in many Cretaceous floras of Africa (Barale and Ouaja, 2002), United States (Axsmith et al., 2004; Haworth et al., 2005), South America (Kunzmann et al., 2006; Sucerquia et al., 2008), England (Alvin et al., 1994), Portugal (Mendes et al., 2010a), eastern Europe (Falcon-Lang et al., 2001; Iamandei and Iamandei, 2005), and Asia (Kimura, 2000; Ren et al., 2008).

The pollen record of Cheirolepidiaceae is represented by the genus *Classopollis*, which dates from the Late Triassic (Reyre, 1973; Zavialova et al., 2010). It was later through the Jurassic and Cretaceous when its morphological patterns became more diverse and its worldwide distribution at low-mid palaeolatitudes was fully established (Watson, 1988). The continuous decline of Cheirolepidiaceae pollen abundance in North America suggests that they were competitively replaced by angiosperms (Lupia et al., 1999).

Palynological studies show that conifer diversity decreased during the Cretaceous (Fig. 3.11), while the abundance of angiosperm pollen suggests a gradual rise to ecological dominance (Fig. 3.12) (Crane and Lidgard, 1989). This suggests that Cretaceous conifer decline is largely attributed to being out-competed by angiosperms.

3.4.1.2. Angiosperms

Angiosperms are the most diverse group of land plants. They are seed-producing plants and can be distinguished from the gymnosperms by a series derived characters, such as flowers, the presence of endosperm within the seeds, and the production of seed-contain fruits, however, a definition of precisely what constitutes an angiosperm and what characters define the group it is still under debate (Taylor et al., 2009).

Origin and stratigraphic distribution

One of the most important events in the Cretaceous Period is the first appearance of flowering plants. The revolutionary rise of angiosperms initiated the global ecological transformation that changed the evolutionary trajectory of many lineages (Beerling and Woodward 1997; Boyce et al. 2010). This change radically affected ecosystem richness and is responsible for over 90% of the present-day terrestrial plant biodiversity at species level (Boer et al., 2012).

The earliest evidence of angiosperms in the geological record is based on fossil pollen (e.g. *Clavatipollenites*) from the Valanginian–Hauterivian (140–130 Ma) sediments of China, Europe and Israel (Brenner, 1996; Hughes, 1994; Zhang, 1999). However, pollen grains of angiosperm in Valanginian strata are rare and not diverse (Fig. 3.11) (Friis et al., 2011; Lidgard and Crane, 1988).

The earliest megafossil evidence is represented by fossil flowers (Friis et al., 1999), fruits (Dilcher, 1989), and leaves (Doyle, 1973; Hughes, 1994) in the Barremian and Aptian (127–112 Ma) (Friis et al., 2011; Willis and McElwain, 2002). The earliest record of Cretaceous wood is reported from the Aptian of southern England by Marie

Stopes in 1912; however the age and identification remain uncertain (Crawley, 2001) (see chapter 6 for more detail). *Archaefructus liaoningensis*, a flowering plant fruiting axis, from the Barremian Yixian Formation in the Liaoning Province of China described by Sun et al. (1998) is considered the earliest macrofossil evidence of angiosperms in the fossil record (Sun et al., 2002, 2011), although its attribution is still under debate.

The discussion about the origin of angiosperms yields many theories. Gnetales, Bennettitales and some Pteridosperms are plant groups that share some characters with modern angiosperms (Fig. 3.13) (Wang, 2010). An origin from Gnetales is suggested by many authors due to the presence of anatomical features such as axillary buds, vessel elements, circular bordered pits in protoxylem, a terminal ovule with two integuments, lack of archegonia, and ribbed pollen (Crane, 1996; Eames, 1952; Ickert-Bond et al., 2003; Maheshwari, 2007). Authors propose a possible link between early angiosperms and features found in Bennettitales such as orthotropous ovules with elongated funiculi and whorls of bracts resembling tepals (Crane and Herendeen, 2009; Friis et al., 2009; Nixon et al., 1994; Rothwell et al., 2009). Some authors (e.g. Cronquist, 1988; Long 1966; Takhtajan, 1969) consider that the cupule of seed ferns was modified to form the carpel in flowering plants and therefore Pteridosperms are the most probable ancestor of angiosperms. There is evidence of earlier angiosperm-like plants from the Jurassic (Table 3.1); however, they remain controversial since they possess some, but not all, of the characteristics necessary for assignment to angiosperms and some my be incorrectly dated (Cornet, 1993; Cornet and Habib, 1992; Friis et al., 2011; Wang, 2010).

Diagnostic features of angiosperms

In the Early Cretaceous angiosperms developed novel vegetative and reproductive characters that made them very distinctive from any other existing plants, their diagnostic features consist in modified structural tissue or phloem and presence of vessel and vessel elements, high leaf shape diversity, and modified stomatal anatomy, among the main particular vegetative characters found in angiosperms (Friis et al., 2011). However, the main characters of angiosperms are related to their reproductive system, which consist of flowers composed of organs such as (1) the carpel that encloses the developing ovules and future seeds; (2) the perianth (sepals, petals or tepals); (3) the androecium or the pollen-producing male organ; (4) the gynoecium, an ovary that encloses the ovules and (5) a stigma that receives the pollen grains (Friis et al., 2011). The reproductive strategy of double fertilization, the double layer pollen wall and the development of double coated seeds with a nourishing tissue known as the endosperm are other distinctive features exclusively develop by angiosperms (Friis et al., 2011).

Taxon	**References (order by year)**
Caytonia	Thomas 1925; Harris 1964; Reymanowna 1973; Krassilov 1977; Nixon et al. 1994; Barbacka and Boka 2000; Taylor et al. 2006; Wang 2010
Dirhopalostahys	Krassilov 1975, 1977
Furcula	Harris 1932
Gigantopterids	Asama 1982; Li et al. 1996; Li and Taylor 1999
Glossopteridales	Retallack and Dilcher 1981; Doyle 2008
Ktalenia	Taylor and Archangelsky 1985
Leptostrobus	Krassilov 1977; Liu et al. 2006
Problematospermum	Krassilov 1982; Liu 1988; Wu 1999
Pentoxylon	Nixon et al. 1994; Biswas and Johri 1997
Sanmiguelia	Brown 1956; Ash 1976; Tidwell et al. 1977; Cornet 1989
Umkomasia	Zan et al. 2008; Taylor et al. 2009

Table 3.1. Other possible angiosperm sister groups (after Wang, 2010).

However, it is important to mention that one or more of these characters are also found in what some consider early angiosperms (Table 3.1), which are not necessarily closely related to angiosperms. For example, pre-angiosperm ancestors (e.g. *Sanmiguelia, Furcula*) showing angiosperm-like leaf characters are considered to have arisen independently in several clades (Taylor et al., 2009). Joining together fossil evidence and molecular analyses suggest that the first angiosperms were woody plants with pinnately veined leaves, multiparted flowers, uniovulate ascidiate carpels, and columellar monosulcate pollen (Doyle, 2012).

Pollen evidence of angiosperms is well documented from the Potomac Group in Virginia, where monocolpate pollen, laminate leaves and flowers have been reported (Friis et al., 1994; Doyle and Hickey, 1976). Throughout the geological succession represented by the Potomac Group the transition of simple pollen forms to more complex can be observed, finding monosulcate pollen in Aptian formations, tricolpate pollen in early-middle Albian formations and tricolporate pollen for late Albian and younger strata (Doyle, 2012). This stratigraphic order of appearance of angiosperm pollen types that corresponds to their sequence of evolution is now confirmed by molecular analysis (Doyle 2005, 2009).

A similar trend can be observed in fossil leaf evidence from various localities in Portugal, Kazakhstan, Colombia, Brazil, and Argentina, where in Aptian–early Albian strata irregular shaped and pinnate leaves are common, and by middle–late Albian leaves present palmately venation, toothed margins and other more complex features such as 3rd and 4th venation orders (Doyle, 2012; Hickey and Doyle 1977).

Further studies of fossil flowers confirmed the evolutionary trend seen in pollen and leaves, and provided more detail on the relations among clades. Some of the best flower evidence available in the fossil record comes from the latest section of the early

Albian of Portugal where many mesofossils of charcoalified flowers have been studied by Friis and colleagues (e.g. Friis et al., 2000 and 2010). For example, from mesofossil floras of Vila Verde locality a fragment of Araceae inflorescence show in detail small naked staminate flowers, each consisting of a single stamen arranged in spiral around an elongate axis (Friis et al., 2010). Remarkable evidence of carpels in the fossil record can be observed in *Pluricarpellatia peltata* B. Mohr, Bernardes-de-Oliveira & David W. Taylor, a whole plant reconstruction from the late Aptian of Brazil possibly related to Nymphaeales (Mohr et al. 2008).

Diversity, abundance and dominance

The new characters developed by angiosperms resulted in more efficient reproductive strategies such as the positioning of pollen and seed organs in close proximity of one another, the production of fleshy fruits, coloured flowers and aroma (Dilcher, 2000). These developments are strongly linked to coevolution with insects and animals that permitted a more effective dispersal and pollination of seeds (Doyle, 2008; Friis et al., 2011).

The diversification of angiosperms also was shaped and enhanced by changes in climate and its effects in other groups of plants (Endress, 2010). In has been suggested that early angiosperms were limited to disturbed (e.g. Hickey and Doyle, 1977; Feild et al., 2004), aquatic (e.g. Cronquist, 1988) or extremely dry sites (e.g. Axelrod, 1970; Sun et al., 2002), however, these hypothesis agree angiosperms were suppressed in most places by the gymnosperms and other groups of plants that still dominated the world (Berendse and Scheffer, 2009).

There is abundant evidence that points out there were many other evolutionary aspects that created key ecological advantages in response to the changing environment, for example, leaf evolution during the Cretaceous facilitated angiosperms to develop leaves with better CO_2 exchange capabilities (de Boer et al., 2012). More efficient gas exchange is believed to be linked to the dominance of angiosperms due to their ability to adapt better to changes in CO_2 atmospheric concentrations (McElwain et al., 2005; McKown et al., 2010). This facilitated angiosperms to outcompete previously dominant coniferous species at middle and low latitudes (Feild et al., 2011). A key advantage for the success of angiosperms was the development of closed carpels, which allowed seeds to develop enclosed within a structure that protected seeds from desiccation as they grew and matured, as well as helped in the dispersal of seeds (Davies et al., 2004).

Deciduousness is also an important adaptation developed by angiosperms to climates that have periods unfavorable to growth (Wolfe, 1987). It also offers an explanation for the rapid success of angiosperms as a result of producing litter that is more easy to decompose, which makes available additional nutrient supply and therefore creating an environmental positive feedback (Berendse and Scheffer, 2009).

These advantages are consistent with the abundance of angiosperm pollen in the palynological record, which indicates that angiosperms became locally abundant in the Albian–Cenomanian and that they became dominant at global scale in the Late Cretaceous (Crane and Lidgard 1989; Heimhofer et al., 2005; Lidgard and Crane 1988; Lupia et al., 1999). The evidence of this shift is well documented in fossil floras in North America with the decline of pteridophytes in lower latitudes and Cheirolepidiaceae (Fig. 3.11) (Lupia et al., 1999). Early analyses of large-scale floristic trends through the Cretaceous indicated that angiosperms competitively replaced all gymnosperm groups (Gothan and Remy, 1957), but more recent studies demonstrate there was a more selective replacement of some but not all gymnosperm groups (Lidgard and Crane, 1988). Although there are many hypotheses on the dominance of angiosperm, the underlying mechanisms involved in this angiosperm revolution remain not completely understood (Brodribb et al., 2005).

3.4.1.3. Pteridophytes

Pteridophytes is a term used to refer to the polyphyletic group of vascular plants that reproduce only by spores; they are divided into two major divisions, Lycopodiophyta and Pteridophyta (Yatskievych, 2002).

Lycopodiophyta includes three major classes; Lycopodiopsida including Lycopodiales (club mosses) and Drepanophycales; Isoetopsida including Selaginellales (spike mosses), Lepidodendrales, Pleuromeiales and Isoetales (quillworts); and the extinct class Zosterophyllopsida (Taylor et al., 2009). Early occurrences are in the Devonian (Drepanophycales and Lepidodendrales); Pennsylvanian (Lycopodiales and Selaginellales); and Triassic (Pleuromeiales) (Banks, 1960; Retallack, 1997; Taylor et al., 2009).

Although the study of Cretaceous club mosses is not particularly extensive, they are present in fossil floras of North America (e.g. Crandall-Stotler, 1996; Herendeen et al., 1999; Konopka et al., 1997, 1998; Magallón et al., 2001), Alaska (Heinrichs et al., 2011), Asia (e.g. Heinrichs et al., 2012; Ignatov and Shcherbakov, 2011), and Antarctica (Vera, 2011).

The division Pteridophyta is formed by four extant classes (Equisetophyta, Psilotophyta, Polypodiopsida and Marattiopsida) and four extinct classes (Cladoxylopsida, Rhacophytales, Stauropteridales, and Zygopteridales) (Smith et al., 2006). They form a monophyletic group that is considered the closest living relative to seed plants (Pryer et al., 2001). The Cretaceous was a time of great Pteridophytic diversification and saw the rise of most extant fern lineages (Watkins and Cardelus, 2012). During this period the ferns grew under warm (subtropical to tropical) conditions in moist environments, including peat-forming swamps, freshwater marshes, riverbanks and understory vegetation in forests (Crane, 1987; van Konijnenburg-van Cittert, 2002). Ferns also formed savannah type vegetation and early successional (pioneer) vegetation after volcanic events (Blackburn and Sluiter, 1994; Crabtree, 1988).

Fossil evidence of ferns is globally abundant in Cretaceous strata in Europe (Collinson et al., 1999; Diéguez and Mélendez, 2000), North America (Gandolfo et al., 1997; Tidwell and Nishida, 1993), South America (Villar de Seoane, 1999), Asia (Krassilov, 1978), Australia (Blackburn and Sluiter, 1994), and Antarctica (Cantrill, 1998). Abundance and diversity of pteridophyte spores show an important decline in the Late Cretaceous concurrent with the dominance of angiosperms (Fig. 3.12) (Lidgard and Crane 1988; Nagalingum et al., 2002).

3.4.2. Cretaceous terrestrial fauna

The Cretaceous fauna was formed by many groups of land animals such as reptiles and mammals but insects were also abundant (Grimaldi and Engel, 2005). Cretaceous mammals were carnivorous and also had a much greater range of body sizes than previously known; they even fed on small vertebrates, including young dinosaurs (Hu et al., 2004; Mirzaie Ataabadi, et al., 2011). Mammals occupied diverse niches and some of them probably competed with dinosaurs for food and territory (Hu et al., 2004).

Among the Cretaceous fauna the rise of many diverse types of dinosaurs, the principal groups were carnosaurs, ceratopsians, coelurosaurs iguanodonts, hadrosaurs, and pachycephalosarus (Brusatte et al., 2010). Among the most interesting recent findings are the feathered dinosaurs from the middle Early Cretaceous Yixian Formation in China (Xu et al., 2012; Zhou et al., 2000). The study of early dinosaur feathers is possible thanks to the great detail included in amber (McKellar et al., 2011). The discovery of polar dinosaurs demonstrates that dinosaurs were highly diversified and well adapted to relatively cool climates just before the Cretaceous/Paleocene mass extinction event (e.g. Browers et al, 1987; Buffetaut, 2004; Fiorillo and Tykoski, 2012; Godefroit et al., 2009; Nelms, 1989; Rich et al., 2002).

The Cretaceous is also considered as the golden age of insect evolution because it was during this geological period that most recent insect families first appeared (Grimaldi and Engel, 2005). The major events of the Cretaceous, such as the origin and radiation of angiosperms and the fragmentation of Gondwana had immense impact on insect evolution, however, post bolide impact (3–7 Ma) evidence in insect damage diversity (e.g. Wappler and Denk, 2011; Wing et al., 2009) suggests balanced and fully functional ecosystems that were not significantly affected by the rapid changes during the K-T transition (Labandeira and Currano, 2013; Krogmann, 2011; Whalley, 1987).

3.5. CRETACEOUS-TERTIARY EXTINCTION

A thin layer of clay deposited about 65.6 Ma marks the transition from the Cretaceous to Tertiary (K-T boundary), representing the end of an era and a significant shift of Earth's biotic evolution and natural heritage (Macleod et al., 1997). Towards the latest Cretaceous a global ecosystem collapse brought in its wake the death of numerous living species on Earth (MacLeod et al., 1997; Twitchett, 2006).

It has been estimated that around 50% of biological genera and 20% of families disappeared (MacLeod et al., 1997). The phenomenon consisted of a selective extermination, that is, while some species groups completely disappeared, others survived. It seems that small freshwater invertebrates, such as shellfish from rivers and lakes were not affected. Regarding the terrestrial animals, those of medium to large size were extremely vulnerable, such as non-avian dinosaurs and pterosaurs (MacLeod et al., 1997). Organisms capable of photosynthesis, including phytoplankton and land plants, formed the foundation of the food chain in the Late Cretaceous as today. Evidence suggests that herbivorous animals died when the plants they depended became rare, hence the top of the chain predators also perished (Wilf and Johnson, 2004).

The marine record shows the disappearance of many families of foraminifera, echinoderms, corals and sponges, as well as the totality of belemnites, ammonites, rudists, teleost fish, mosasaurs and plesiosaurs (MacLeod et al., 1997). But the extinction of animals and plants was not the only impact of this event on biodiversity. Disappearances allowed the adaptive radiation of the groups that survived the ecological niches that became vacant. The best example of this phenomenon was the explosion of diversity of placental mammals, which until then were mostly small animals, solitary and nocturnal (Robertson et al., 2004).

The duration of the event has not been agreed. Some extinct groups give clear signs of a slow fade during the last 10 Ma of the Cretaceous. However, various other groups seem to be disappeared right in the K-T event (MacLeod et al., 1997; Twitchett, 2006). Various explanations have been proposed for this phenomenon, however the reliability of the different hypothesis studies is subject to controversy.

Alvarez et al. (1980), initially suggested that this massive extinction was caused by a meteorite impact. The clay layers of K-T boundary showed levels iridium and osmium 160 times higher than normal, and this abnormality was found at 40 sites around the earth. The high amount of iridium found in sediments from many K-T sections was a clear proof of this event since iridium is a common element in asteroids and comets, and suggested that the size of the colliding body should be of around 10 km in diameter.

This hypothesis, once considered very controversial, progressively gained substantial support from subsequent studies on shocked quartz and microtektites which chemical analysis ruled out volcanic origin (Bohor et al., 1987; Dressler and Sharpton, 1999). Subsequently, large-scale tsunami deposits at the K-T boundary were found in Texas, showing evidence that an impact must have taken place near by (Bourgeois et al., 1988). Looking back to geological studies since 1960 onwards, the 180 km diameter Chicxulub crater in Yucatan, Mexico could be identified as the cause of Iridium anomalies and thus, the responsible of the K-T cataclysm (Hildebrand et al., 1991, 1995).

Further studies attempted to explain the consequences of the Chicxulub impact. Such explosion would have caused the excavated material, along with the debris of the asteroid would have been ejected into the atmosphere causing wildfires around the world, and in turn, large shock waves would have caused global earthquakes and volcanic eruptions (Toon et al., 1997). The emission of dust and particles could have covered the entire surface of the Earth for several years, possibly a decade, creating an environment of difficult life for organisms. The production of carbon dioxide caused by the shock and destruction of carbonate rocks would have caused a dramatic greenhouse effect (Hildebrand et al., 1991, 1995). Another consequence of the impact is that the dust particles in the atmosphere would have prevented sunlight reached the surface of the Earth, lowering the temperature drastically. The photosynthesis of plants would have been interrupted, affecting the entire food chain (Pope et al., 1997).

Conversely, Courtillot et al. (1988) proposed that the mass extinction was provoked over a longer length of time by a significant volcanic activity known as the Deccan Traps in India. The basalts, which nowadays cover about 500,000 km^2, with individual sequences of 10,000 km^2 and over 10,000 km^3 of volume, have been estimated to run from 69 to 63 Ma approximately, and consisted of a series of episodic eruptions (Courtillot and Fluteau, 2010). The activity was of such magnitude that emissions of carbon dioxide and sulphur gases might have altered the climate and poisoned the oceans (Courtillot and Fluteau, 2010).

Furthermore, some studies suggest the combination of both, the Deccan volcanism together with the asteroid impact in Yucatan, the latter being what triggered the extinction (Officer et al., 1992, Schulte et al., 2010). This could explain the massive extinction of various primary producers and its effects causing major starvation higher up in the food chain and therefore the collapse of many ecosystems (Schulte et al., 2010).

Other research propose that the biotic effects of this impact have been vastly overestimated and that the Chicxulub crater is 300,000 years older than the K-T boundary, thus suggesting that the asteroid impact and K–T mass extinction are two separate and unrelated events (Adatte et al. 1996; Keller et al., 2008). On the contrary, this hypothesis attributes an important marine regression as an important cause of extinction. Evidence from planktonic foraminifera analysis from core samples in Chicxulub revealed that a strong decline in sea level took place during the Maastrichtian. These findings suggest that global cooling led to a sea level regression of about 80 to 30 m, which would be more harmful to the foraminifera that the Chicxulub impact (Adatte et al. 1996). This study also insinuates, that the possible cause of the K-T mass extinction could have been another cosmic impact or cumulative rapid climatic and environmental change effects. (Keller et al., 2004, 2009). However, recent studies contradict this hypothesis, emphasizing that it does not fully explain other global events related to the extinction, and stating that on its own it could not achieve such significant loss of life (Schulte et al., 2006, 2008).

In addition to the Chicxulub impact, a study conducted by Chatterjee (2003) proposed that the collision of several meteorites or a fragmented asteroid provoked the mass extinction. Other possible craters could be Silverpit in the North Sea, Boltysh in Ukraine (Kelley and Gurov, 2002), and Shiva in India. The research mainly focused on the submerged Shiva crater, which shows an oblong shape of 600 km long and 400 km wide. Such vast impact could have formed a rise in the Earth's mantle through fractures, explaining the geological origin of the Deccan Traps (Chatterjee et al., 2003). Despite the evidence of impact from shocked quartz, tsunami deposits and iridium anomaly shown by Chatterjee (2003), to the majority of the scientific community, the lack of research, possible misinterpretation of results and odd shape of Shiva crater may imply it is not in fact an impact crater.

In summary, the Mesozoic era concluded in a substantial global ecosystem collapse, which triggered one of the most recognized mass extinctions on Earth, resulting into a major biotic turnover. Through decades, numerous scientific studies have been taking place in order to understand and explain the origin of such phenomenon. Varying from the possibility of a single or multiple asteroid impacts, to resilient volcanism, and remarkable marine regression, argument for and against the validity of these investigations are extensive. If the cataclysm occurred due to one of the existing hypothesis, the combination of them, or some other event yet to discover, the reconstruction of the latest Cretaceous scenario remains unresolved. Further attempts to comprehend the K-T extinction and its source might be vital to handling nowadays environmental position, thus, further research on the matter is needed.

FIGURES CHAPTER 3

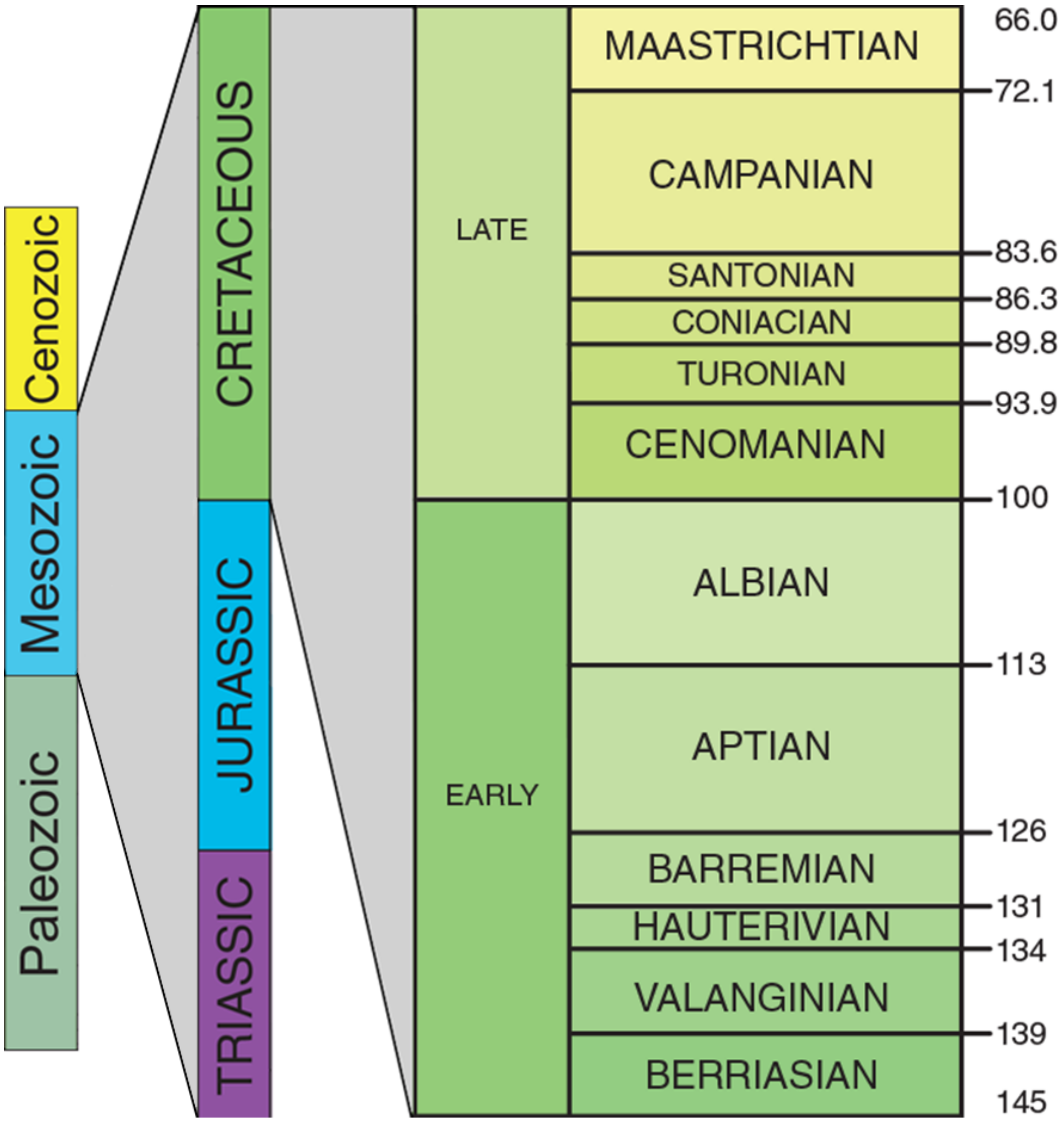


Figure 3.1. Cretaceous time scale, modified from Cohen et al., (2012).

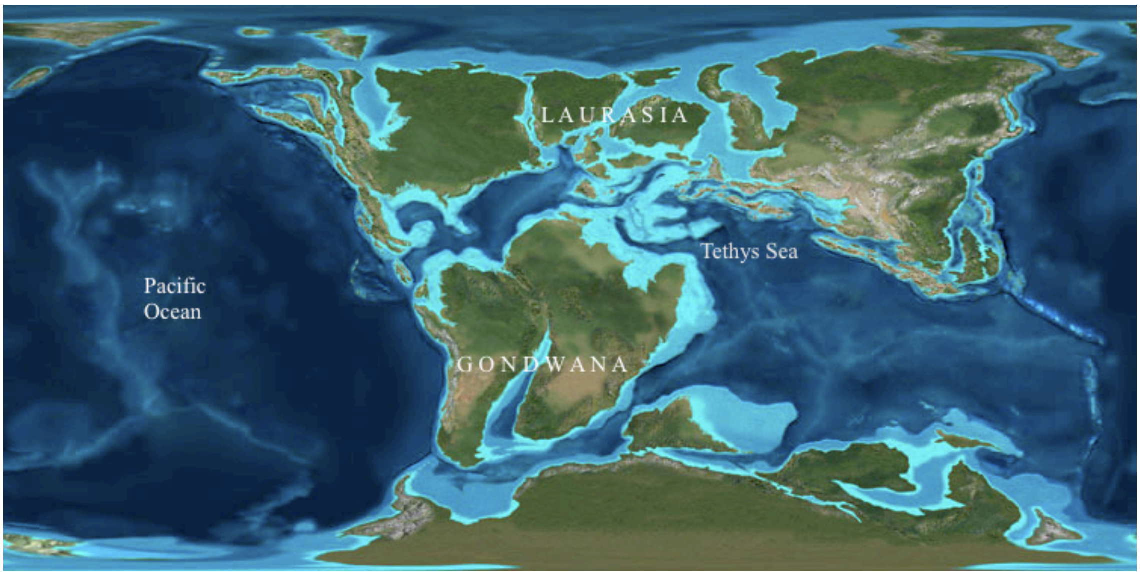


Figure 3.2. Early Cretaceous (Berriasian) 145 Ma. (Blakey, 2011 date accessed).

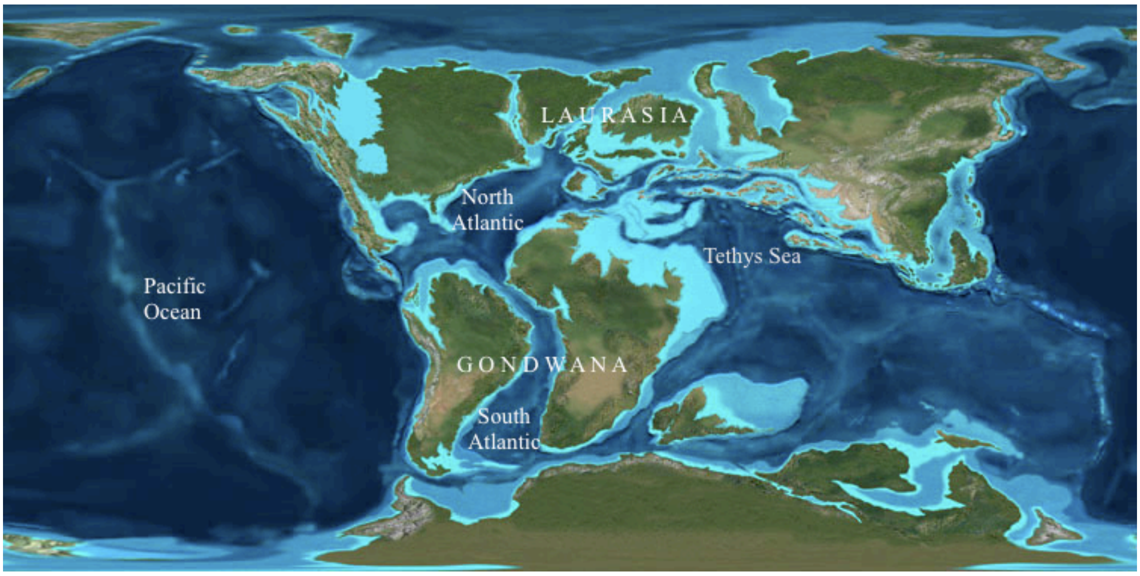


Figure 3.3. Middle Cretaceous (Albian–Cenomanian) 105 Ma. (Blakey, 2011 date accessed).

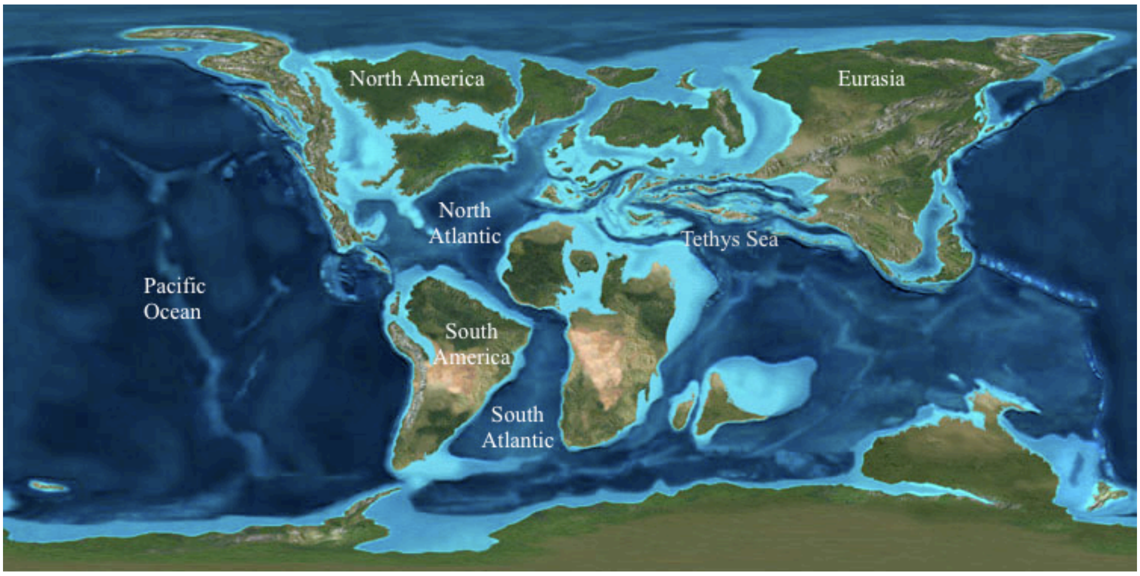


Figure 3.4. Middle Late Cretaceous (Turonian–Santonian) 93.9–83.6 Ma. (Blakey, 2011 date accessed).

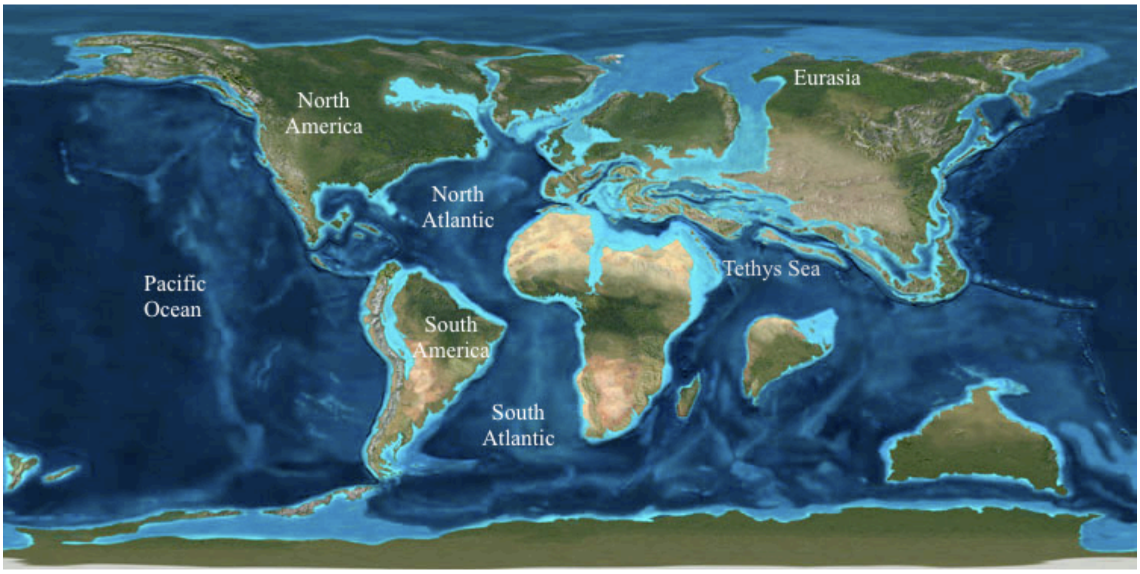


Figure 3.5. Cretaceous–Tertiary 65 Ma. (Blakey, 2011 date accessed).

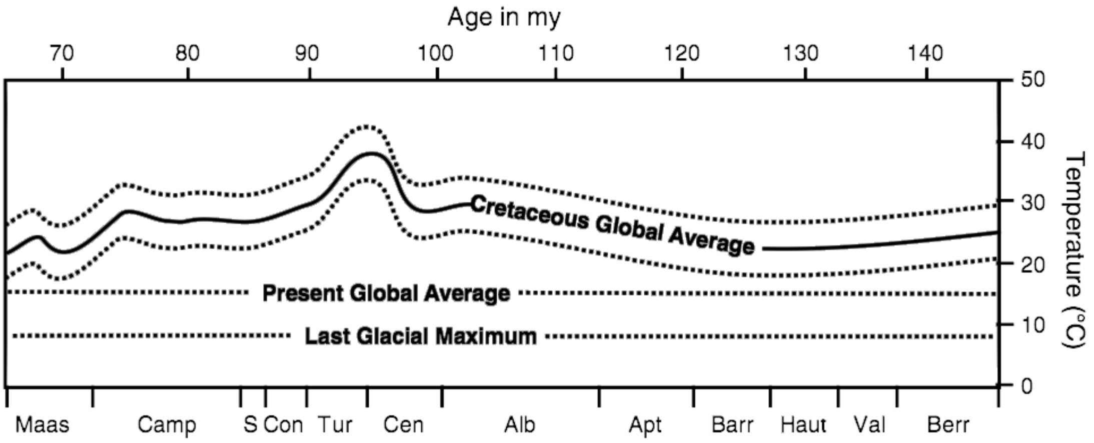


Figure 3.6. Cretaceous global average temperatures based on sea-surface temperature models (after Frakes, 1999; Frakes et al., 1994) compared to Present and Last Glacial Maximum global average temperatures (modified from Hay and Floegel, 2012).

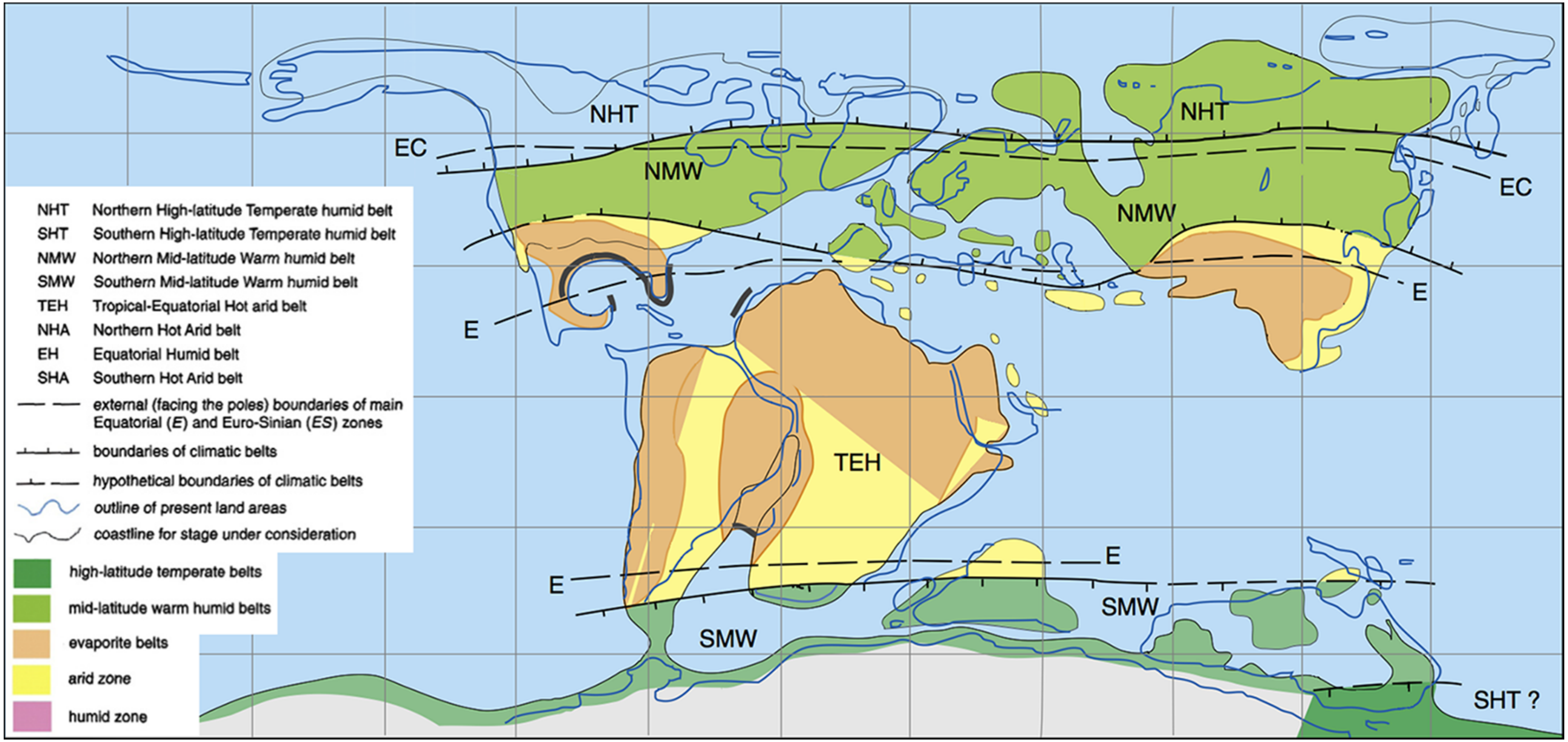


Figure 3.7. Aptian climate indicators and zones (after Chumakov et al., 1995; Hay and Floegel, 2012).

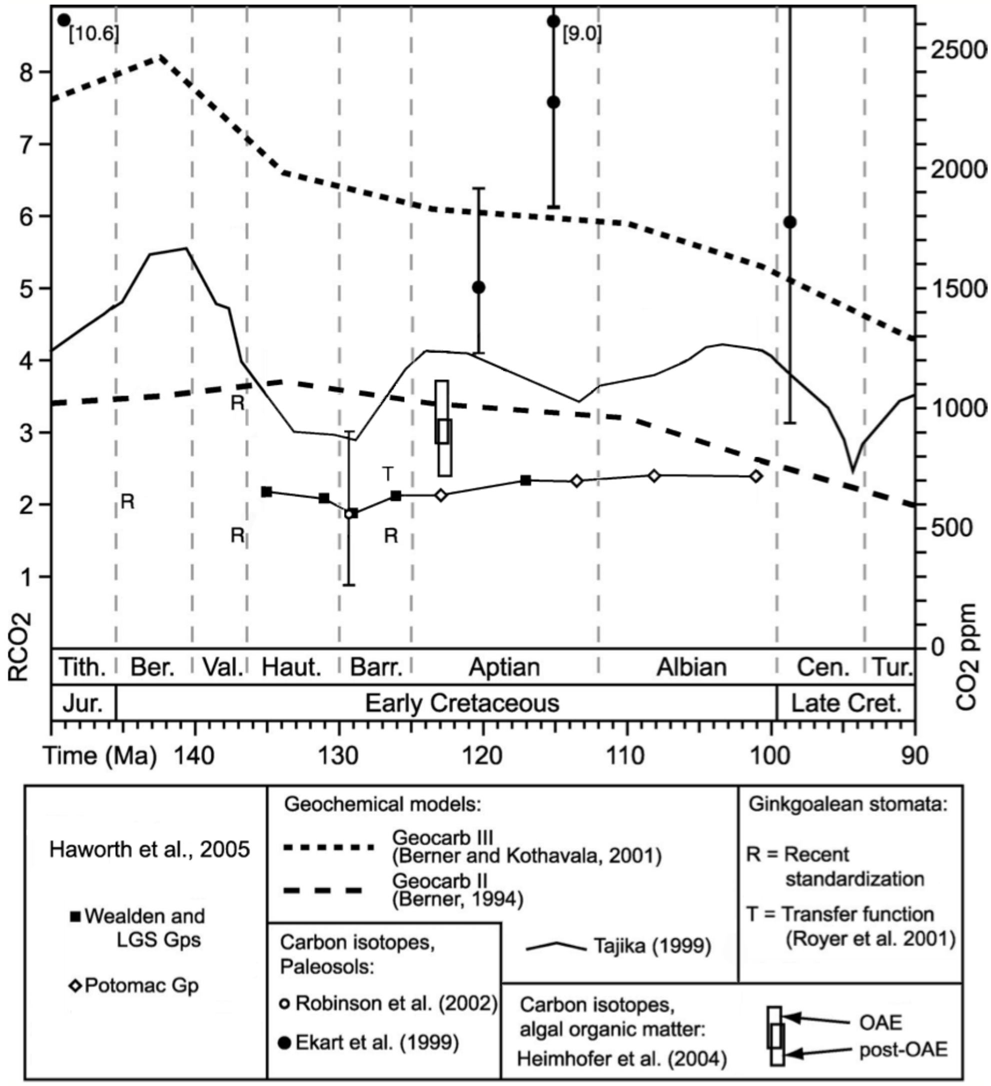


Figure 3.8. Estimated of mid-Cretaceous atmospheric CO_2 levels based on different analyses such as biogeochemical models, carbon isotope composition of soil carbonates and marine algal organic matter, and stomatal indices of fossil ginkgoaleans. Where $pCO_2 > 9RCO_2$, true value is in brackets. RCO_2—ratio of paleo-pCO_2 value to preindustrial atmospheric CO_2 value of 300 ppm. Filled squares: England localities; Open squares; U.S. localities; error bars—1σ either side of data point. Samples at 129 and 99 Ma, with a minimum uncertainty of 0.2 of mean RCO_2. Oceanic anoxic event (OAE); Lower Greensand (LGS) (after Haworth et al., 2005).

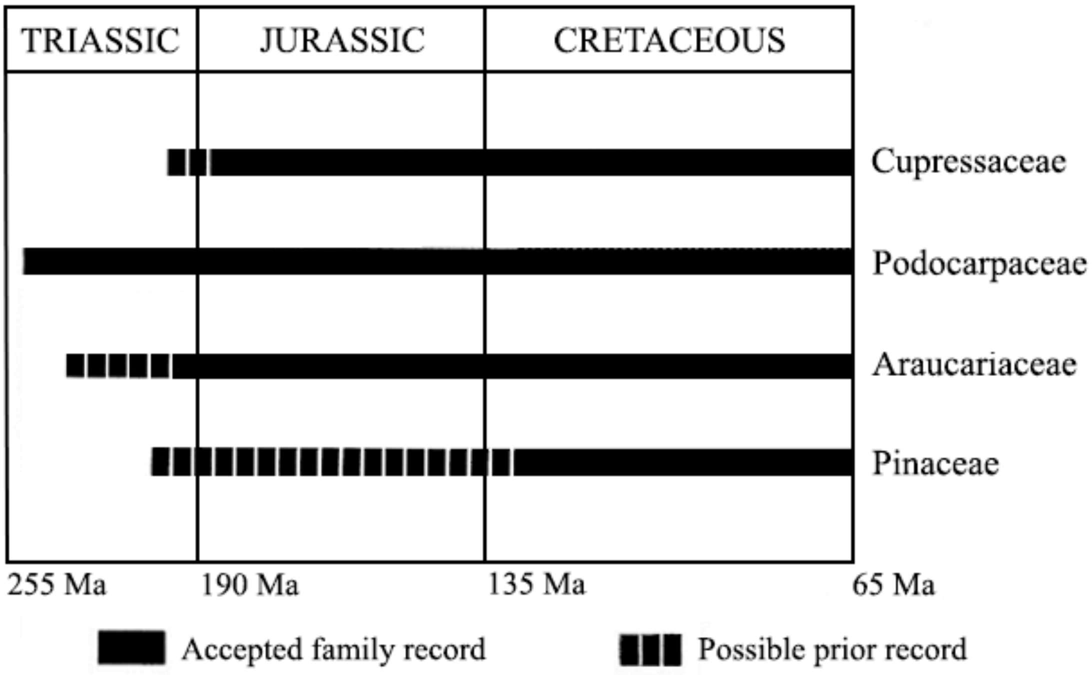


Figure 3.9. The fossil record of conifers during the Mesozoic (modified from Miller, 1977).

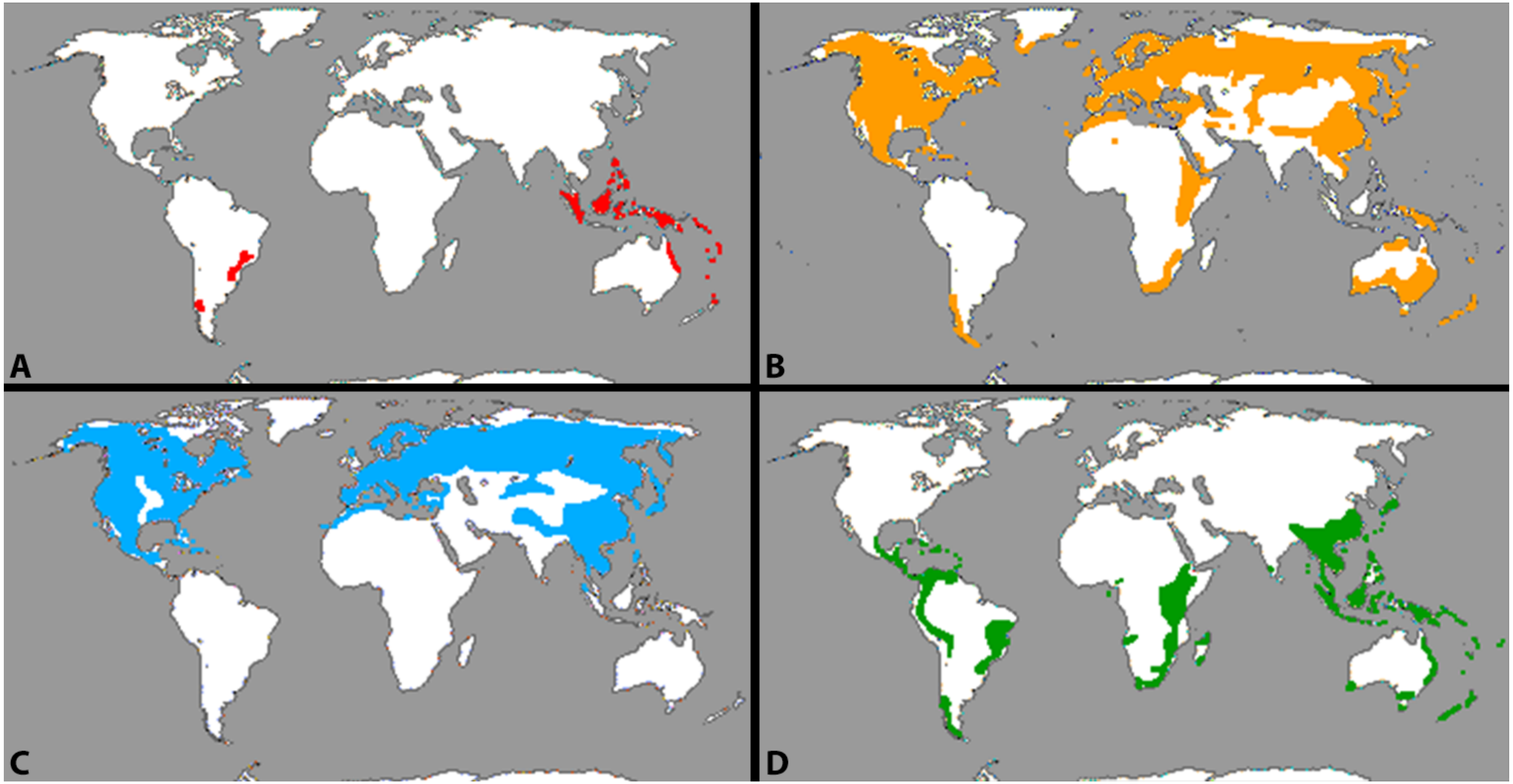


Figure 3.10. Present natural distribution of Araucariceae (A), Cupressaceae (B), Pinaceae (C), and Podocarpaceae (D) after Missouri Botanical Gardens (2010).

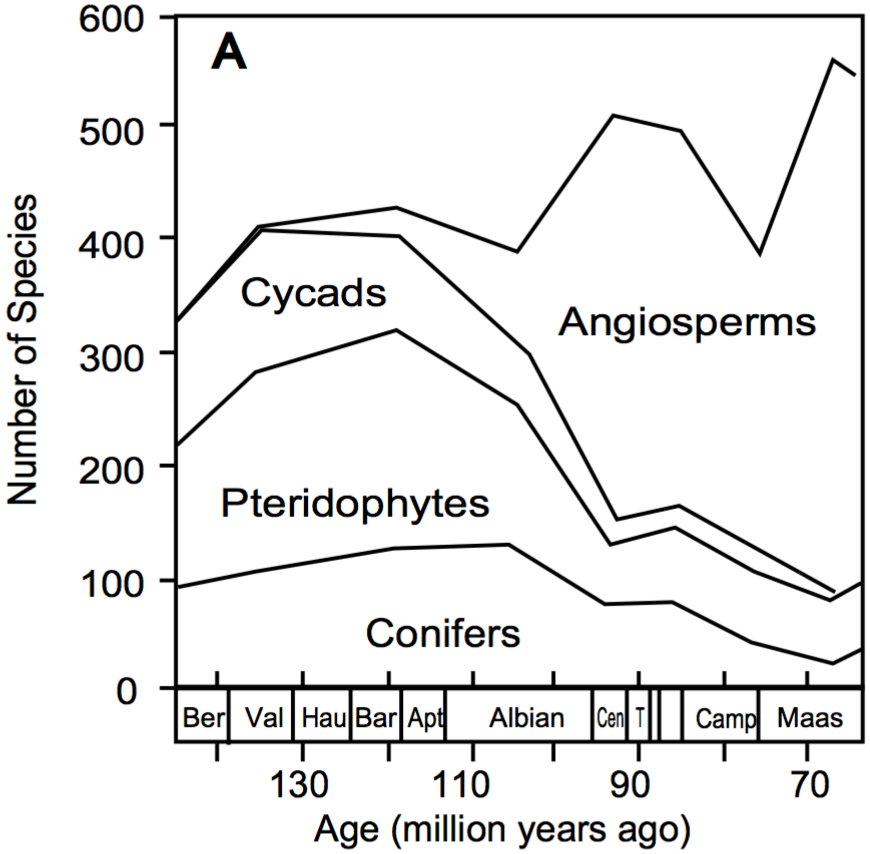


Figure 3.11. Total pollen species diversity changes during the Cretaceous illustrating the taxonomic radiation of angiosperms (from Lidgard and Crane 1988).

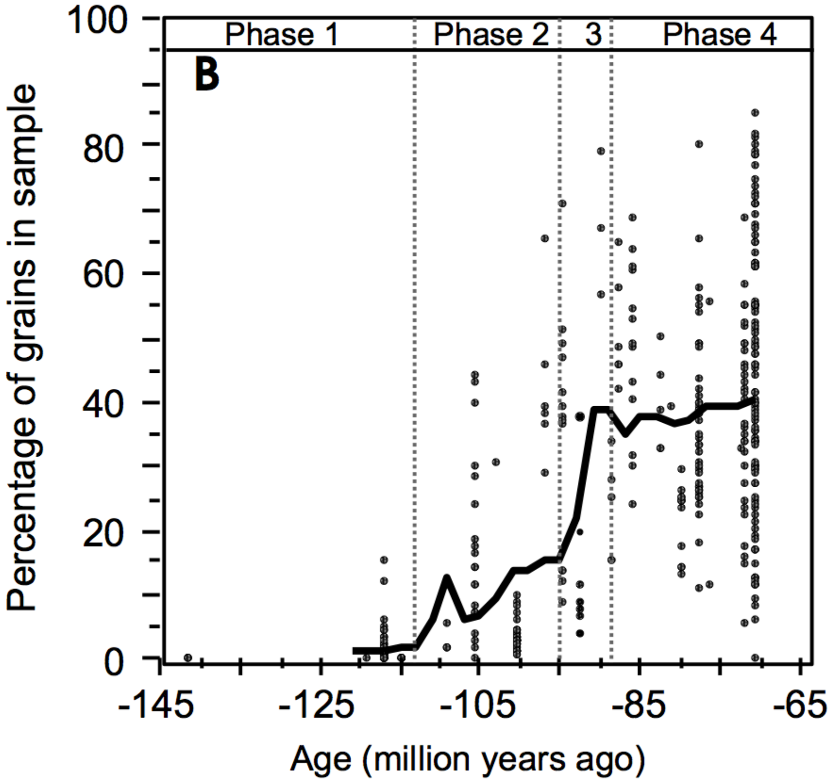


Figure 3.12. Increase in relative angiosperm abundance within Cretaceous palynoflora. Each point on the graph represents the average abundance within 7.5 Ma intervals (from Lupia et al., 1999).

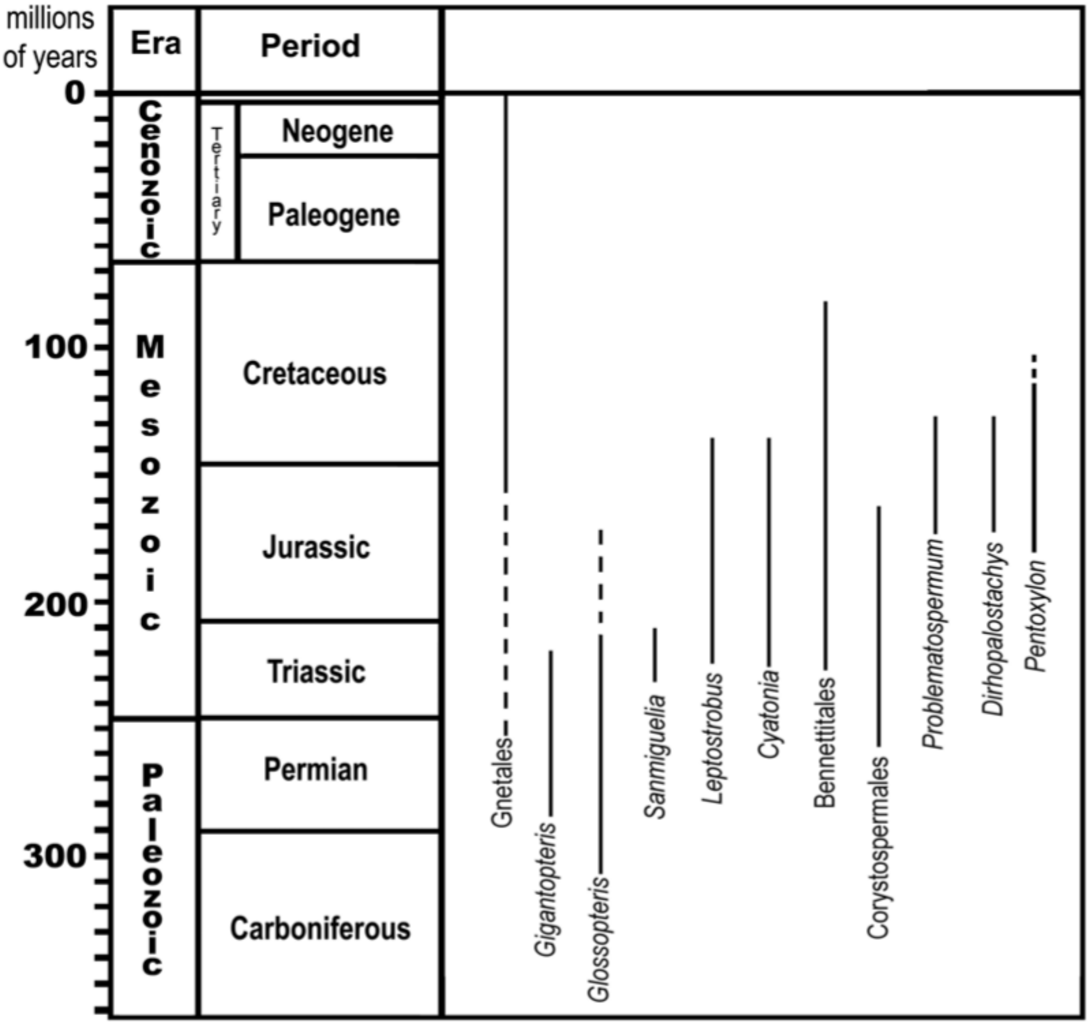


Figure 3.13. Approximate temporal distribution of possible angiosperm ancestors. *Dashed lines* indicate uncertainty (taken from Wang, 2010).

CHAPTER 4: CRETACEOUS FOREST COMPOSITION AND PRODUCTIVITY INFERRED FROM A FOSSIL WOOD DATABASE

4.1. INTRODUCTION

Fossil wood is widely preserved in Cretaceous strata worldwide (Stewart and Rothwell, 1993; Taylor et al., 2009). Where preserved in a charcoalified or permineralised (silicified or calcified) state, the identity of plants may be determined (Taylor et al., 2009). Because fossil wood is derived from arborescent plants (trees), global analysis of fossil wood assemblages has the potential to reveal biogeographic patterns of Cretaceous forests (Philippe et al., 2004). However, fossil wood also commonly preserves tree-rings, which further allows the annual growth rate (productivity) of trees to be determined (Creber and Chaloner, 1985). In this chapter, I build a comprehensive database of records of Cretaceous fossil wood to elucidate global patterns in forest composition and productivity. I relied on fossil wood records rather than other types of fossil, e.g., leaves, reproductive structures, or pollen because only wood provides unequivocal evidence for canopy-forming trees. Although wood is occasionally transported for long distances (Philippe et al., 2008), in the analysis I assume that this effect was negligible when averaged over the global database in which only ~15% of the records are related to marine facies.

Although such analyses have been earlier attempted based on limited data (e.g, Creber and Chaloner, 1985; Florin, 1963), this work is the first truly comprehensive and quantitative global study. Specifically, the work allows the following key questions to be addressed. What were the patterns of Cretaceous forest distribution? How were they affected by the rise of angiosperms? To what extent were modern biogeographic patterns established in Cretaceous time? Was Cretaceous forest productivity equator centered, pole centered, or did it have some other pattern? Was productivity elevated compared to the present? The answers to these questions may improve the knowledge of Cretaceous vegetation biomes, help test the results of computer climate models, and give insights into the future effects of long-term global warming.

4.2. BACKGROUND AND ASSUMPTIONS

The construction and interpretation of the fossil wood database presented in this chapter requires inferences to be made about (1) the identity of fossil trees, and their natural groups (Cretaceous forest composition), and (2) the significance of tree-rings preserved in the woods, for tree growth and climate (Cretaceous forest productivity). Before presenting the new findings, I first discuss some of the issues and assumptions that undergird this work.

4.2.1. Forest composition

Cretaceous fossil wood assemblages include remains of conifers, angiosperms, cycads/cycadeoids, ginkgos, ferns, and possibly other groups, too (Taylor et al., 2009). Identification of fossil wood involves study of anatomical properties in three sections (transverse, TS; radial, RLS; and tangential, TLS) (IAWA Committee, 1989). Of particular significance, amongst other features, are the nature of vertically orientated lignified cells (tracheids in gymnosperms; vessels and fibres in angiosperms with few exceptions) best seen in TS, the type of tracheid and cross-field pitting observed in RLS, and the dimensions of horizontally-orientated parenchymatous rays observed in TLS (Hass and Rowe, 1999).

Wood (secondary xylem) is of two basic types: manoxylic, containing a high proportion of parenchyma, and pycnoxylic, containing smaller amounts of parenchyma (Bamford and Philippe, 2001). Fern and cycads/cycadeoid wood is characteristically manoxylic. The other groups show typically pycnoxylic wood, although some angiosperms may be somewhat manoxylic (e.g., palms, Friis et al., 2011). Most angiosperm woods are distinguished by the presence of vessels and fibres, although a few vesselless forms also occur in the Cretaceous and survive to the present (Feild et al., 2002). Conifer woods are distinguished by their compact tracheid structure, and dominantly narrow rays (Bamford and Philippe, 2001). Ginkgo woods are very similar to those of conifers but are distinguished by the presence of inflated axial parenchyma cells and very short rays (Falcon-Lang, 2004; Kvacek, 1999; Ulicny et al., 1997). This latter difference is subtle and probably ginkgo woods are under-reported in the fossil record (Falcon-Lang, 2004).

Most of the records in the database (Appendix 1) are from conifers and therefore it proved to be advantageous to sub-divide this group. General sub-division of conifer wood into various types is based on features such as tracheid pitting and cross-field pit type (Falcon-Lang and Cantrill, 2000, 2001; Philippe et al., 2004). Due to the large number of fossil wood records, it was not possible undertake a detailed systematic analysis of all specimens in the database. Therefore, conifer specimens were merely grouped in four major categories based on general anatomical features as follows: Araucarioid woods show alternate tracheid pits and araucarioid cross-field pits (Bamford and Philippe, 2001; IAWA Committee, 2004). Podocarpoid woods generally show opposite tracheid pits and podocarpoid cross-field pits (Bamford and Philippe, 2001; IAWA Committee, 2004). Cupressoid woods generally show opposite tracheid pits and cupressoid or taxodioid cross-field pits (Bamford and Philippe, 2001; IAWA Committee, 2004). Pinoid woods show opposite tracheid pits and piceoid to open cross-field pits (Bamford and Philippe, 2001; IAWA Committee, 2004).

Woods with these general characters are seen in members of the extant families, Araucariaceae, Podocarpaceae, Cupressaceae, and Pinaceae (Greguss, 1955; IAWA Committee, 2004), but whether the Cretaceous fossil wood categories conform to these families is less certain (Bamford and Philippe, 2001). In addition, some Cretaceous conifer woods cannot be easily lumped into this four-part system (e.g. *Xenoxylon*) and therefore form a fifth heterogeneous category. Their identity is uncertain, but might include one or more of the extinct Cretaceous conifer families such as the Cheirolepidiaceae (Bamford and Philippe, 2001; Philippe and Thevenard, 1996).

In summary, only generalized patterns of changing forest composition can be inferred from a Cretaceous fossil wood database, and I stress that how these patterns relate to the distribution of extinct and extant families is somewhat uncertain also. Nonetheless, this approach has great potential for showing global geographic patterns in woody vegetation.

4.2.2. Tree productivity

The study of tree-rings as indicators of tree productivity and therefore past climate conditions and was first proposed by Seward (1892) in his influential essay, building on early work dealing with tree-rings in extant trees (Falcon-Lang, 2005). The approach of using tree-rings for deep-time research was further developed by Geoff Creber and Bill Chaloner in an influential set of papers (Creber, 1977; Creber and Chaloner, 1984ab, 1985). Their methods are based on the fact that wood (secondary xylem) development is subject to environmental factors, which influence its structure. Tree-rings in fossil woods thus represent a natural form of "data storage system", particularly of climatic effects which can be "read back" by examining the wood (Creber, 1977; Creber and Chaloner, 1984a, b). Among the several definitions of tree-rings, the analysis and measurements presented in this thesis are based on the concept proposed in publications by Creber and Chaloner (1984a,b). They state that wood (secondary xylem) tissue is produced, centripetally by the activity of a layer of cells known as the vascular cambium, which divides in a tangential plane (Creber and Chaloner, 1984b). In temperate latitudes cells grow to different extents, depending upon the time of year. In early summer the tracheids achieve a greater radial diameter and have thinner walls (earlywood) than those differentiated later in the growing season, which show thick-walled cells (latewood) (Creber and Chaloner, 1984b). A marked boundary is seen between the last-formed cells of one season and the first of the next. The growth increment between two such boundaries is known as a tree ring (Creber and Chaloner, 1985). The occurrence of growth interruptions (*sensu* Falcon-Lang, 2003) and false rings were also taken into account for this analysis.

The presence of tree-rings therefore typically indicates a seasonal climate, either a temperate climate (temperature variations) or more locally a tropical climate (rainfall variations) (Creber and Chaloner, 1984a,b). Conversely, the lack of tree-rings or the development of weak tree-rings suggests a humid tropical (non-seasonal) climate (Brison et al., 2001; Wheeler and Baas, 1993). However, many other factors influence the occurrence and markedness of tree-rings including position in tree, taphonomic biases (Chapman, 1994), leaf phenology (Falcon-Lang, 2000), and environmental factors such as floods, fires, or insect attacks (Falcon-Lang, 2003). In the fossil wood study, where tree-rings occur with clearly marked boundaries (based on visual inspection of fossils or plates in publications), I have assumed that they represent annual growth increments, and therefore a measure of forest productivity (Creber and Chaloner, 1985). In the paratropical conditions that dominated the Cretaceous world (Frakes and Francis, 1990; Wilson et al., 2002), I acknowledge that this assumption may be questionable for some specimens.

Even if Cretaceous tree-rings are accepted as annual increments, the interpretation of mean tree-ring width data is fraught with difficulties. As Falcon-Lang (2005) showed, based on analysis of the International Tree-Ring Database, there is huge variation in annual growth rate for a given climate, mostly caused by interspecific differences and differences resulting from aspect of the growth site. However, in general terms mean tree-ring width does positively correlate with Mean Annual Temperature (MAT), where rainfall is non-limiting, with relatively narrow rings produced in the taiga biome and wider rings in the warm temperate zone (Falcon-Lang, 2005).

Therefore, comparison of global modern tree-ring width data with comparable global fossil data may shed light on relative changes in global growth rates (productivity) in Cretaceous times. Such a comparison is useful in placing, in global context, the results of local Cretaceous studies such as evidence for elevated growth rates in the polar forest biome based on studies in the Antarctic (Francis, 1986; Jefferson, 1982, 1983) and Arctic (Kumagai et al., 1995).

4.3. DATABASES

In this first research project, I constructed two databases. The first database containing Cretaceous fossil wood occurrences (including the “wood” of tree ferns and cycads/cycadeoids) was constructed from an extensive literature review including published literature from peer-reviewed journals, regional palaeontological catalogues, books, and conference abstracts with the help of various publication searchers and online resources (e.g. Scopus, Google Scholar, Google Books, Web of Knowledge, JSTOR, PUBMED, and GeoRef). Searches continued until the daily hit rate was consistently close to zero for several days.

Data on fossil woods was also obtained from pre-existing databases such as InsideWood Database (2004-present) and the Palaeobiology Database (paleodb.org). Inventories of major museums, including paper records and online catalogues, such as University of California Museum of Paleontology, Colecion Nacional de Paleontologia at UNAM, Mexico, Paleobotanique Université Lyon 1, the Smithsonian Institution, and many others in France, Germany, Canada, the UK, and the Netherlands, were requested and included in the database.

The second database comprises mean tree-ring width data obtained from (1) tabulated data in publications; (2) measurement of fossil woods in shown in plates; and (3) studies of fossil wood collections at the following repositories: Colecion Nacional de Paleontologia at UNAM, Mexico, Paleobotanique Université Lyon 1, Sedwick Museum, Cambridge, Natural history Museum London, and University of Utrecht, The Netherlands. Where new data were obtained from museum collections, measurements were made to an accuracy of 0.1 mm using a transmitted light microscope.

4.3.1. Fossil wood database

4.3.1.1. Database quality and completeness

Not all the records in the databases of fossil wood occurrences were, at first, suitable for biogeographical analysis due to incomplete information given about their age, locality or affinity in associated literature (this was especially true for historical records). To improve the quality of geological information associated with each record, a further literature review was undertaken to establish the geological context and age of the fossil using the most up to date literature available. For each record, the location (geographic coordinates to the nearest degree of modern latitude and longitude), stratigraphy, and age were tabulated.

In order to check the completeness of the database, I plotted a global map of Cretaceous rock outcrop using regional and national geologic maps. Fossil wood records were then plotted on the map, and any gaps identified. The geologic map did not distinguish terrestrial and marine strata so some geographic data gaps may be due to the presence of marine sediments. Alternatively, other gaps could be due to low levels of collection in remote areas. Once gaps were identified, targeted searches were made to try and fill them with variable success. Overall Cretaceous rocks seem to be fairly well sampled for fossil wood, showing only some extended gaps at very high latitudes in the Northern Territories of Canada and in Siberia, as well as in the Middle East, all of which can be attributed to the difficulty of geologists reaching those places.

The whole dataset of Cretaceous fossil wood occurrences is shown in Figure 4.1. It comprises 2238 records from almost 500 localities in more than 70 countries and recorded in more than 550 publications. In addition, it includes almost 200 unpublished specimens housed at 10 different paleontological collections and museums. This map represents the first compilation of Cretaceous woods at a global scale. The data from this plot is accessible for anyone in the electronic format of this thesis, as well as in the following link of the journal Geology: ftp://rock.geosociety.org/pub/reposit/2012/2012053.pdf (Peralta-Medina and Falcon-Lang, 2012)

While I cannot claim that this process of data harvesting has resulted in an exhaustive or complete database, it is at least comprehensive, including probably > 90% of records in publications available on the internet and collection databases, suggested by the lack of new data obtained from academic searching engines.

4.3.1.2. Identification problems

Where possible, original material or published photomicrographs were examined to confirm assignment of fossil wood records to a particular plant group category. However, in many cases, anatomical preservation was too poor and material could only be assigned, for example, to indeterminate conifers. Consequently, of the 2238 records in the database, only 1597 records could be identified with sufficient precision for inclusion in the analysis.

4.3.1.3. GIS analysis of database

The remaining 1597 fossil wood records were sorted into four time bins as follows: T1, Berriasian–Hauterivian (145.5–125 Ma); T2, Aptian–Albian (126–98 Ma); T3, Cenomanian–Santonian (99–83 Ma); and T4, Campanian–Maastrichtian (84–65.5 Ma). These bins were selected because they reflect marked changes in angiosperm wood abundance (T1, absent; T2, rare; T3, common; T4, abundant; Wheeler and Baas, 1991).

Records were then plotted, by hand, on printouts of Ron Blakey's global palaeogeographic maps rectangular format (Blakey, 2011 date accessed) to obtain palaeo-coordinates. Four base maps were selected for each time bin as follows: T1 (120 Ma), T2 (105 Ma), T3 (90 Ma), T4 (65 Ma). These were selected because they are the maps with ages that most closely match the four time-bins. They are available here: www2.nau.edu/rcb7. The original colour palaeogeographic map images were then edited using Photoshop CS6 and turned into lower resolution, black and white JPG format. The black and white outline was then imported into ArcGIS and georeferenced in order to permanently assign palaeocoordinates to every fossil wood record.

To analyse the co-occurrence of plant groups, data were manipulated in ArcGIS using the Proximity and Overlay tool. In this technique, buffer areas with a diameter of 1°, 2°, 3°, 4°, and 5° of palaeo-coordinates are created around each fossil record. The overlay tool is then used to calculate the percentage co-occurrence (overlap) of each pair of plant specimens for each buffer diameter. Analysing the whole dataset allows the degree of co-occurrence of different plant groups to be established quantitatively.

Associations were further analysed with Chi-squared test to determine if a certain type of wood (e.g. araucarioid, cupressoid) happened in the same sample unit more or less frequently than expected or if they occur together only by chance. In other words, Chi-squared test helps to clarify if the number of observations of each category differs significantly from the expected value or if they differ due to sampling error (Preacher, 2001).

4.2.2. Tree-ring database

To analyse forest productivity, mean tree-ring width data were obtained for conifers from the literature (n = 134) or direct measurement of sections (n = 150) in museum collections. Tree-ring data available on the literature may include measurements based on several different ring definitions (e.g. Creber and Chaloner, 1984a; Falcon-Lang, 2003; Taylor and Ryberg, 2007). Data obtained from short (<20 rings) and long (>20 rings) sequences were analysed separately, but values for both data sets were similar. Where it was possible to make a judgment about the position of the wood in the tree, I excluded specimens inferred to represent stumps and branches because those tree rings can be exceptionally wide due to buttress effects. The data set was subdivided into three groups (low, mid, and high palaeolatitude, 0°–30°, 30°–60°, and 60°–90°, respectively) and the mean and variance were obtained and compared with modern data from the International Tree-Ring Data Bank (see Falcon-Lang, 2005).

4.4. RESULTS

Based on analysis of the two databases, the following patterns are evident for Cretaceous forests.

4.4.1. General composition of Cretaceous forests

The database of Cretaceous fossil wood (n = 2238) is composed by ferns (2.5%), cycadeoids (1.7%), ginkgo (0.7%), conifers (59%), and angiosperms (20.6%) (Fig. 4.2). Conifers are further subdivided into four anatomical categories (araucarioid, podocarpoid, cupressoid, and pinoid) as follows: Araucarioids (22.2% of total wood records) comprise *Agathoxylon, Araucarioxylon, Araucariopitys,* some *Brachyoxylon, Dadoxylon, Dammaroxylon,* and some *Planoxylon.* Podocarpoids (11.7%) comprise *Circoporoxylon, Metapodocarpoxylon, Phyllocladoxylon, Podocarpoxylon, Protocircocarpoxylon, Protophyllocladoxylon,* and *Protopodocarpoxylon.* Cupressoids, including cheirolepids (10.1%) comprise *Chamaecyparixylon, Cupressinoxylon, Cupressoxylon,* some *Elatides,* some *Frenelopsis, Juniperoxylon, Metacupressinoxylon, Paracupressinoxylon, Protocupressinoxylon, Prototaxodioxylon,* some *Pseudofrenelopsis, Sequoioxylon, Taxaceoxylon, Taxodioxylon,* and *Thujoxylon.* Pinoids (6.5 %) include *Abiocaulis*, *Cedroxylon*, *Keteleerioxylon*, *Laricioxylon*, *Palaeopiceoxylon*, *Piceoxylon*, *Pinoxylon*, *Pityoxylon*, *Protocedroxylon*, *Protopiceoxylon*, and *Protopinuxylon*. Conifers that have complex taxonomy (e.g., *Xenoxylon*) represent 8.6% and other not identified samples 15.5% (Fig. 4.2).

As my aim was only to group woods into the broad anatomical categories, I did not update all generic names based on modern revisions (e.g. Bamford and Philippe, 2001). Emended species by recent publications (e.g. Herbst et al., 2007; Oh et al., 2011) were included in the database and records were updated, therefore the above lists contain a mixture of historical and revised taxa.

From the original 2238 records included in the database, 641 (28.6%) records were excluded for the biogeographic analysis due to incomplete data about their age, provenance and/or affinity (Fig. 4.3).

4.4.2. Geographic distribution of plant groups through the Cretaceous

Forest composition analysis shows that araucarioid and podocarpoid conifers were the most abundant (33.9 % of all records) and globally widespread (80°N to 80°S) taxa, especially in time bins T1–T3 (Fig. 4.4, column 1). In contrast, cupressoid (cf. frenelopsids and taxodioids) conifers had a more restricted range in mid-palaeolatitudes (mean palaeolatitude 39.5°) in both hemispheres while pinoid conifers were mostly confined to mid- to high palaeolatitudes (mean palaeolatitude 46.1°) exclusively in the Northern Hemisphere (Fig. 4.4, column 2), where they strongly intergraded with cupressoids. Angiosperm records were widely dispersed in the earliest time bin (T2) in which they occur, and only extended their latitudinal range minimally over time (Fig. 4.4, column 3). See detailed distribution maps in Appendix 2.

4.4.3. Abundance of conifers and angiosperms through time

All conifer groups underwent decline during Late Cretaceous time, with araucarioid and, to a lesser extent, podocarpoid conifers undergoing drastic reduction. Conifer loss shows an antithetic trend to the rise of angiosperms (Fig. 4.5), the major changeover occurring in latest Cretaceous (Campanian–Maastrichtian) time when the proportion of angiosperms increased from 31% to 77% (Fig. 4.5). No patterns are evident in the cycadeoid, tree fern, and ginkgo data, probably due to low sample size (collectively <5% of total analysed records), and these data are not shown on the palaeomaps (Fig. 4.4).

4.4.4. Plant spatial analysis

Spatial analysis using a 3° buffer diameter (my analyses of 1 – 5° buffer diameters showed that values plateau above 3° of buffer) to explore the co-occurrence of all pairs of plant groups (for all time bins) reveals the following associations (Fig. 4.7): cupressoids are most closely associated with pinoids (at 63% of sites) and podocarpoid conifers are most closely associated with araucarioids (60.7% of sites), while araucarioids and podocarpoids rarely co-occur with pinoids (25.7% and 19.8% of sites, respectively). Spatial analysis also reveals that araucarioids more closely co-occur with angiosperms (50.2% of sites) than cupressoids (40.1%), podocarpoids (37.2%), or pinoids (27.1%). Chi-square test supports a higher degree of associations between araucarioid with podocarpoid, angiosperm and cupressoid co-occurrences, as well as the cupressoid–angiosperm association (Table 4.1). On the other hand, cupressoid–pinoid and cupressoid–podocarpoid observed frequencies are less than the expected frequency value (Table 4.1).

4.4.5. Productivity inferred from tree ring data

Forest productivity analysis (Fig. 4.8) shows that annual tree growth rate was elevated compared to the present. Annual growth rate was elevated, but not significantly so, at low palaeolatitudes (mean 2.37 ± 0.75; cf. modern mean 1.48 ± 0.53); however, at mid-palaeolatitudes (mean 2.56 ± 0.94; cf. modern mean 1.18 ± 0.51) to high palaeolatitudes (mean 2.03 ± 0.70; cf. modern mean 0.68 ± 0.59), rates were elevated (×2) at a significant level (Fig. 3.5). In addition, the humid tropical belt was wider than at present, as indicated by the near absence of woods with tree rings in low latitudes (10°– 30º), and the temperate belt was displaced >15º poleward, as indicated by mean ring width of ~2 mm at 80º palaeolatitude; trees do not produce ~2 mm rings above latitude 63º today (Falcon-Lang, 2005).

4.5. DISCUSSION

There have been few previous studies of Cretaceous wood distribution at a global scale. One of the few works on this subject is the classic paper published by Florin (1963) entitled “The distribution of conifer and taxa in time and space” in which he showed some maps of distribution of conifers related to genera such as *Podocarpus*, *Araucaria* and *Taxodium*; however the amount of records and data included in this maps are not sufficient to establish biogeographic patterns. In a similar semi-quantitative vein, Creber and Chaloner (1985) examined tree-ring patterns across the Cretaceous world and inferred a generally equable climate. My more comprehensive and quantitative analysis extends these classic studies.

Patterns of Cretaceous forest composition and productivity collated here are based on a nearly complete compilation of fossil wood, synthesizing >175 yr. of data. My work builds on those earlier attempts to analyse the nature of Cretaceous terrestrial biomes and climates using fossil databases (e.g., Creber and Chaloner, 1985; Florin, 1963; Philippe et al., 2004), but takes a more quantitative approach similar to that used in palynological studies (Crane and Lidgard, 1989; Lidgard and Crane, 1988).

Global biogeographic analyses are frequently complicated by sampling biases (e.g. continental fragmentation, temporal resolution, depositional hiatuses, taphonomic and facies-related biases), however, these types of studies are not only subjected to the quality and the incomplete nature of the fossil record but also to a significant amount of geological information and data overlooked in some published works. More conscious and meticulous analysis of these Cretaceous datasets, beyond the general approach and aims of this study, will confirm or correct conclusions herein reached. An interesting example would be to assess whether the amount of fossil wood records related to marine deposits (i.e. ~15%) challenge distribution patterns previously discussed.

Whilst my analysis is not immune to sample biases, general patterns of Cretaceous wood that here emerge are consistent when compared with compilations of climate-sensitive sediments (Chumakov et al., 1995; Hay and Floegel, 2012; PALEOMAP project, 2001-present) and climate model results (Sellwood and Valdes, 2006). They agree araucarioid and podocarpoid conifers were centered in humid tropical and paratropical regions with relatively few records from warm and cool temperate settings, while cupressoid conifers dominated along the seasonally dry ecotone between humid tropical and arid mid-latitude belts (30°– 45°). The distribution of pinoid conifers, centered in temperate, and to some extent, in cool temperate northern latitudes (mostly 40°– 65°), suggest that their present-day distribution was established in Cretaceous time. This is consistent with the origin of Pinaceae in high latitudes of the Northern Hemisphere (LePage, 1999). Furthermore, these ancient patterns may also explain modern trends in conifer leaf physiognomy; extant araucarians and podocarps mostly have broad leaves, cupressaceous conifers mostly have scale leaves (except for taxodioids), and pinaceous conifers mostly have needle leaves, consistent with humid, dry, and cool conditions, respectively (Farjon, 2001). One caveat is that the Cretaceous wood categories (araucarioid, podocarpoid, cupressoid, pinoid) may not precisely correspond to extant families.

My data suggest that the drastic global decline in conifer dominance could be linked to the rise of angiosperms, which initially proliferated in the humid tropical and paratropical belt dominated by araucarioid conifers, explaining why this group was the most seriously affected while higher latitude pinoid populations underwent less decline. It is interesting that compilations of pollen records indicate that angiosperms rose to dominance in the Albian–Cenomanian (Heimhofer et al., 2005), whereas the major changeover in the fossil wood record occurred in the Campanian–Maastrichtian. This suggests that while weedy angiosperms diversified at an early stage, they did not become forest dominants at mid and low latitudes until 25 Ma later.

Global patterns of forest composition and productivity herein presented are mostly consistent with Cretaceous climate models (Beerling et al., 1999; Sellwood and Valdes, 2006), indicating expansion of the tropical belt and poleward extension of forests. Tree-ring data also support the hypothesis that extreme greenhouse warmth and/or CO_2 fertilization may have had significantly influenced terrestrial biomes, more than doubling global forest productivity (Beerling et al., 1999). As such, my findings have implications for understanding the long-term effects of future global warming.

4.6. CONCLUSIONS

1. Global patterns of Cretaceous forest composition and productivity are analysed using a comprehensive fossil wood database (n = 2238). To ascertain forest composition, records were classified by botanical affinity, plotted on palaeomaps, and analysed with GIS tools.

2. Results confirm previous conjecture that araucarioid and podocarpoid conifers were globally co-dominant in Early Cretaceous times, especially in humid (para)tropical biomes, but drastically reduced in numbers and range during the Late Cretaceous. Cupressoid conifers, which were most common in seasonally dry mid-latitudes, although taxodioid and pinoid conifers, which were associated with temperate conditions at higher northern latitudes, also declined at the same time, though less markedly.

3. Spatial analysis shows that loss of conifer forests (especially araucarioids) was directly linked to the rise of co-occurring angiosperms. My data also show that woody angiosperm ascendancy was not achieved until Campanian-Maastrichtian times (somewhat later than previous analyses), when the use of vessels and more efficient leaf transport became established, by which time the modern relictual pattern of conifer distribution had been largely established.

4. Mean ring width data ($n = 284$) of long tree-ring sequences were obtained to ascertain forest productivity along the palaeolatitude gradient. Comparison with modern data shows that Cretaceous forest productivity was significantly elevated (x2) in mid- and high palaeolatitudes and further implies a poleward displacement of the temperate belt by >15°.

FIGURES CHAPTER 4

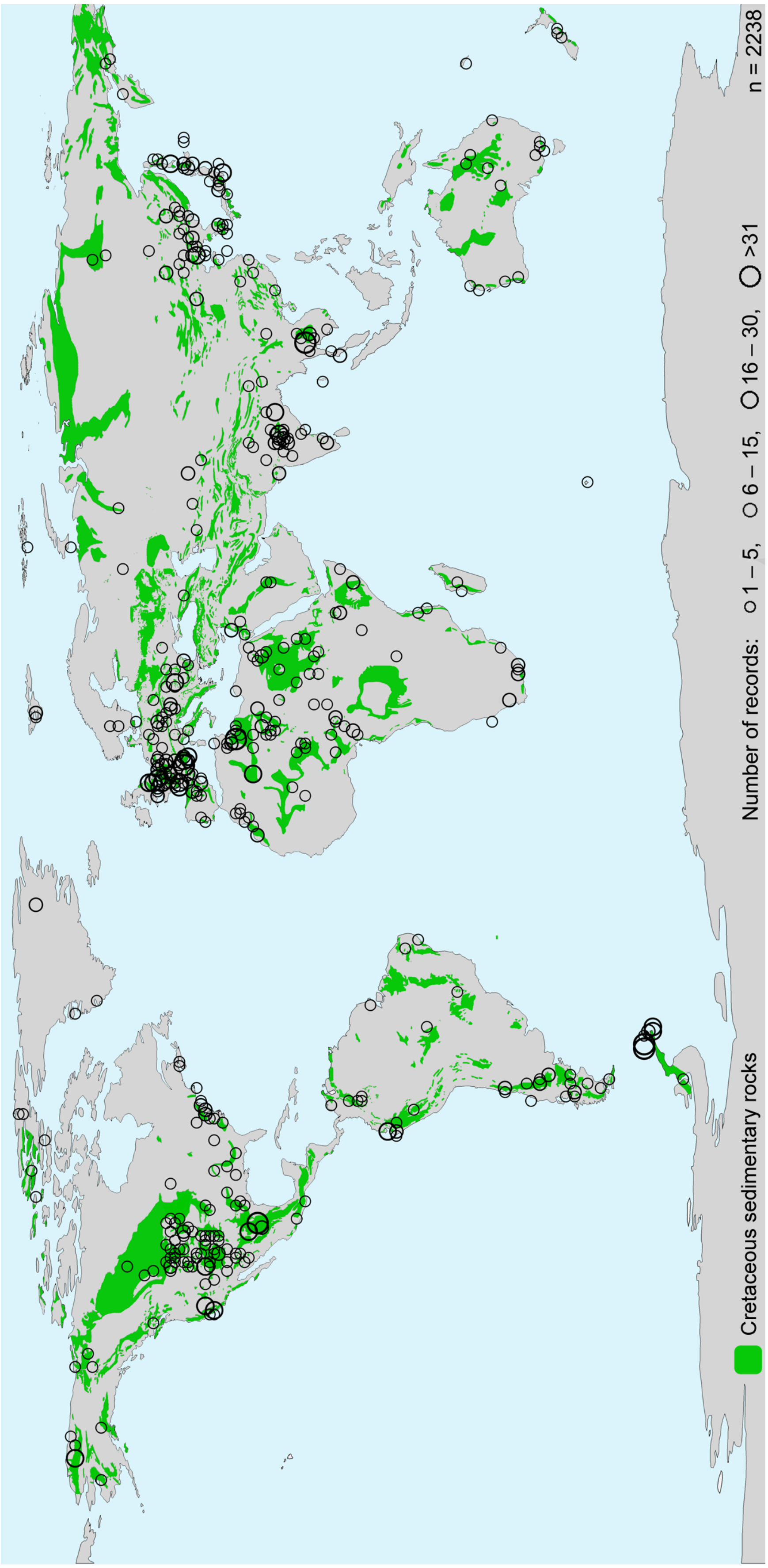


Figure 4.1. Fossil wood records (n = 2238) plotted on world map showing Cretaceous outcrops (dark grey; collated from various map sources). The only data gaps are for poorly sampled Cretaceous outcrops in Middle East, Arctic Russia, and northwest Canada

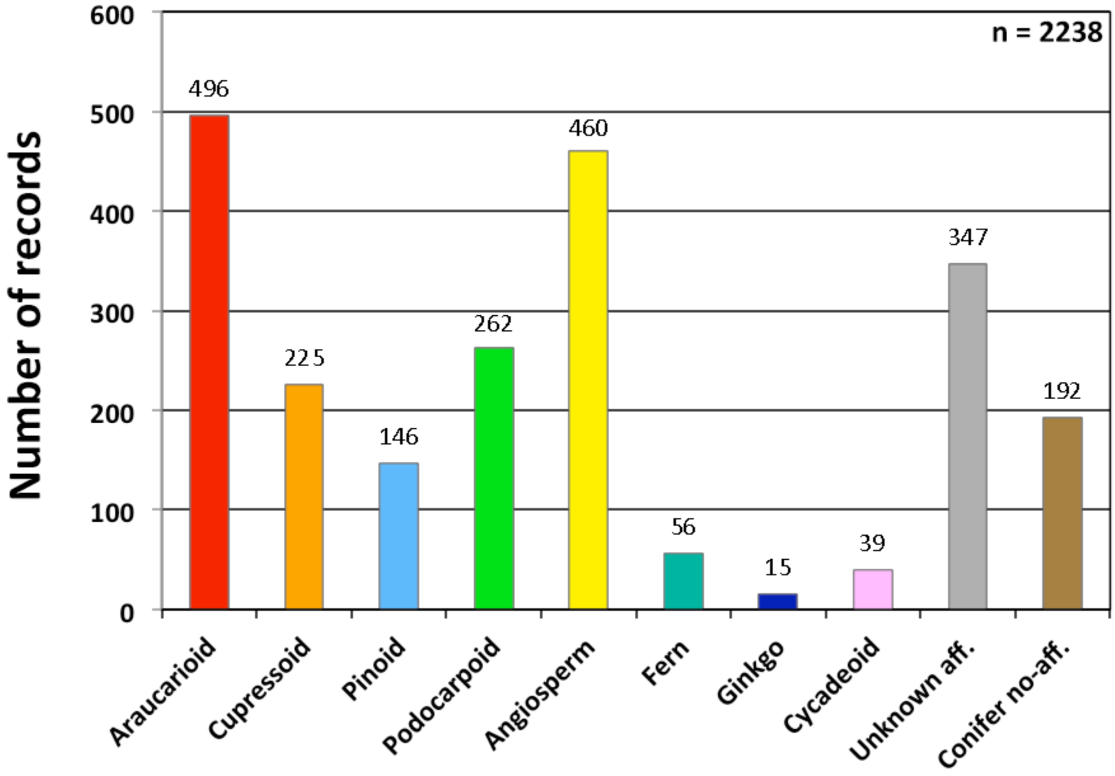


Figure 4.2. Number of records of Cretaceous wood.

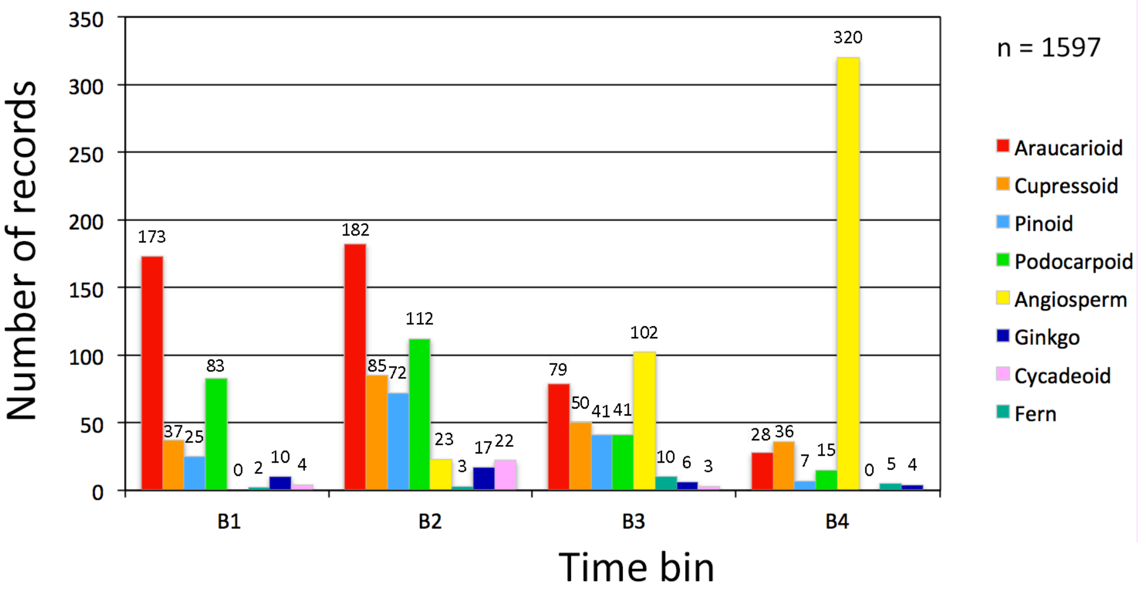


Figure 4.3. Numbers of identified samples of Cretaceous wood included in the biogeographic analysis.

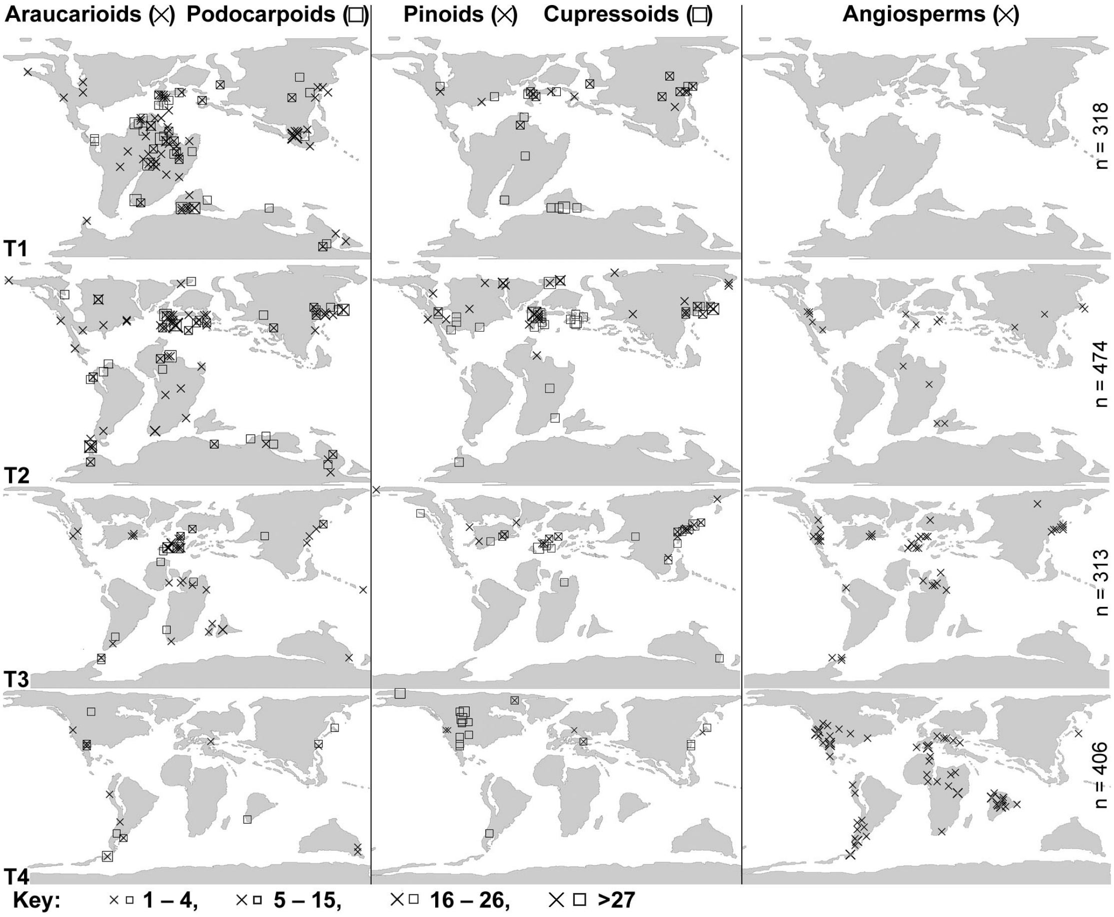


Figure 4.4. Palaeogeographic distribution of Cretaceous conifers and angiosperms plotted with ArcGIS. Columns show (1) araucarioids and podocarpoids, (2) cupressoids and pinoids, and (3) angiosperms; rows show time bins: T1, Berriasian–Hauterivian (145.5–125 Ma); T2, Aptian–Albian (126–99 Ma); T3, Cenomanian–Santonian (99–83 Ma); T4, Campanian–Maastrichtian (84–65.5 Ma). See appendix 2 for detailed maps.

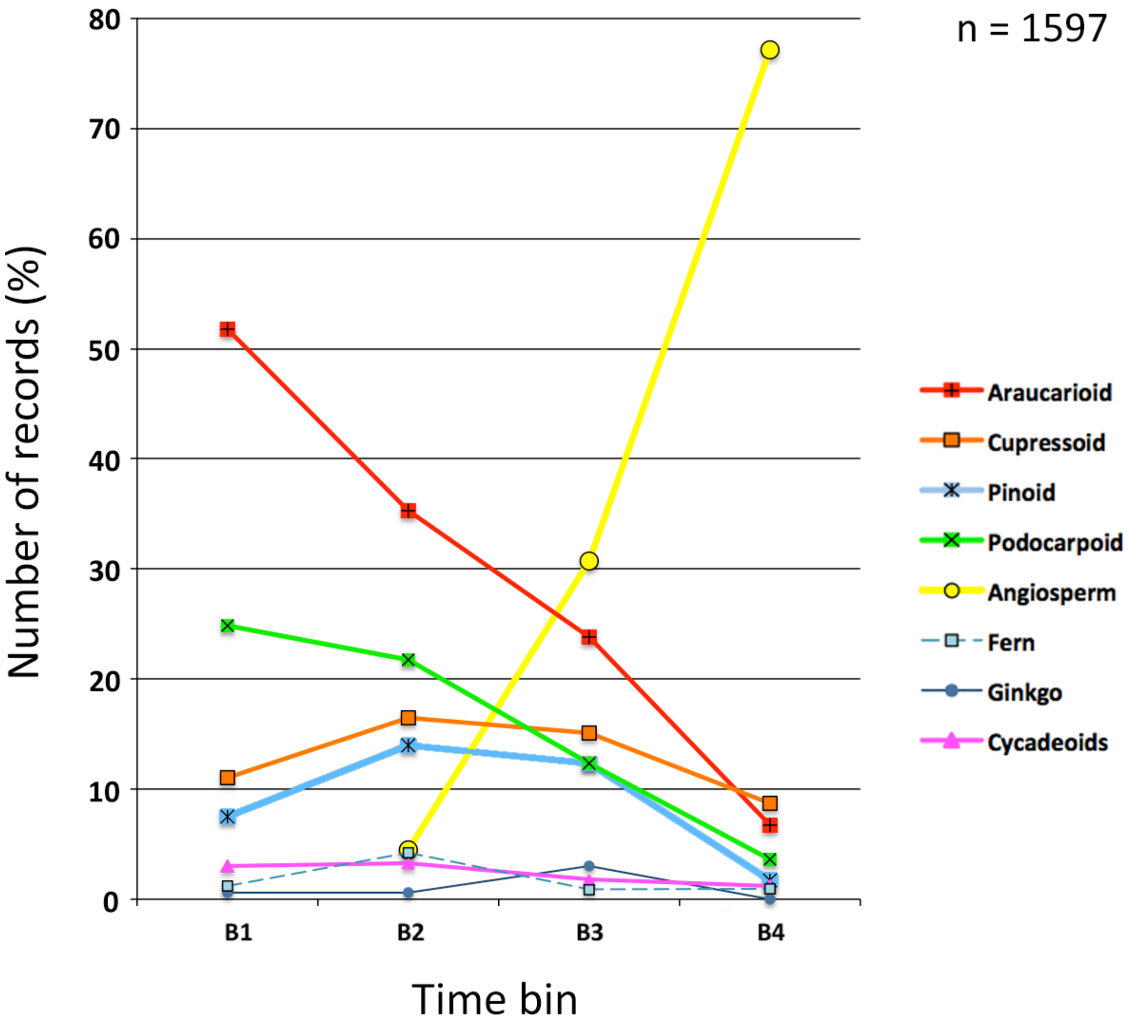
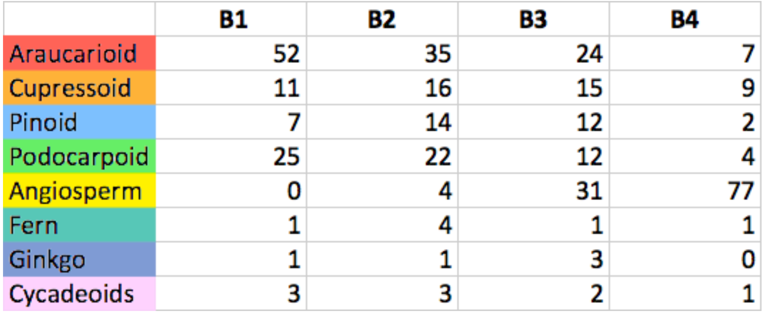


Figure 4.5. Percentage of abundance of wood records through the Cretaceous.



	B1	B2	B3	B4
Araucarioid	52	35	24	7
Cupressoid	11	16	15	9
Pinoid	7	14	12	2
Podocarpoid	25	22	12	4
Angiosperm	0	4	31	77
Fern	1	4	1	1
Ginkgo	1	1	3	0
Cycadeoids	3	3	2	1

Figure 4.6. Changes in percentage of abundance of Cretaceous wood records plotted in figure 4.5.

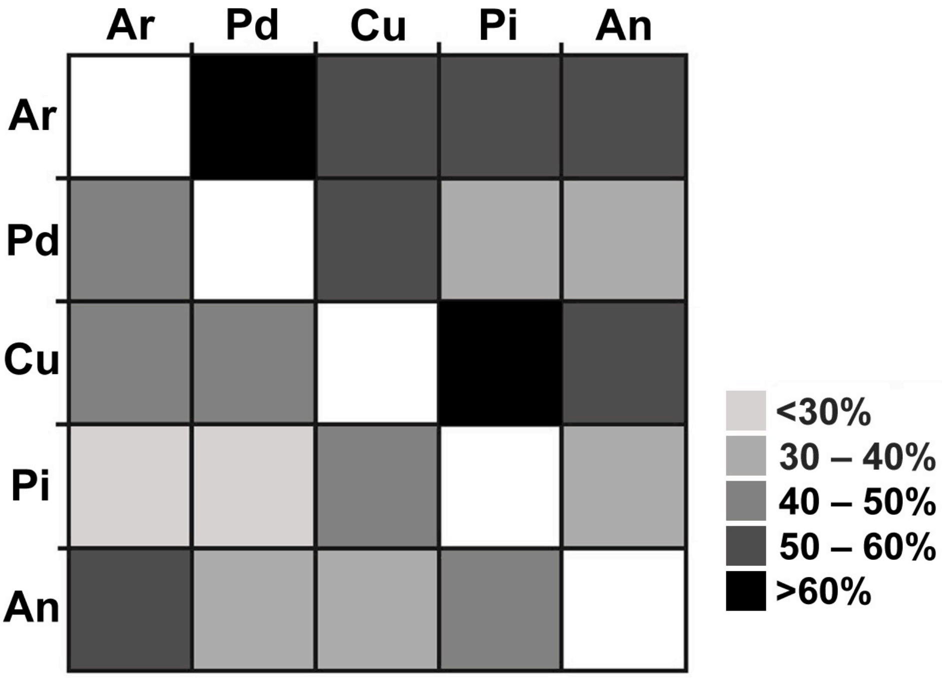


Figure 4.7. Co-occurrence matrix for each pair of plant groups. Abbreviations: Ar- araucarioid; Pd- podocarpoid; Cu- cupressoid; Pi- pinoid; An- angiosperm.

	Observed N	Expected N	Residual
Pino - Podo	63	117.2	-54.2
Arau - Pino	83	117.2	-34.2
Angio - Podo	95	117.2	-22.2
Cupr - Pino	99	117.2	-18.2
Cupr - Podo	102	117.2	-15.2
Pino - Angio	103	117.2	-14.2
Arau - Cupr	142	117.2	24.8
Cupr - Angio	147	117.2	29.8
Arau - Podo	160	117.2	42.8
Arau - Angio	178	117.2	60.8
Total	1172		

Table 4.1. Chi-square test of fossil wood co-occurrences. (Chi value = 105.765, df = 9, *P* = 0.0001).

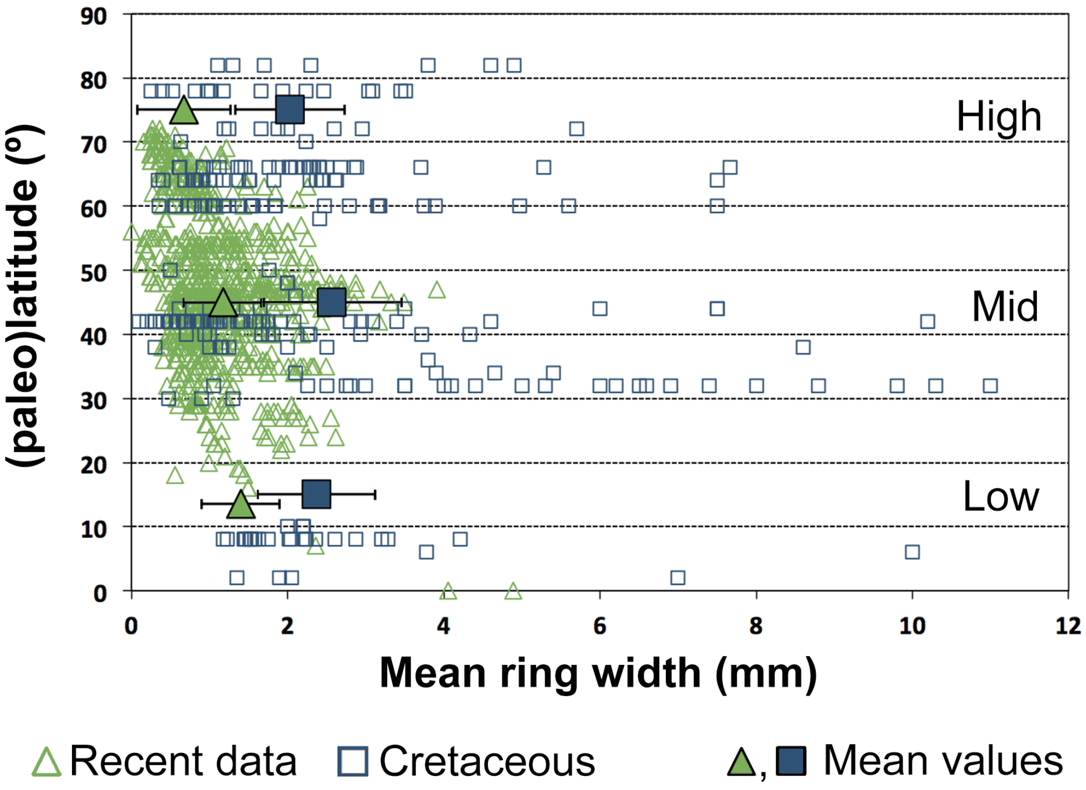


Figure 4.8. Comparison of modern and Cretaceous forest productivity, based on mean tree-ring width for low (0º – 30º), mid (30º – 60º), and high (60º – 90º) latitudinal zones. Data source: Cretaceous fossil wood (n = 284, this study); modern trees (n = 727; International Tree-Ring Data Bank (web.utk.edu/~grissino/itrdb.htm); e.g., see Falcon-Lang, 2005).

CHAPTER 5: BIOGEOGRAPHY OF CRETACEOUS CHEIROLEPID CONIFERS

5.1. INTRODUCTION

5.1.1. The Cheirolepidiaceae family

The Cheirolepidiaceae Takhtajan ex Doludenko, 1978 is a family of Mesozoic conifers with a long and complex taxonomical background (Watson, 1982). As previously documented and summarized by Alvin (1982) and Watson (1988), the *Hirmeriella-Cheirolepis* group and Frenelopsid conifers were considered to be two unrelated conifer families (Watson, 1988). The relation between these two groups was discovered when Hlustik and Konzalova (1974) and Alvin (1977) reported cones of *Frenelopsis alata* and *Pseudofrenelopsis parcemosa*, respectively, associated with *Classopollis* pollen *in situ* (Axsmith et al., 2004). These discoveries established the relation between these two groups and Cheirolepidiaceae was established as a single family (Watson, 1988).

Conifers of Cheirolepidiaceae first appear in the Late Triassic, being a dominant element throughout the Jurassic and Early Cretaceous vegetation (Barnard, 1973; Vakhrameev, 1978). They were mainly present in southern Laurasia and northern Gondwana (Archangelsky, 1963; Batten and MacLennan, 1984; Kunzmann et al., 2006; van Waveren et al. 2002), and they are commonly found at low palaeolatitudes (Alvin, 1982). Evidence of the presence of these conifers at high latitudes is rarely found (e.g. Cantrill and Falcon Lang, 2001; Falcon Lang and Cantrill, 2000; Mohr and Gee, 1992).

The maximum diversity and abundance of Cheirolepidiaceae was in the Jurassic-Early Cretaceous (Kunzmann et al., 2006). During the rise and subsequent dominance of angiosperms by the Early-Middle Cretaceous, the family declined in abundance (Lupia et al., 1999), and became extinct during the late Maastrichtian (van der Ham et al., 2003). Although pollen has been found in Early Tertiary sediments (Vakhrameev, 1970), it is regarded as reworked (Balme, 1995; Srivastava, 1976;).

Some of the most representative vegetative and reproductive structures reported are *Cupressinocladus, Classostrobus*, *Frenelopsis, Pseudofrenelopsis, Protocupressinoxylon,* and *Tomaxellia*, which are found in many Cretaceous floras of Africa (e.g. Barale and Ouaja, 2002; Lejal-Nicol, 1987; Watson, 1983), United States (e.g. Axsmith et al., 2004, 2005; Doyle, 1992; Haworth et al., 2005; Srinivasan, 1995; Watson, 1977, 1988; Watson and Fisher, 1984), South America (e.g. Archangelsky, 1968; Del Fueyo et al., 2008; Sucerquia et al., 2008), England (e.g. Alvin et al., 1978; Alvin et al., 1994; Francis, 1983; Watson, 1977), Portugal (e.g. Alvin, 1977; Dinis, 2001; Mendes et al., 2010b), eastern Europe (e.g. Alvin and Hlustik, 1979; Falcon-Lang et al., 2001; Iamandei and Iamandei, 2005; Krassilov, 1982; Kvacek, 2000; Reis, 2000), and Asia (e.g. Kimura, 2000; Ren et al., 2008; Saiki, 1999; Zhou, 1995; Yang, 2008).

The pollen record of Cheirolepidiaceae is represented by the genus *Classopollis*, which dates from the Late Triassic (Reyre, 1970, 1973), by the time its distinctive morphology also became established (Zavialova et al., 2010). It was later through the Jurassic and Cretaceous when its morphological patterns became more diverse and its worldwide distribution at low-mid palaeolatitudes was fully established (Watson, 1988). The continuous decline of Cheirolepidiaceae pollen abundance suggests that they were competitively replaced by angiosperms (Lupia et al., 1999).

5.1.2. Paleoecology of Cheirolepidiaceae conifers

The paleoecology of the Mesozoic conifer family Cheirolepidiaceae has been the subject of much speculation. The presence of scale-like leaves and thick cuticles in Cheirolepidiaceae are considered xeromorphic adaptations related to reduction of solar radiation, reduction of drought-air circulation, reduction of evapotranspiration, and trapping of surface external water (Thevenard et al., 2004). Based on anatomical characters and sedimentological data many authors construed that the Cheirolepidiaceae were drought resistant, low-growing thermophilous trees and shrubs preferring well-drained soils and upland slopes (Kunzmann et al., 2006; Sun et al., 2010; Upchurch and Doyle, 1981; Vakhrameev, 1970).

On the other hand, their occurrence in a wide range of palaeoenvironmental conditions at many localities and great morphological diversity support the earlier conclusions that Cheirolepidiaceae conifers are not absolute proofs of dry, heat- or salt-constrained habitats (Alvin et al., 1978; Alvin, 1982; Mendes et at., 2010a).

There have been a series of studies (e.g. Aucour et al., 2008; Haworth et al., 2005; McElwain and Chaloner, 1996; McElwain, 1998; Thevenard et al., 2004; Passalia, 2009) on palaeoclimates based on proxy data of stomata index on Cheirolepidiaceae to calculate variations of atmospheric CO_2 (Royer, 2001; Woodward and Kelly, 1995). The method is founded on the observation that plants' stomatal densities adjust in response to changing atmospheric pCO_2 to minimize transpiration (Haworth et al., 2005; Woodward, 1987). However, these observations are based on calibrations of stomatal frequency using "living fossils" and therefore relying on the assumption that no evolutionary shifts in ecophysiological responses have occurred over time (Grein et al., 2013).

5.1.3. Climate-sensitive sediments

Climate-sensitive sediments are one of the main proxies to study palaeoclimates through extrapolation of modern distribution of types of rocks formed under specific climate conditions (Parrish, 1998). For example, glacial sediments require the presence of glaciers and thus cold climate; shallow-water limestones require warm water and highly concentrated carbonate waters; and evaporite deposits require higher evaporation rates than precipitation and water in restricted basins (Sohl and Chandler, 2007). Other detailed studies on mineral content, such as kaolinite, are also used to obtain information on precipitation rates and weathering (Holmes, 1992).

Oxygen isotopes studies in different types of sediments are also good indicators of palaeotemperatures (Clarke and Jenkyns, 1999), although variations in salinity, diagenetical alterations, erosion, weathering, and deposition of climate-sensitive sediments may affect their reliability (Gornitz, 2009).

Important attempts to reconstruct the distribution of climate sensitive sediments at global scale include the palaeogeographic maps published by Christopher Scotese (and Sriroop Chaudhuri) on his website (PALEOMAP project, 2001-present) which is based on a compilation made by J. Boucot (U. of Oregon) with help form Chen Xu (Nanjing University). The work of Chumakov et al. (1995) offers a series of detailed palaeoclimate maps based on climate-sensitive sediments and fossil material is perhaps one of the most comprehensive studies on Cretaceous climate zones.

5.2. MATERIALS AND METHODS

I constructed a database of Cheirolepidiaceae conifers comprising 478 records from 220 localities worldwide. Data compiled from 242 publications include vegetative (i.e. leaves, shoots and wood) and reproductive (i.e. male/female cones and pollen) (Appendix 3) material. Records were sorted into two main time bins: Early Cretaceous (145.5–99.6 Ma), and Late Cretaceous (100–65.5 Ma) in order to match climate paleogeographic maps available at PALEOMAP project (2001-present). Records were then plotted by hand on Ron Blakey's global palaeogeographic maps of 120 Ma and 90 Ma respectively (Blakey, 2011 date accessed) to obtain palaeo-coordinates.

To analyse the spatial correlation of Cheirolepidiaceae conifers and climate-sensitive sediments occurrences data were manipulated in ArcGIS using the *Proximity* and *Overlay* tools. Buffer areas of 1º, 2º and 3º in diameter were created for sediments and their co-occurrence with Cheirolepidiaceae conifers was ascertained by the percentage of localities that fell in each buffer (Fig. 5.1).

Cheirolepidiaceae occurrences were later plotted on palaeoclimate maps republished and edited by Hay and Floegel (2012) after Chumakov et al. (1995). Early Cretaceous localities were plotted in the Aptian climate map (Fig. 5.10) while fossil localities of Late Cretaceous age were plotted on the Santonian climate map (Fig. 5.11).

Statistical analyses were employed to test for normal distributions and also for the correlation/association of two or more samples. Chi-square test was selected as the number of frequencies was higher than 5. In this case, Chi-square test allows calculating the significance of the association between and climate-sensitive sediments distribution, as well as to test for the relation between fossil's age and the rock type associations.

5.3. RESULTS

5.3.1. Proximity analysis of climate-sensitive sediments and Cheirolepidiaceae fossil evidence.

Results of the proximity analysis of cheirolepid occurrences in relation to climate-sensitive sediments show that during the Early Cretaceous, these fossils in general tend to be closer to evaporites and coal (Table 5.2, Fig. 5.2; A1, B1 and C1). In figure 5.2 C2, 22% of localities where cheirolepid fossils occur are related to evaporites, 15% to coal, 11% to kaolinite, 10% to bauxite, and 4% to calcrete.

The correlation between Early Cretaceous cheirolepid conifers and sediments indicative of arid/dry conditions at a global scale can be observed in figure 5.5. This map shows that fossil localities follow a similar distribution pattern across the globe with Central America being the only major geographical gap of Cheirolepid occurrences. Although cheirolepid occurrences tend to be found closer to evaporites, when using the 3º buffer, a significant percentage of sites (27%) show a high proximity with coal which indicates more humid/wet environments (Table 5.2 and Fig. 5.2 C3, Fig. 5.4).

During the Late Cretaceous, localities where cheirolepid records occur tend to be closer to sediments that indicate wet/humid environment conditions (Table 5.2, Fig. 5.3 F1; Fig. 5.6). Although both *Classopollis* and mega/mesofossils distributions are related to wet/humid climate-sensitive sediments, the former shows a strong affinity to coal which represents wet/temperate climates (Fig. 5.3; D1 and D2), while the latter tends to be more related to kaolinite suggesting humid/warm tropical environments (Fig. 5.3; E1, E2 and E3). Forty six localities included in the proximity analysis (18%) were not related to any of the five climate-sensitive sediments (Table 5.1).

Results are further confirmed by the Chi-squared test, which indicates there is a significant (*P* = 0.02) difference in the frequency of fossil occurrences in certain rock types depending on their age (Table 5.3). In the Early Cretaceous fossils occur more often in evaporites (Table 5.4), while in the Late Cretaceous cheirolepids are predominantly found in kaolinite, coal and, bauxite (Table 5.5).

The latitudinal analysis of cheirolepids shows that during both Early and Late Cretaceous these conifers were primarily abundant at mid-latitudes between 20 – 40º (Fig. 5.8). The latitudinal distribution of both types of fossils (micro and mega/mesofossils) shows a very similar pattern (Fig. 5.9). Although, the number of pollen records at the equatorial region pollen is distinctively more abundant than mega/mesofossils. On the other hand, mega/mesofossils reach latitudes between 60 –70º where record of pollen is not found (Fig. 5.9). The statistical analysis, however, showed no significant correlation between fossil type of fossil and the rock where they occur (Chi-square value: 0.732, *P* = 0.947).

5.3.2. Cheirolepid distribution comparison with other global palaeoclimate records

The dataset plotted over palaeoclimate data and maps created by Chumakov et al. (1995) showed that during Early Cretaceous times, localities with cheirolepid fossils tend to lie on the limits of the Northern Mid-latitude Warm humid belt (NMW) and the Tropical-Equatorial Hot arid belt (TEH). This is also the case of southern hemisphere localities, which lie mostly between the TEH and the Southern Mid-latitude Warm humid belt (SMW) (Fig. 5.10). Mega and mesofossils are clearly restricted to 3 latitudinal ranges 20–50º N, 10º N –15º S and 40–50 ºS (Fig. 5.10). 55% of those localities are found in the in tropical regions (NMW and SMW), and the other 45% of fall in the evaporite/arid belt. In contrast *Classopollis* distribution tends to be relatively wider since it covers the latitudinal gaps close to the evaporite belt and arid zones. 66% of *Classopollis* occurrences are found in arid regions while 34% in humid topics.

In the Late Cretaceous 76% of localities with cheirolepid mega and mesofossils are located in the tropical belt (NMW) (Fig. 5.11) while the other 24% represent localities in the arid regions (Fig. 5.11). Localities with *Classopollis* are evenly divided 50–50% between arid and tropical regions (Fig. 5.11).

5.4. DISCUSSION

The idea of cheirolepids as indicators of aridity has been widely assigned to this extinct conifer family based on anatomical characters such as thickening of the cuticles, subsidiary cells with large papillae, and anticlinal walls with strong cutinisation (Alvin 1982; Hlustik 1978; Sun et al., 2010; Vakhrameev 1970; Watson 1988). More recently, however, the classic palaeoecological interpretations of cheirolepids as strict arid coastal xerophytes have been challenged by studies with a more detailed taphonomic approach. It has been proposed that only certain species of the family can be used as ecological indicators of saline or marine influences since these conifers are found in a wide range of environments ranging from inland areas to coastline habitats (Gomez et al., 2002).

Biogeographic analyses of cheirolepid occurrences presented in this work show that although they tend to be closely related to evaporites, a fair amount of localities occur near kaolinite and coal which indicate a certain affinity with paratropical climate. This has also been observed in the Cretaceous floras from Portugal where the majority of samples collected are found in kaolinite deposits (Mendes et at., 2010a). My results support the idea of these conifers being able to reach less arid climates and to even be abundant in humid tropical regions. The distribution patterns of Early Cretaceous

Cheirolepidiaceae reveal they were more abundant in the transitional regions between the mid-latitude humid belt and the evaporite-arid zone than in the arid equatorial province. This idea is sustained by reports of Cheirolepidiaceae found in tropical floras where ferns, bryophytes, and non-xeromorphic angiosperms are common too (Axsmith, 2005; Crane et al., 1994). The biogeography of Early Cretaceous cheirolepids suggest that although their anatomical features made them dominant in arid regions they were also capable of adapting to a certain extent to more humid environments. This is idea coincides with alternative explanations for the presence of xeromorphic characters, which suggest they are the result of adaptation to extreme seasonality and growth on poor-developed/well-drained sandy soils (Gomez et al., 2012) and high evaporation rates similar to mangrove habitats (Upchurch and Doyle, 1981). The global distribution of the family Cheirolepidiaceae suggest that even though they were more abundant in arid regions they were not restricted to them, implying that they covered a wider range of habitats including inland freshwater floodplains, lakeshores and brackish coastal environments as previously suggested (Alvin et al., 1978; Alvin, 1982; Gomez et al., 2002).

The analysis of Late Cretaceous occurrences shows the drastic decline in abundance of Cheirolepidiaceae previously reported in palynological studies (Lupia et al., 1999). Although the causes are still debated, studies in Portuguese Cretaceous floras suggest that climate variations had an important effect on the warm/humid and hot/arid mid-latitude belts (Mendes et at., 2010a). Willis and McElwain (2002) indicate that a wet winter (Mediterranean) biome prevailed during the Late Cretaceous, with an important decrease in temperature at low- and mid-palaeolatitude regions by the Late Turonian (Gale, 2000). Evidence of the contraction of the arid regions and further expansion of tropical belt is also observed in palaeoclimate reconstructions by

Chumakov et al. (1995), showing a more restricted distribution of evaporites during the Late Cretaceous compared with the Early Cretaceous, and an significant increase in the distribution and number of coal occurrences found at mid- and higher palaeolatitudes. These cooler and more humid conditions are reflected in the drastic shift in the correlation between cheirolepids and climate-sensitive sediments that goes from being mostly related to evaporites during the Early Cretaceous to be more related to wet/humid sediments during the Late Cretaceous. While humid zones became more extensive by the end of the Cretaceous the number of Cheirolepidiaceae records decrease in abundance. Nevertheless, the percentage of samples across the latitudinal gradient remains stable suggesting a global decline that affected simultaneously the different environments they inhabited.

In addition to the climatic variation that affected the global arrangement of Cretaceous biomes, the ecological change caused by the dominance of angiosperms could have also aided the later extinction of Cheirolepidiaceae as previously observed in chapter 4 in the record of fossil wood of the other conifer lineages.

The main limitation of this analysis is the low number of cheirolepid occurrences and climate-sensitive records that do not allow grouping the samples in time bins relevant to their age (Cretaceous stages) without affecting the significance of statistical analyses. The different time frame of sediment deposition between rock types analysed is a caveat that may also affect the interpretations of the biogeographic analysis.

5.5. CONCLUSIONS

Biogeographic analysis of Cheirolepidiaceae conifers shows a strong spatial correlation between the distribution of arid climate-sensitive sediments (i.e. evaporites) and Cheirolepid occurrences during the Early Cretaceous. In contrast, Late Cretaceous localities where these conifers are found tend to occur in humid tropical environments. This suggests that the presence of cheirolepid fossils not necessary imply dry-arid environments as previously thought. Although they were more abundant in dry/arid environments during the Early Cretaceous, they also had a strong presence in mid-latitudes where tropical and arid belts converge. The findings in this work agree with the idea of a more cosmopolitan capability of Cheirolepidiaceae conifers even though they were more adapted and success for dry environments.

The drastic decrease and subsequent extinction of this family of conifers is clearly reflected in the lower abundance and fewer localities reported for the Late Cretaceous in comparison to their climax during the Early Cretaceous. The causes of extinction could be related to the expansion of the tropical zone towards the arid/dry regions as well as the dominance of angiosperms, which affected all groups of conifers during the Late Cretaceous.

Although the number of cheirolepid megafossils is not particularly large, further collecting and inclusion of *Classopollis* occurrences to the dataset will allow grouping the samples in smaller time-bins that would reflect more accurately the changes of distribution of Cheirolepidiaceae family during the Cretaceous.

FIGURES CHAPTER 5

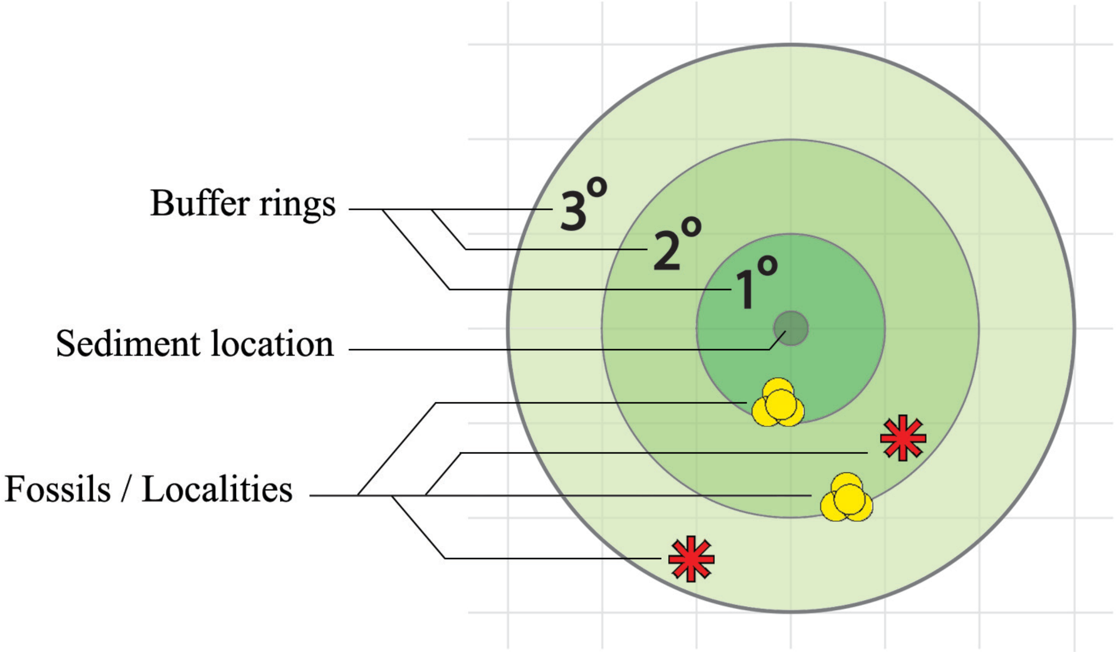


Figure 5.1. Proximity analysis of Cheirolepidiaceae fossils and climate-sensitive sediments.

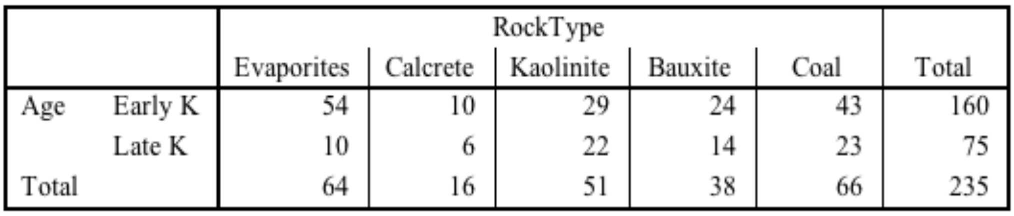
CLIMATE-SENSITIVE SEDIMENTS		**EARLY K**	**LATE K**
Arid / Dry	Evaporites	63	59
	Calcrete	25	31
		88	**90**
Humid / Wet	Kaolinite	32	52
	Bauxite	24	48
	Coals	142	133
		198	**233**
Number of fossil localities (251)		193	58
Localities related to sediments		153	52
Localities not related to sediments		40	6

Table 5.1. Details on number of sediment occurrences and the amount of fossil localities related to them.

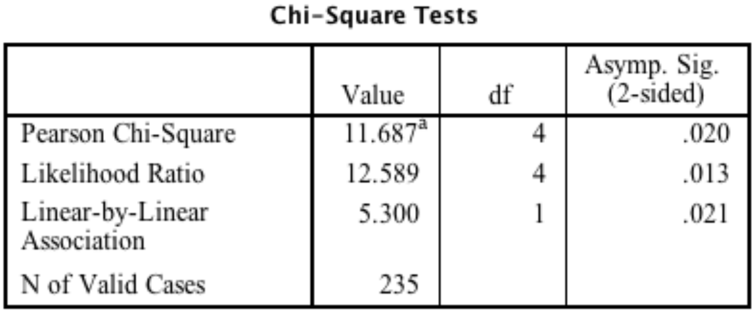
EARLY CRETACEOUS						
Pollen (n= 92)	Localities in **1**° buffer	%	Localities in **2**° buffer	%	Localities in **3**° buffer	%
Evaporites	4	*4*	18	*20*	28	*30*
Calcrete	0	*0*	2	*2*	5	*5*
Kaolinite	4	*4*	8	*9*	18	*20*
Bauxite	3	*3*	8	*9*	12	*12*
Coal	2	*2*	11	*12*	23	*25*
Mega and mesofossils (n = 69)						
Evaporites	5	*7*	16	*23*	26	*38*
Calcrete	1	*1*	3	*4*	5	*7*
Kaolinite	2	*3*	8	*12*	11	*16*
Bauxite	5	*7*	8	*12*	12	*17*
Coal	3	*4*	13	*19*	20	*29*
All fossils (n = 161)						
Evaporites	9	*6*	34	*21*	54	*33*
Calcrete	1	*1*	5	*3*	10	*6*
Kaolinite	6	*4*	16	*10*	29	*18*
Bauxite	8	*5*	16	*10*	24	*15*
Coal	5	*3*	24	*15*	43	*27*

LATE CRETACEOUS						
Pollen (n= 34)	Localities in **1**° buffer	%	Localities in **2**° buffer	%	Localities in **3**° buffer	%
Evaporites	2	*6*	4	*12*	6	*18*
Calcrete	1	*3*	3	*9*	4	*12*
Kaolinite	5	*15*	9	*26*	11	*32*
Bauxite	4	*12*	6	*18*	7	*21*
Coal	7	*21*	12	*35*	15	*44*
Mega and mesofossils (n = 24)						
Evaporites	2	*8*	4	*17*	4	*17*
Calcrete	0	–	1	*4*	2	*8*
Kaolinite	5	*21*	11	*46*	11	*46*
Bauxite	4	*17*	6	*25*	7	*29*
Coal	5	*21*	8	*33*	8	*33*
All fossils (n = 58)						
Evaporites	4	*7*	8	*14*	10	*17*
Calcrete	1	*2*	4	*7*	6	*10*
Kaolinite	10	*17*	20	*34*	22	*38*
Bauxite	6	*10*	8	*14*	10	*17*
Coal	12	*21*	20	*34*	23	*40*

Table 5.2. Percentage of the total number of localities with cheirolepidiaceous fossils related to a climate-sensitive sediment (shaded in grey).



		RockType					
		Evaporites	Calcrete	Kaolinite	Bauxite	Coal	Total
Age	Early K	54	10	29	24	43	160
	Late K	10	6	22	14	23	75
Total		64	16	51	38	66	235

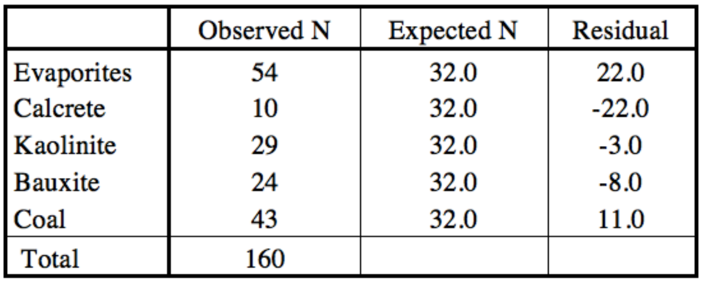


Chi-Square Tests

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	11.687^a	4	.020
Likelihood Ratio	12.589	4	.013
Linear-by-Linear Association	5.300	1	.021
N of Valid Cases	235		

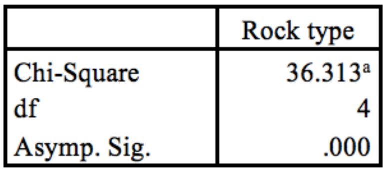
Table 5.3. Chi-square test of Cretaceous cheirolepids (n = 235). Chi-square calculated value of 11.687 with 4 degrees of freedom and a statistical significance of *P* = 0.02. Therefore we reject the null hypothesis (Ho: there is no significant relationship between rock type and the age fossil occurrences), and we accept the alternate hypothesis (Ha:), which indicates there is a significant relationship between rock type and the age of fossil.

Occurrences



	Observed N	Expected N	Residual
Evaporites	54	32.0	22.0
Calcrete	10	32.0	-22.0
Kaolinite	29	32.0	-3.0
Bauxite	24	32.0	-8.0
Coal	43	32.0	11.0
Total	160		

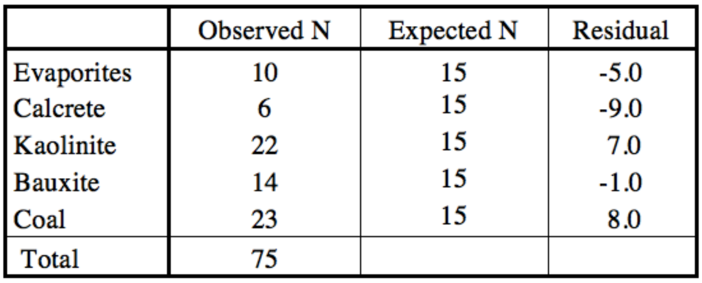
Test Statistics



	Rock type
Chi-Square	36.313[a]
df	4
Asymp. Sig.	.000

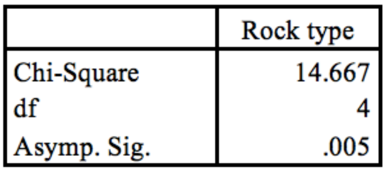
Table 5.4. Chi-square test of Early Cretaceous cheirolepids (n = 160). Chi-square value = 36.313, df = 4, and *P* = 0.0001. Therefore we reject the null hypothesis (Ho: there is no significant relationship between rock type and the frequency of fossil occurrences), and we accept the alternate hypothesis (Ha:), which indicates there is a significant relationship between rock type and the frequency of fossil occurrences.

Occurrences



	Observed N	Expected N	Residual
Evaporites	10	15	-5.0
Calcrete	6	15	-9.0
Kaolinite	22	15	7.0
Bauxite	14	15	-1.0
Coal	23	15	8.0
Total	75		

Test Statistics



	Rock type
Chi-Square	14.667
df	4
Asymp. Sig.	.005

Table 5.5. Chi-square test of Late Cretaceous cheirolepids (n = 75). Chi-square value = 14.667, df = 4, *P* = 0.005. Therefore we reject the null hypothesis (Ho: there is no significant relationship between rock type and the age fossil occurrences), and we accept the alternate hypothesis (Ha), which indicates there is a significant relationship between rock type and the age of fossil.

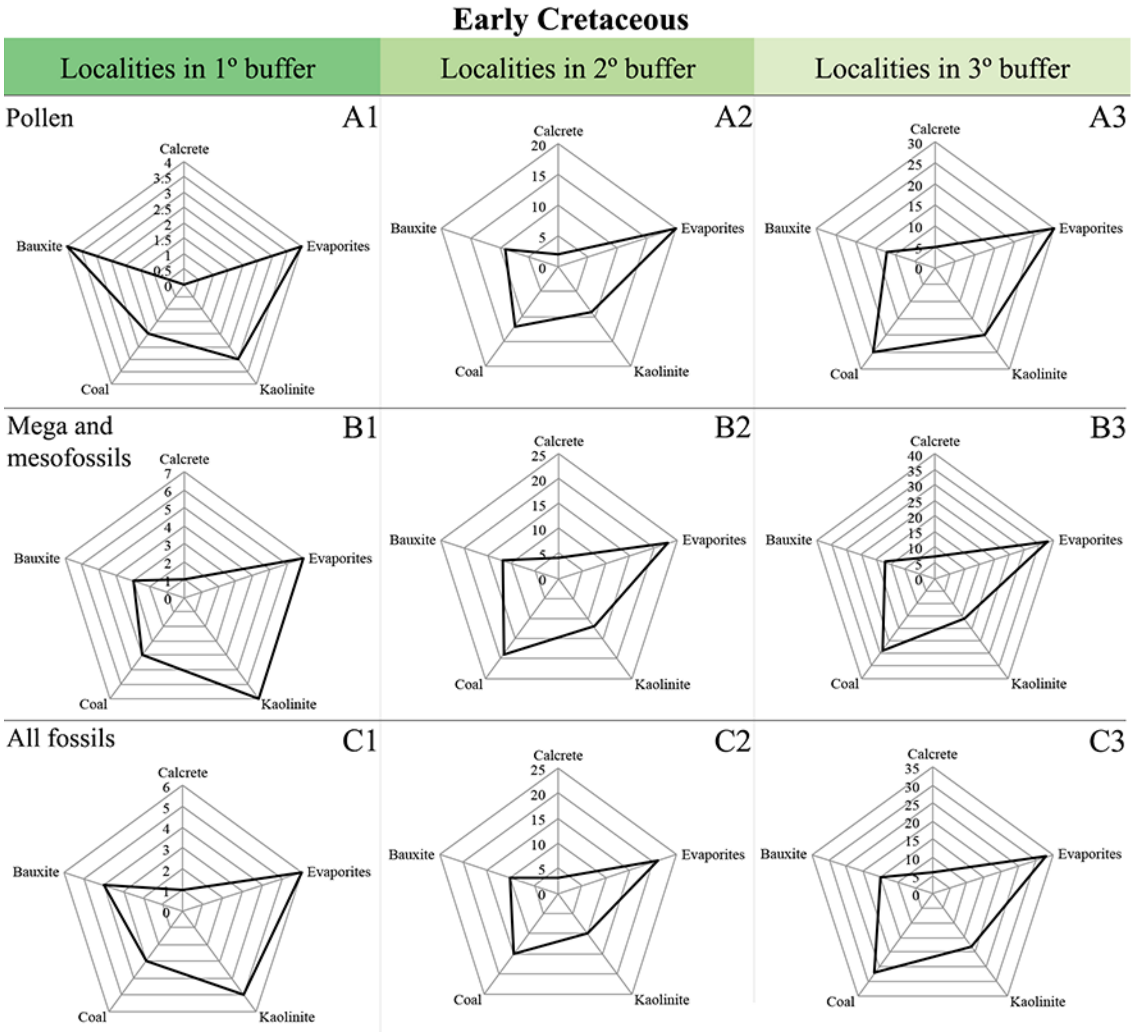


Figure 5.2. Percentages of the total number of Cheirolepidiaceae Early Cretaceous localities related to certain climate-sensitive sediment for each buffer ring.

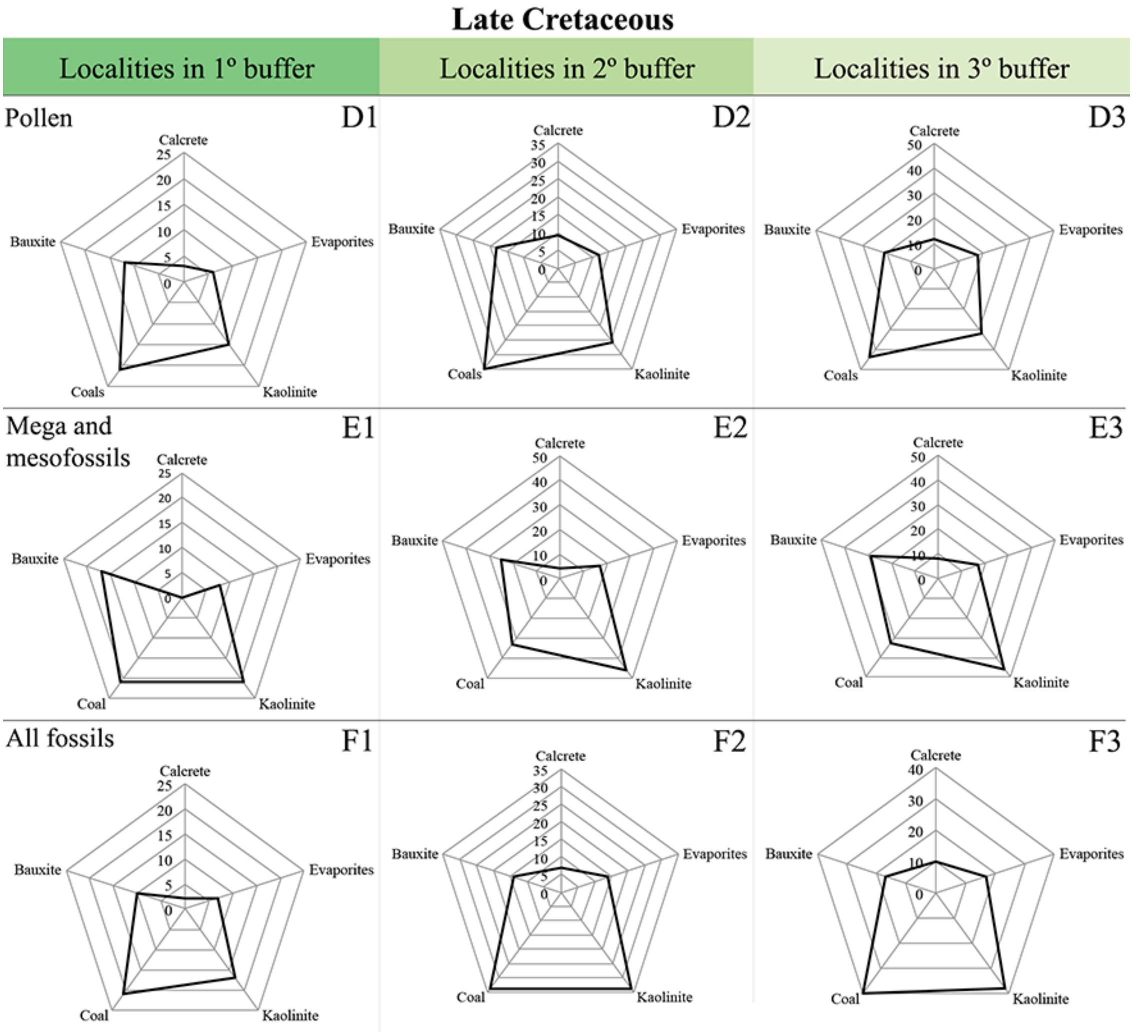


Figure 5.3. Percentages of the total number of Cheirolepidiaceae Late Cretaceous localities related to certain climate-sensitive sediment for each buffer ring.

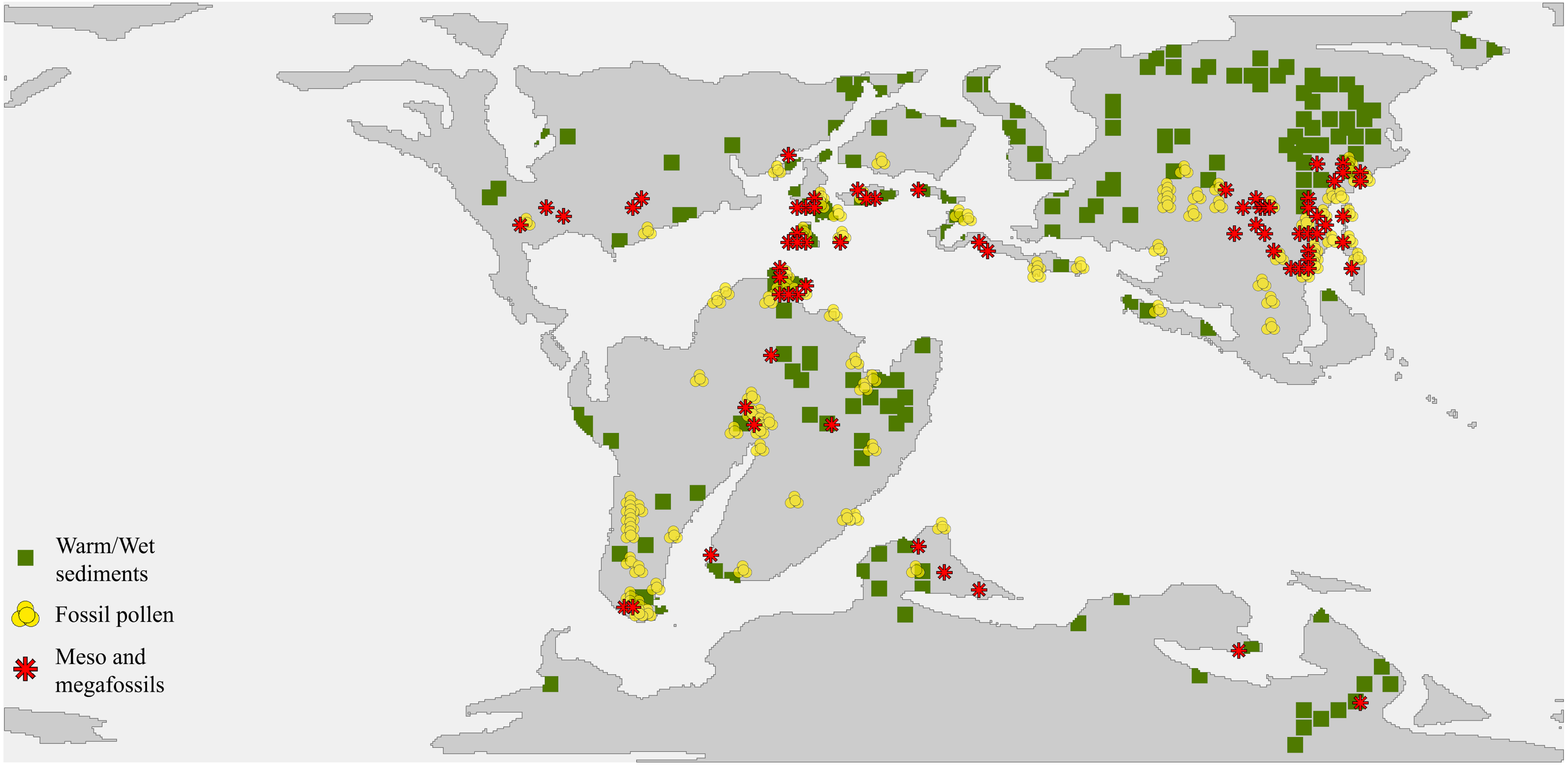


Figure 5.4. Distribution of Early Cretaceous localities (n =153) where Cheirolepidiaceae conifers are found, in relation to the distribution of warm/wet sediments (Coal, Bauxite, and Kaolinite). Data obtained from PALEOMAP project, 2011 date accessed).

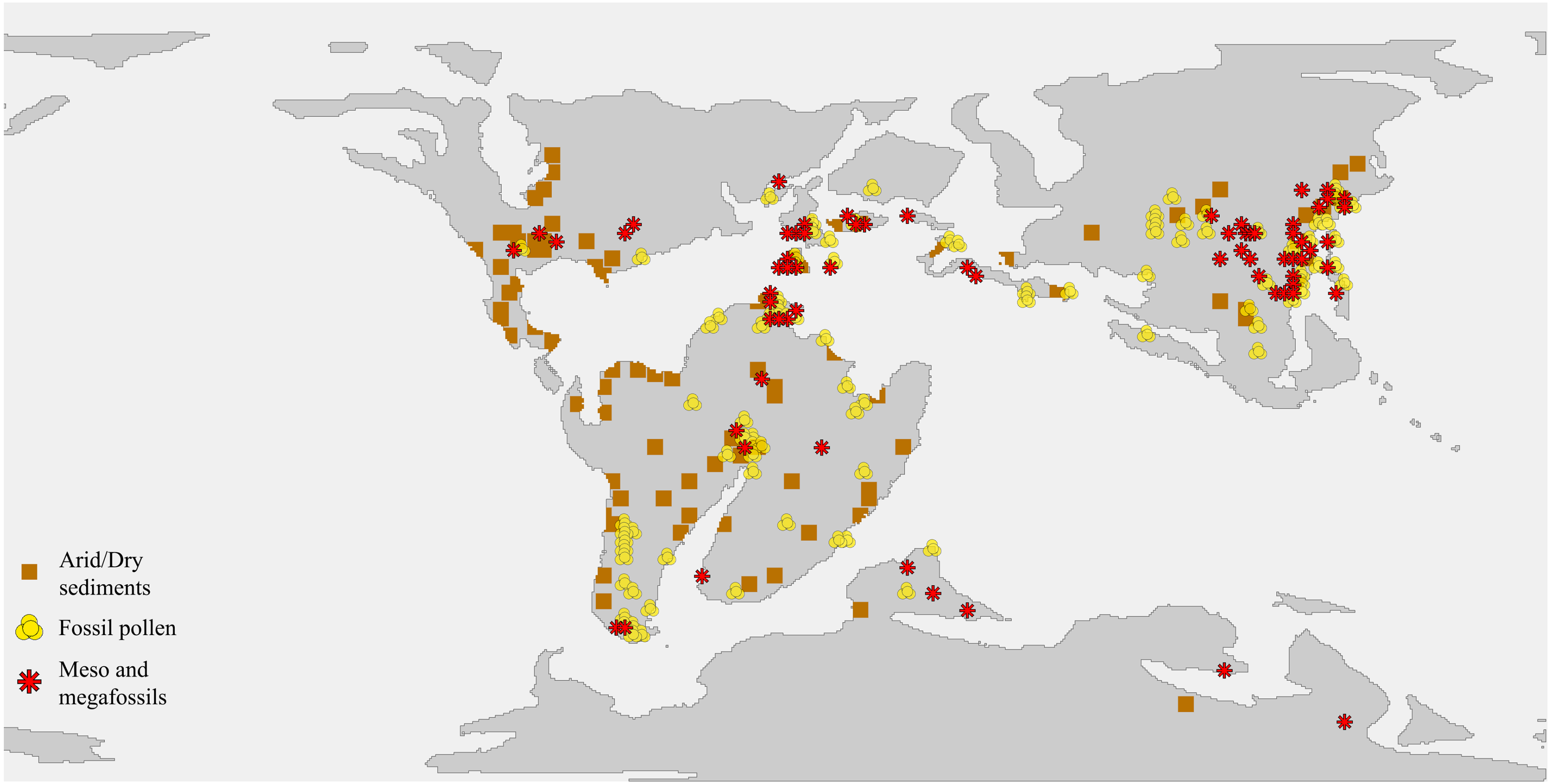


Figure 5.5. Distribution of Early Cretaceous localities (n =153) where Cheirolepidiaceae conifers are found, in relation to the distribution of arid/dry sediments (Evapotites and Calcrete). Data obtained from PALEOMAP project (2011 date accessed).

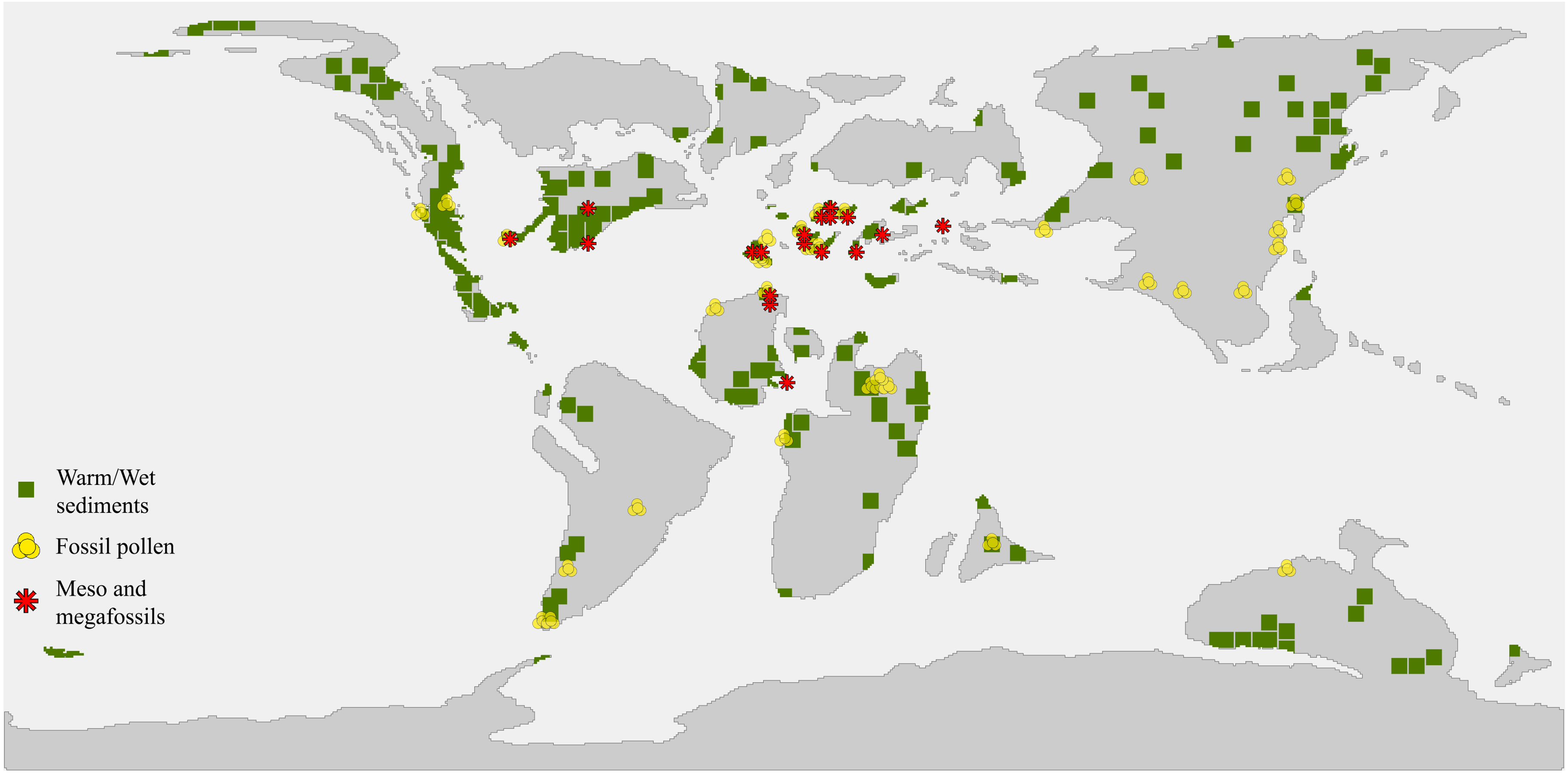


Figure 5.6. Distribution of Late Cretaceous localities (n =52) where Cheirolepidiaceae conifers are found, in relation to the distribution of warm/wet sediments (Coal, Bauxite, and Kaolinite). Data obtained from PALEOMAP project (2011 date accessed).

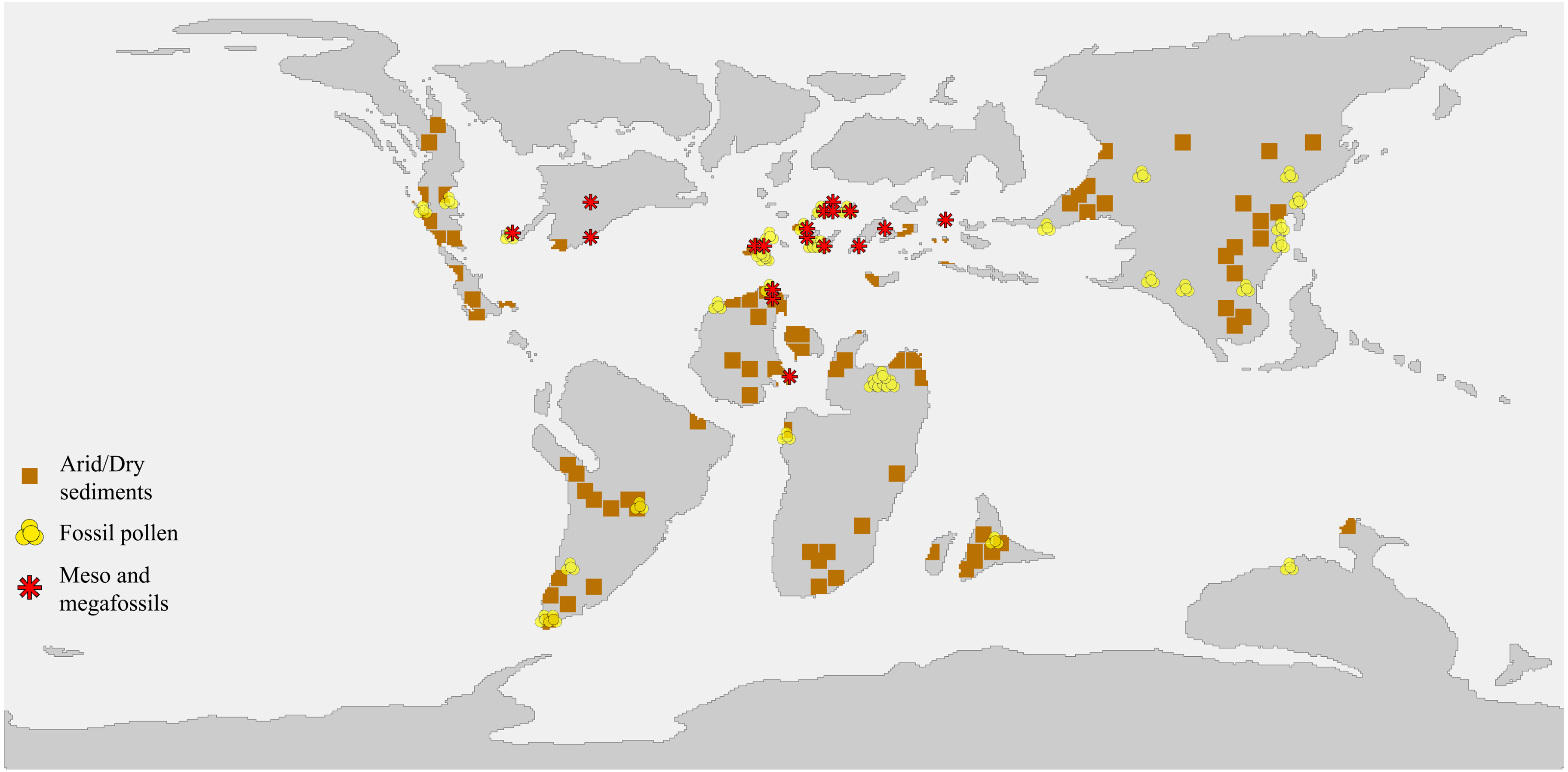


Figure 5.7. Distribution of Late Cretaceous localities (n =52) where Cheirolepidiaceae conifers are found, in relation to the distribution of arid/dry sediments (Evapotites and Calcrete). Data obtained from PALEOMAP project (2011 date accessed).

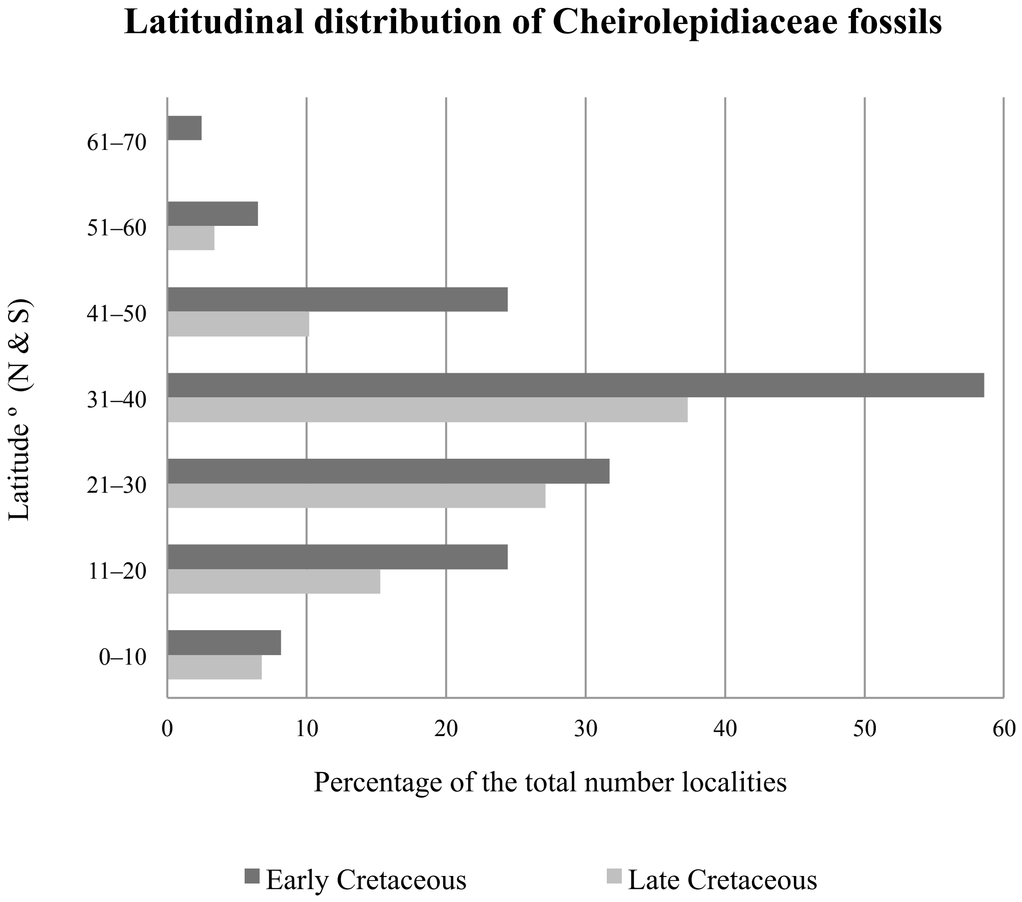


Figure 5.8. Distribution of Cheirolepidiaceae localities across the latitudinal gradient. Both North and South palaeolatitudes are grouped in ten degrees bins and plotted on the same axis.

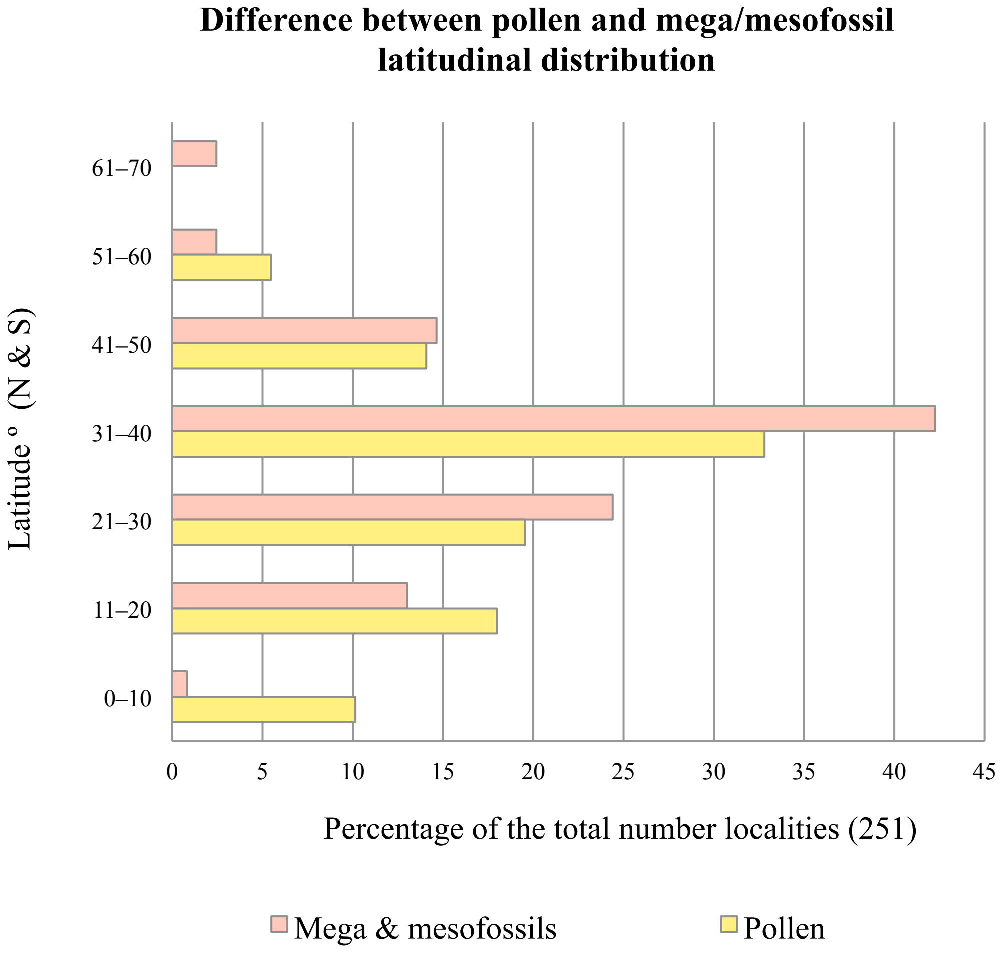


Figure 5.9. Difference between pollen and mega/mesofossil latitudinal distribution in the Cretaceous. Both North and South palaeolatitudes are grouped in ten degrees bins and plotted on the same axis.

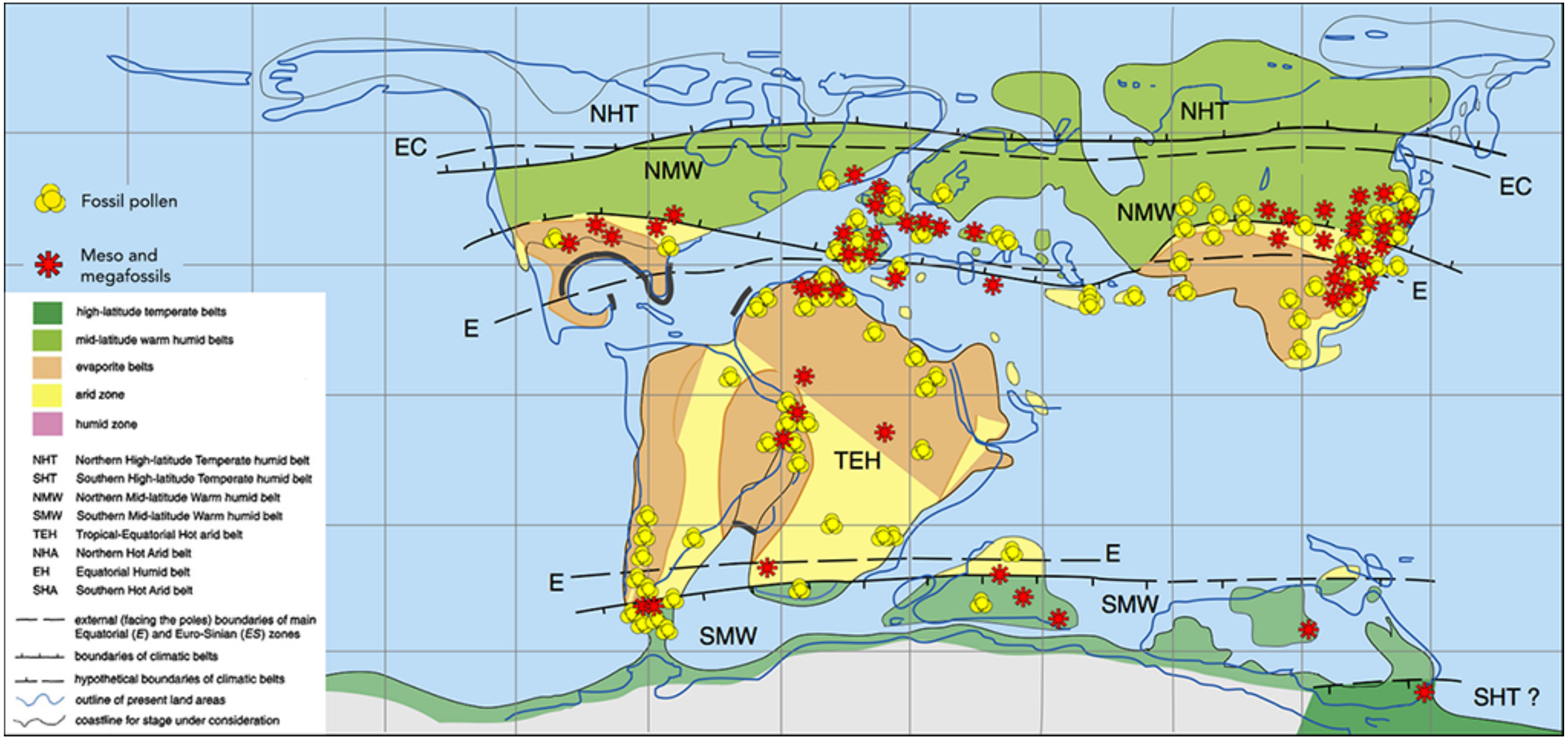


Figure 5.10. Early Cretaceous localities (n =193) where Cheirolepidiaceae conifers occur, plotted on Aptian palaeoclimatic zones proposed by Chumakov et al. 1995. Map modified after Hay and Floegel, 2012.

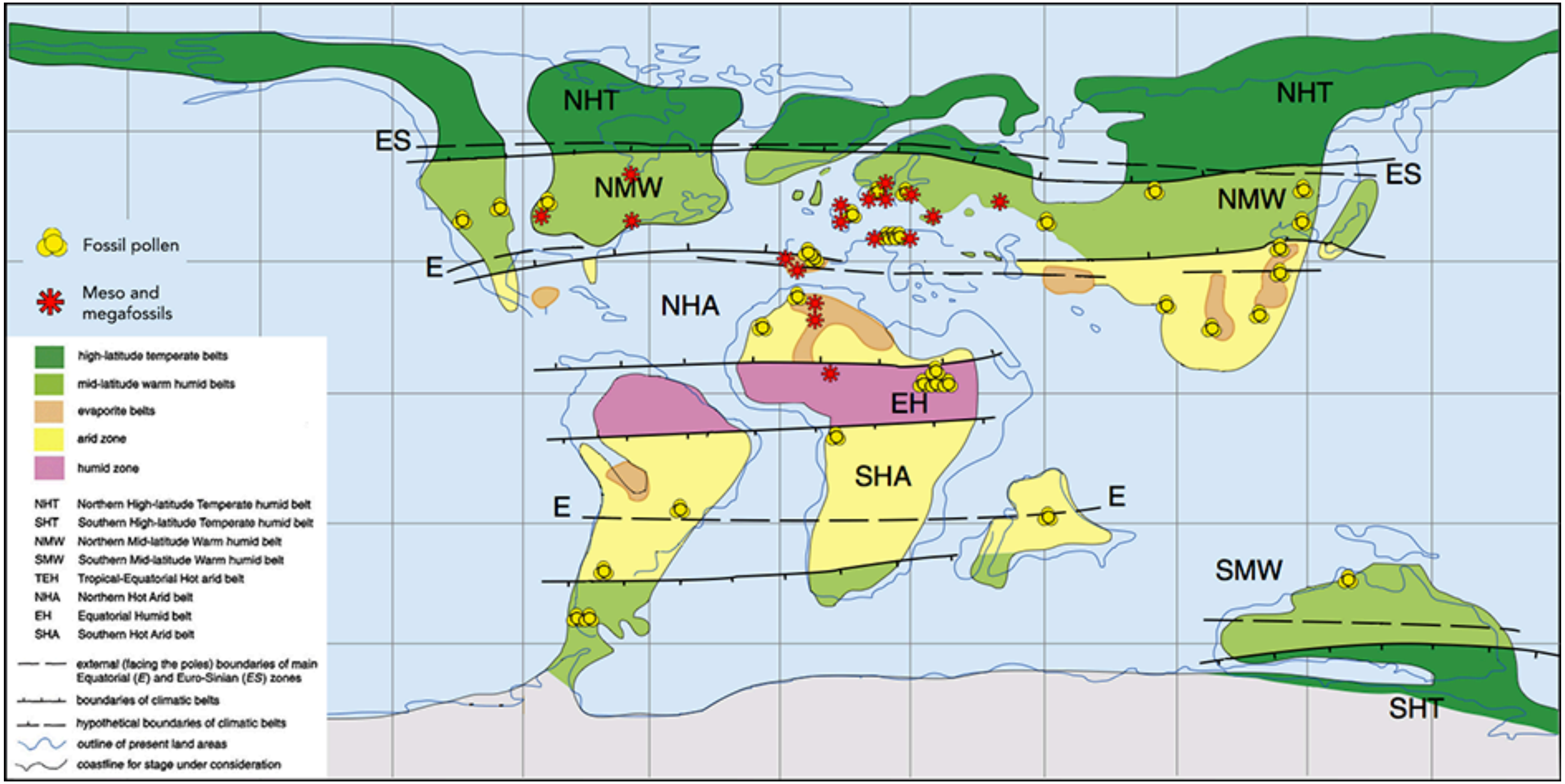


Figure 5.11. Late Cretaceous localities (n =58) where Cheirolepidiaceae conifers occur, plotted on Santonian palaeoclimatic zones proposed by Chumakov et al. 1995. Map modified after Hay and Floegel, 2012.

CHAPTER 6: PUTATIVE "CRETACEOUS" DIPTEROCARPOID FOSSIL WOOD IN THE COLLECTIONS OF NATURALIS, LEIDEN, THE NETHERLANDS, AND ITS IMPLICATIONS FOR THE CONTROVERSIAL AGE AND PROVENANCE OF *WOBURNIA POROSA* STOPES

6.1. INTRODUCTION

In order to augment the Cretaceous fossil wood database analysed in Chapter 4, and to get some first-hand experience of wood anatomical description, in this chapter I describe in detail a new specimen of angiosperm fossil wood accessioned in the collections of Naturalis, Leiden, Netherlands. The locality information for this fossil specimen in the museum records was given as the Cretaceous (Maastrichtian) of South Limburg, The Netherlands. However, as the descriptive and identification work reached an advanced stage, it became clear that the wood was a dipterocarpoid (Dipterocarpaceae) taxon and therefore the museum records were almost certainly incorrect. Specifically, a detailed study of (1) the dipterocarpoid wood anatomy, (2) the geographic and stratigraphic distribution of fossil and extant dipterocarps and (3) comparative material of known provenance allowed me to infer that the genuine origin of the specimen was from Neogene strata of Indonesia (as explained in detail below).

Despite not being a Cretaceous specimen, the amount of time devoted to this fossil wood meant that it had to be included in this Cretaceous thesis. Nonetheless, my research dealing with this specimen does have significance for Cretaceous wood assemblages because it shows how easy it is for fossil wood specimens (that require sectioning for proper identification) to become incorrectly accessioned in museums and allows the Cretaceous fossil record to be critically reviewed. More specifically, my re-examination of another problematic dipterocarpoid wood (*Woburnia porosa* Stopes), which was thought to derive from the Cretaceous of England, suggests that this specimen was also, probably, derived from Neogene strata of Indonesia (although I am unable to infer a more precise provenance). This kind of critical review of the fossil record is essential if the kind of biogeographic analyses conducted in Chapter 4 and 6 are to be correct.

6.2. MATERIAL AND METHODS

The fossil specimen that comprises the focus of this study is a large (0.28 m incomplete diameter) silicified tree trunk accessioned as RGM 232138 in the collections of NCB Naturalis, Leiden, The Netherlands. Standard petrographic thin sections were prepared for specimen RGM 232138 in transverse (TS), tangential longitudinal (TLS) and radial longitudinal sections (RLS). Three sections (one of each orientation) were cut from mature wood, approximately 140 mm from the pith, and a further six sections (two of each orientation) were cut through the pith and surrounding juvenile wood. Anatomical features were described using the International Association of Wood Anatomists (IAWA) list of microscopic features for hardwood identification and the specimen description is preceded by a list of the IAWA Hardwood List feature numbers (IAWA Committee, 1989). In that list, the following modifiers are used: "?" before a feature number indicates it is uncertain if that feature is present or absent in the sample; "v" following a feature number indicates that the feature is variable in occurrence or there is a tendency towards showing the feature.

The identity of the specimen was initially investigated using the InsideWood Database (2004-present) using recommended search strategies (Falcon-Lang et al., 2012; Wheeler, 2011). In addition, the specimen was compared with slides in two major wood collections in the Jodrell Laboratory, Kew Gardens, U.K., and the National

Herbarium of The Netherlands, Leiden.

I also utilized Principal Component Analysis (PCA) to quantitatively compare the anatomical characters of the fossil specimen with other extant and fossil woods. PCA is an ordination technique in which a multivariate dataset is projected onto few dimensions defined by the axes of maximal variance (Hammer et al., 2001; Hammer and Harper, 2006). It is a common tool used to analyse multivariate data and identify clusters. It has been widely used in studies of the systematics of extant wood (Hellberg and Carcaillet, 2003; Oskolski et al., 2007; Wickremasinghe and Heart, 2006), as well as fossil woods (Martínez-Cabrera and Cevallos-Ferriz, 2004; Oakley and Falcon-Lang, 2009; Oakley et al., 2009). In addition to PCA, Cluster Analysis (CA) was employed to corroborate the anatomical similarities between fossils herein described and other dipterocarpaceous fossil woods reported in the literature. CA was also used in the anatomical comparison to extant Dipterocarpaceae woods. CA is a multivariate analysis for presence/absence data sets that group taxa producing a dendrogram based on Jaccard similarity (Harper, 1999; Hammer et al., 1999-2013).

6.3. FOSSIL WOOD DESCRIPTION

6.3.1. Systematic palaeobotany

Order Malvales Dumortier, 1829

Family Dipterocarpaceae Blume, 1825

Subfamily Dipterocarpoideae Burnett, 1835

Genus Dryobalanoxylon Den Berger, 1923

Species Dryobalanoxylon bangkoense Schweitzer, 1958 emended nov., Plates I – III

Type material: Utrecht 04527, slides 1987, 1988 and 1989.

Type locality: Province of Jambi, western Sumatra, Indonesia; southwest of Bangko, Merangin River, Point 201 (Posthumus, 1929). An explanation of how I arrived at this inferred provenance is given later in the chapter (see chapter 6.5 for a detailed justification).

Repository: Collection of the Laboratory of Palaeobotany and Palynology, Utrecht University Collection, The Netherlands.

Description of Dryobalanoxylon bangkoense *type material using IAWA list character codes:* 2, 5, 9, 13, 22, 25, 31, 42, 27, 56, 60, 62, 63, 69, 70, 79, 80, 82, 92?, 93, 97, 98v, 102, 107, 108v, 110, 115, 127

Original diagnosis of Schweitzer (1958, p. 41): Zuwachszonen fehlend, Gefäße zu 7 bis 13 auf den Quadratmillimeter, sehr oft in Gruppen. Das apotracheale Holzparenchym häufig, meist maschenförmig angeordnet. Fasertracheiden und Libriformfasern die Grundmasse des Holzes bildend, nicht zu radialen Reihen angeordnet, Markstrahlen meist 3- bis 4 schichtig, bis zu 70 Zellen hoch.

Emended diagnosis: Growth rings indistinct; vessels diffuse-porous, exclusively solitary; perforation plates simple; intervessel pits alternate, circular to polygonal shape, and vestured; vessel – ray pits with reduced borders; vessel tangential diameter 105 – 215 μm; tyloses and vasicentric tracheids common; fibres non-septate, with distinctly bordered pits in both radial and tangential walls; fibres mostly very thick-walled, thin- to thick-walled fibres rare; axial parenchyma adjacent to axial canals; rays rarely uniseriate or common multiseriate rays, 2 – 5 cells wide; body ray cells procumbent with mostly 2 – 4 rows of square marginal cells or more; sheath cells locally present; ray density 2 – 6 rays per mm; axial canals, in long (and ?short) tangential lines.

New material: Hand specimen labeled RGM 232138 and 9 thin sections labeled RGM 232138a – i.

Repository: Netherlands Biodiversity Center, Leiden, The Netherlands.

Locality: Neogene of Indonesia, and possibly, the Pliocene of Jambi, western Sumatra Indonesia, in particular (see chapter 6.5 for a detailed justification).

Description using IAWA list character codes: 2, 5, 9, 13, 22, 23, 25, 26v, 29, 30, 42, 43v, 47, 48v, 54, 56, 60, 62, 63, 66, 69v, 70, 77?, 78?, 79?, 85?, 92, 93, 97, 98v, 107, 110, 115, 127, 128v.

Description of mature wood: Growth rings absent or indistinct; vessels diffuse-porous; vessels circular in outline, exclusively solitary (96%) (Plate I, 1, 2); simple perforation plates (Plate I, 3, 5), orientated at >55° to longitudinal direction; intervessel pits, circular to polygonal shape, 3 – 7 µm (mean 4.7 ± 0.7, n = 50), distinctly bordered, with alternate arrangement (Plate I, 3, 4); vessel – ray pits with reduced borders, somewhat larger than intervessel pits (Plate I, 6, 7); intervessel pits, vestured (Plate I, 8); vessel tangential diameter, 105 – 215 µm (mean 168 ± 25.8, n = 50); vessel density, 9 – 20 per mm^2 (mean 14 ± 2.38, n = 50) (Plate I, 1); vessel element length, 0.5 – 1.7 mm (mean 0.9 ± 0.3, n = 50). Tyloses common (Plate I, 9). Vasicentric tracheids, 22 – 43 µm diameter (mean 32 ± 5, n = 50), very common, showing 2 – 4-seriate, alternate bordered pits (Plate I, 10).

Fibre tracheids, 15 – 31 µm diameter (mean 22 ± 3, n = 50), non-septate, with distinctly bordered pits, 10 – 21 µm diameter (mean 14 ± 1.3, n = 50); pits common in both radial and tangential walls (Plate I, 11, 12). Fibres very thick-walled, up to 11 µm, measured to the middle lamella (mean 6 ± 2, n = 50); thin- to thick-walled fibres rarely present (Plate II, 1).

Axial parenchyma, difficult to observe in TS, rare or absent except when adjacent to axial canals, where it is abundant in tangential lines, 3 – 5 cells wide and in strands, 3 – 8 and > 8 cells high (Plate III, 1, 3, 4). Axial parenchyma cells, rectangular in TLS, 17 – 38 µm diameter (mean 26 ± 4, n = 50) and 21 – 66 µm high (mean 46 ± 12, n = 50) (Plate II, 2, 3; Plate III, 5, 6).

Rays of two types, rare uniseriate or common multiseriate rays, 2 – 5 cells wide (mean 3 ± 0.9, n = 50), commonly with uniseriate tails (Plate II, 4, 5; Plate III, 5, 6); uniseriate rays, 0.1 – 0.6 mm high (mean 0.3 ± 0.1, n = 50) composed mainly of square cells (Plate II, 4, 5); multiseriate rays, 0.3 – 1.2 mm high (mean 0.7 ± 0.2, n = 50), inclusive of uniseriate tails present (Plate II, 4); body ray cells procumbent with mostly 2 – 4 rows of square marginal cells or more (Plate II, 6); weakly developed sheath cells locally present (Plate II, 4, 5); ray density, 2 – 6 per tangential millimetre (mean 3.3 ± 1.5, n = 65).

Axial canals, 38 – 127 µm diameter (mean 76 ± 23, n = 50), in long (and ?short) tangential lines (Plate III, 1, 3, 4).

Description of ontogenetic trends: Tangential vessel diameter increases from 57.5 ± 12.0 µm (n = 50) at 5 mm from the pith to 168 ± 25.8 µm (n = 50) at a distance of 140 mm from the pith (Fig. 6.1). Vessel density decreases from 31.7 vessels per mm^2 at 5 mm from the outer edge of the pith to mean 14.00 ± 2.38 vessels per mm^2 at a distance of 140 mm from the pith (Fig. 6.1). Both these parameters reach a plateau at about 100 mm from the pith, confirming that the outer part of the trunk described in the systematics section is indeed mature wood (Zobel and Buijtenen, 1989).

6.4. IDENTIFICATION

Specimen RGM 232138 contains an unusual combination of characters that allows very precise identification. Of key importance is the co-occurrence of vasicentric tracheids (IAWA feature 60) and axial canals in long tangential lines (IAWA feature 127), a combination found only in the subfamily Dipterocarpoideae (Dipterocarpaceae) according to the InsideWood Database (accessed 17 November 2011).

The Dipterocarpaceae family comprises between 15 – 19 genera and 470 – 580 species, mostly distributed in the tropics (see Maury-Lechnon and Curtet, 1998 for a review). Three sub-families are recognized as follows: (1) The Pakaraimoideae is a monospecific group of small trees and shrubs restricted to the seasonal tropical forests of Guyana; (2) The Monotoideae (3 genera) is a group of mostly small trees and shrubs found in dry deciduous subtropical forests in Africa with isolated occurrences in Colombia; and (3) The Dipterocarpoideae (up to 15 genera) is a diverse group of rainforest trees widespread across southeast Asia, the Seychelles and the Andaman Islands (Fig. 1; Londoño et al., 1995; Maguire and Ashton, 1977; Meher-Homji, 1979; Whitmore, 1998) (Fig. 6.2). The Dipterocarpoideae is the subfamily that today dominates much of Indonesia (Borneo, Sumatra, Java), the Malay Peninsula and the wetter parts of the Philippines (Whitmore, 1998); this subfamily includes many large (> 50 – 80 m high) canopy-forming trees (Corlett and Primack, 2011) and has a reliable fossil record beginning as early as the Oligocene (Maury-Lechnon and Curtet, 1998; Morley, 2003). There are competing evolutionary hypotheses to explain its disjunct biogeography (Sasaki, 2006), but a growing consensus is that the Dipterocarpaceae originated, possibly, as early as the latest Cretaceous-Paleogene of Gondwana and reached Asia via the Indian tectonic plate in the Eocene-Oligocene (Dayanandan et al., 1999; Dutta et al., 2011; Morley, 2003; Prasad et al., 2009; Rust et al., 2010).

The Dipterocarpoideae is subdivided into two clades, the Dipterocarpeae (comprising *Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Stemonoporus*, *Upuna*, *Vateria*, *Vateropsis*, and *Vatica*) and the Shoreae (comprising *Dryobalanops*, *Hopea*, *Neobalanocarpus*, *Parashorea*, and *Shorea*) (Ashton, 1982). Specifically, the combination of vasicentric tracheids and axial canals in long tangential lines restricted the identification to one genus of the Dipterocarpeae clade (*Anisoptera*) and all five genera of the Shoreae clade (*Dryobalanops*, *Hopea*, *Neobalanocarpus*, *Parashorea*, and *Shorea* inclusive of *Shorea* sect. *Pentacme*) based on my own observations of material and published reports (Gottwald and Parameswaran, 1968).

6.4.1. PCA and CA analysis of extant Dipterocarpaceae

To further investigate the identity of RGM 232138, I constructed a wood anatomical database for the extant Dipterocarpoideae and its close relatives, the Pakaraimoideae and the Monotoideae, and analysed it using Principle Component Analysis (PCA) and Cluster Analysis (CA). My data were harvested from InsideWood Database (2004-present, accessed 17 November 2011) and supplemented by studies of dipterocarp wood collections at the Jodrell Laboratory, Royal Botanic Gardens, Kew, UK, and the National Herbarium, Leiden, The Netherlands (Appendix 6). The database contains 81 records of dipterocarp wood with nearly complete anatomical data, spanning almost the entire taxonomic and anatomical diversity of the family. The only genera for which no data could be acquired were *Pseudomonotes* (Monotoideae) and *Stemonoporus* (Dipterocarpoideae). The genus, *Shorea*, which is the most diverse dipterocarp genus comprising nearly 200 species (or ~ 40% of total species for the family), is represented by 20 species in the database. In total 66 anatomical characters (IAWA features 1 – 2, 5, 7, 9, 11 – 15, 20 – 22, 29 – 33, 41 – 43, 45 – 49, 56 – 58, 60 –

63, 66, 68 – 70, 91 – 94, 96 – 98, 102 – 109, 111 – 116, 118 – 122, 127 – 130) were coded as 0 for absent and 1 for present; these characters were selected because they are equally useful for fossil wood studies. Two key characters – vasicentric tracheids (IAWA feature 60) and axial canals in long tangential lines (IAWA feature 127) – which, as noted, are particularly distinctive features of the fossil wood, were coded with a weighting of 2.

The resulting PCA (Fig. 6.3a) and CA (Fig.6.3b) show that the Pakaraimoideae and the Monotoideae plot as out-groups some distance from the Dipterocarpoideae and my fossil specimen. Within the cloud of data comprising the Dipterocarpoideae, records of Dipterocarpeae and Shoreae clades form broadly distinct but slightly intergrading groups (Fig. 6.3a and 6.3b). Within these clades, most genera form coherent clusters, with the exception of the highly diverse *Shorea*, which is somewhat more widespread in the PCA. Specimen RGM 232138 plots on the edge of the Shoreae clade, and occurs close to the centroid of a cluster of nine specimens of *Dryobalanops*. A small number of specimens of *Anisoptera* (Dipterocarpeae clade) and *Shorea*/*Parashorea* (Shoreae clade) also plot nearby, but the centroids for these groups (2D), when considered in totality, are somewhat distant (Fig. 6.3a). CA shows a clearer division of the families with the exception of *Vateria*, *Vatica* and *Upuna*, which plot close to Shoreae clade (6.3b).

6.4.2. Qualitative comparison with extant dipterocarp woods

I next directly compared my fossil to specimens of extant dipterocarp wood in the collections of the Jodrell Laboratory, Royal Botanic Gardens, Kew, UK, and the National Herbarium, Leiden (comprising ~ 120 species in 15 genera). As an initial search strategy, the general appearance of extant woods in transverse section was compared with specimen RGM 232138, paying particular attention to qualitative features such as the length and spacing of lines of axial canals, the diameter, density, and distribution of vessels, and the width and frequency or rays. In parallel with the PCA and CA results above, the fossil was most similar to *Anisoptera*, *Dryobalanops* and *Shorea,* all of which contain some species with the unusual combination of vasicentric tracheids and axial canals in long tangential lines seen in the fossil.

Of these three genera, *Anisoptera*, which is represented in the collections by 9 out of 10 extant species, is generally least similar to the fossil. It differs in showing, typically, much shorter lines of canals, or even lacking canals completely. Only two taxa (*A. laevis* and *A. scaphula*) – the two taxa that plot closely to the fossil on the PCA (Fig. 6.3a) – show axial canals in long tangential lines. Another difference is that the axial canals in *Anisoptera* are similar in diameter to the vessels, whereas in the fossil, they are typically only half the diameter. Furthermore, the rays of *Anisoptera* are typically ~ 6 cells wide and always > 1 mm, whereas in the fossil they are 2 – 5 cells wide and somewhat shorter (typically < 1 mm), and ray tails are uncommon in *Anisoptera*, whereas they are a distinctive feature of the fossil. Finally, whereas sheath cells are abundant and well differentiated in *Anisoptera,* they are only weakly developed in the fossil.

Rather more similar to the fossil is *Shorea* (Plate IV), although I qualify this statement by highlighting that only 62 species out of the total ~ 200 extant species were observed. The key differences are that vessels in *Shorea* are usually somewhat larger (> 200 µm) than in the fossil. In addition, vessels may show radial multiples, and rarely, diagonal groupings, whereas in the fossil, vessels are exclusively solitary. Also, the lines of axial canals are generally more widely spaced than in the fossil, and one species shows radial canals. Other differences are that fibres in *Shorea* are commonly thin-walled (but very thick-walled in the fossil) and vasicentric tracheids are absent in about half the *Shorea* species I examined, whereas this is a prominent feature of the fossil. Furthermore, rays are typically narrow (~ 2 cells wide) compared to the fossil (2 – 5 cells wide).

Finally, *Dryobalanops* (Plate V) is a very close match to the fossil, with no significant anatomical differences. In particular, the genus shows axial canals always in long tangential lines, exclusively solitary vessels, vasicentric tracheids, and very thick-walled fibres – all key features of the fossil. Within the genus, the width and height of ray is somewhat variable, but the ray dimensions for the fossil fall well within this variation. Thus, in summary, I infer that the fossils is very closely similar to, if not identical to, the extant genus, *Dryobalanops*.

6.4.3. Comparison with fossil dipterocarp woods

To date, there have been eight genera of fossil dipterocarp wood described in the literature (see Schweitzer, 1958, for the most comprehensive overview). These taxa are *Anisopteroxylon*, *Dipterocarpoxylon*, *Dryobalanoxylon*, *Hopeoxylon*, *Pentacmeoxylon*, *Shoreoxylon*, *Vaterioxylon* and *Vaticoxylon*. The characters that are key to discriminating between these dipterocarp fossil wood taxa include (1) the presence or absence of fibre-tracheids, silica crystals, gums and tyloses, (2) vessel tangential diameter and its size relative to that of the axial canals, and (3) the length of the tangential lines of axial canals (Schweitzer, 1958; Mandang and Kagemori, 2004).

RGM 232138 differs from *Anisopteroxylon* and *Dipterocarpoxylon* in the length of the tangential lines of axial canals and the vessel tangential diameter. In RGM 232138 the axial canals are present in very long lines (> 8) and the mean vessel diameter is ~160 µm, whereas in the above mentioned genera, axial canals typically occur singly, in pairs, or in short tangential lines and mean vessel diameter is significantly larger (typically >200 µm). A diagnostic feature of *Vaticoxylon* is the presence of silica crystals, which are not observed in RGM 232138. In addition mean vessel diameter is significantly smaller (typically ~150 µm) in *Vaticoxylon*. RGM 232138 differs from *Shoreoxylon* in showing vasicentric tracheids. Instead, RGM 232138 shows all the diagnostic features of *Dryobalanoxylon*, including abundant thick-walled fibres and a lack of aliform parenchyma (commonly seen in other dipterocarp taxa).

To date, seventeen specimens comprising twelve species of *Dryobalanoxylon* have been described including eleven from Indonesia, three from India, and single occurrences from both Cambodia and Vietnam (Mandang and Kagemori, 2004). Species level identification of fossil dipterocarp woods is problematic and the diagnostic characters that supposedly distinguish the twelve species of *Dryobalanoxylon* are somewhat equivocal, variable, and not always visible due to locally poor preservation.

The main characters used for discrimination of *Dryobalanoxylon* species are mean vessel diameter, density and shape, ray height, fibre wall thickness as well as the occurrence of storied rays (Mandang and Kagemori, 2004; Schweitzer, 1958). Compared with RGM 232138, the following well-described species differ in a few key characters, and can be excluded from this search: *Dryobalanoxylon khmerinum* commonly shows elliptical vessels and significantly lower vessel density; *D. rotundatum* shows storied rays; *D. neglectum* shows thin-walled fibres; *D. sumatrense* lacks sheath cells; *D. borneense* and *D. spectabile* always show elliptical vessels; *D. tobleri* has vessels > 350µm high. Only *Dryobalanoxylon bangkoense* Schweitzer shows all the characters seen in RGM 232138, including circular vessels (rarely elliptical), unstoried rays, vessels up to 200 µm diameter, and very thick-walled fibres.

Thus, while highlighting the uncertain validity of many *Dryobalanoxylon* species concepts, I am confident that RGM 232138 is anatomically indistinguishable from the holotype of *D. bangkoense* (Utrecht 04527) and associated material from the same area (Utrecht 04480, 04482, 04529 and 04710).

To further investigate the identity of RGM 232138, I constructed a wood anatomical database for all fossil Dipterocarpoideae using data harvested from InsideWood Database (2004-present, accessed 17 November 2011) and other sources. The database contains 62 records of fossil dipterocarp wood. In total 44 anatomical characters (IAWA features 1 – 2, 5, 7, 9, 13, 22, 30, 36, 41 – 43, 46 – 49, 56, 60 – 62, 65, 76 – 80, 83, 85 – 86, 89, 96 – 98, 102, 104, 106 – 108, 110, 114 – 116, 120, 130) were coded as 0 for absent and 1 for present; a smaller number of characters were used compared to the PCA of extant woods due to poor preservation of some fossil features. As with the PCA of extant woods, two key characters – vasicentric tracheids (IAWA feature 60) and axial canals in long tangential lines (IAWA feature 130) – were coded with a weight of 2.

In the PCA of fossil woods (Fig. 6.4a) form loose clusters, genera show a small degree of intergradation. This may reflect descriptive and preservational uncertainties in the fossil material, and suggests a revision of fossil dipterocarp woods is warranted. In the PCA of fossil woods, my *Dryobalanoxylon bangkoense* specimen mostly co-occurs with other specimens of *Dryobalanoxylon* although two *Anisopteroxylon* specimens also plot nearby. Generally, the analysis supports attribution to *Dryobalanoxylon*. The grouping of dipterocarp fossil woods in the Cluster analysis also supports the identification of RGM 232138 as *Dryobalanoxylon* (Fig. 6.4b)

6.5. INFERRED PROVENANCE

As noted in the introduction RGM 232138 (*Dryobalanoxylon bangkoense*) was catalogued in the collections of NCB Naturalis, Leiden, as originating from the Cretaceous (Maastrichtian) of South Limburg, The Netherlands. However, a detailed investigation of the "collection history" of this specimen casts doubt on that repository information. RGM 232138 may have entered the collections of the Rijks Geologisch Museum (RGM) in Leiden in the early Twentieth Century. In those days, newly acquired specimens were not always assigned unique museum numbers, and instead, specimens were boxed together with other specimens (some numbered, others unnumbered) and a label was attached to the exterior of the box. By about the 1950s, the specimen that would be later numbered RGM 232138 was located in Box 2478. This box was labelled as containing fossil woods from the Cretaceous of St. Pietersberg and the area surrounding Maastricht, The Netherlands – one of a number of boxes of fossil wood material from this area.

Around 2000, in the course of a reorganization and redetermination of collections in the new storage facility at Naturalis, Leiden, unnumbered specimens, including the one studied here, were numbered sequentially and entered into the museum catalogue. Most of the specimens in Box 2478 were already numbered; however, two were not (RGM 232137 and RGM 232138) and were assigned, by association, to the Cretaceous of South Limburg, The Netherlands. Specimen RGM 232137 is very likely correctly assigned to the Dutch Cretaceous because it shows *Teredo* borings and an adhering chalk matrix, both features characteristic of wood of this provenance. In contrast, specimen RGM 232138 has a different petrography, lacking those features and showing a 'rusty' haematite rind and some recent plant roots. Specimen RGM 232138 was shown to John Jagt (Natural History Museum, Maastricht), an expert on the Cretaceous of the Maastricht region, who confirmed that it was unlikely to have originated from this area. This is supported by the fact that specimen RGM 232138 is not mentioned in an exhaustive inventory of Cretaceous woods in Dutch museums and private collections (Felder, 1961). Thus, it is very likely that the locality information for this specimen in the museum register is incorrect.

Despite this problem, it is possible to infer the genuine provenance and age of specimen RGM 232138 based on three pieces of information: (1) the geographic and stratigraphic distribution of previously described dipterocarp fossil woods, (2) the general history of collections associated with the Dutch exploration of Indonesia, and (3) direct petrographic comparison of the fossil with other fossil woods accessioned in Naturalis, Leiden and the University of Utrecht. The investigations are described in detail below so that the reader can independently judge the level of certainty of the inferences.

6.5.1. Geographic and stratigraphic distribution of Dipterocarpoideae fossil woods

As documented above, RGM 232138 has a close affinity, if not identity, with the extant genus *Dryobalanops* (Dipterocarpoideae, Dipterocarpaceae) and the fossil taxon, *Dryobalanoxylon bangkoense*. Fossil woods belonging to the dipterocarp subfamily Dipterocarpoideae have been described from many localities over the past century (Appendix 6; InsideWood Database, 2004-present, accessed 12 October, 2012). Fossil woods of this group are relatively easily identified based on their distinctive axial canals – an anatomical feature common to many dipterocarpoid species, and only rarely seen in half a dozen other unrelated taxa (mostly Leguminosae; Gasson, 1994). However, although some possible dipterocarp-like wood types have been noted from the Eocene (Dutta et al., 2011; Poole, 1993), all systematically well-constrained specimens referable to the subfamily Dipterocarpoideae come from a very narrow geographic and stratigraphic window. Of the 121 verified records, the vast majority occur in Miocene and Pliocene strata (n = 85), (Fig. 6.5; InsideWood Database, 2004-present, accessed October 2012; Mandang and Kagemori, 2004; Maury-Lechnon and Curtet, 1998; Schweitzer, 1958). Most of these records come from India (n = 67) or Indonesia (n = 42; in Java, Sumatra or Borneo) with a few others recorded from Ethiopia (n = 2), Somalia (n = 3), Burma (n = 3), Thailand (n = 1), Cambodia (n = 1), and Vietnam (n = 1) (Fig. 6.6). With the exception of the Ethiopian specimens, all fossil specimens are broadly in the same geographic range as occupied by extant Dipterocarpoideae (Fig. 6.6). The richest deposits for Dipterocarpoideae fossil wood comprise the Pliocene strata of Java and Sumatra (Indonesia). Here studies of hundreds of fossil wood specimens have revealed that more than 90% can be referred to the Dipterocarpoideae (Mandang and Martono, 1996), including some spectacular examples of fossil tree trunks, tens of metres long (Mandang and Kagemori, 2004).

Therefore, the overwhelming likelihood is that RGM 232138 originated from the Neogene of the circum-Pacific region, i.e., east Africa, India, or southeast Asia.

6.5.2. History of fossil wood exploration in the former Dutch East Indies

In view of this narrow geographic distribution of fossil wood of the Dipterocarpoideae, it is also significant that – after the fossil wood collection originating from The Netherlands (n = 248 specimens) – the next largest fossil wood collection in NCB Naturalis, Leiden (n = 74) comes from the former Dutch East Indies (Java, Sumatra, Kalimantan and Sulawesi, in present-day Indonesia). Most of this Naturalis collection was obtained through the explorations of Crié (1888) and Molengraaf (1902), mostly from the Pliocene of Java and Kalimantan, and includes many dipterocarpoid fossil woods (Den Berger, 1923, 1927; Kräusel, 1922*a*, 1922*b*, 1925, 1926). Old museum labels on these specimens show that most were originally accessioned in the collections of the Rijks Geologisch Museum, Leiden and the Geologisch en Mineralogisch Instituut, Utrecht. In 1925, Oene Posthumus (1898 – 1945), in the course of an expedition organized by palaeobotanist, W. J. Jongmans (1878 – 1957), obtained a third collection of dipterocarpoid fossil wood from Indonesia.

Some of these Posthumus specimens were sent to Heerlen, but were eventually accessioned in the Naturalis, Leiden collections. However, other specimens from the same expedition were entrusted to Richard Kräusel (1890 – 1966), who gave them to his student Schweitzer to be studied (Posthumus, 1929); these latter specimens are now accessioned in University of Utrecht.

In view of this long history of study of fossil dipterocarp woods from the Neogene of Indonesia by Dutch scientists and institutions, it seems highly likely that RGM 232138 originated from these deposits.

6.5.3. Comparison with fossil woods from Indonesia in Dutch collections

To further test the hypothesis that RGM 232138 originated from the Neogene of Indonesia, the specimen was compared with other fossil woods (both hand specimens, and where available, thin sections) of known provenance in the collections of Naturalis, Leiden and the University of Utrecht. To the naked eye, the large majority of these Indonesian fossil wood specimens differ markedly from RGM 232138 in their general petrography. They are dark grey to black, and often slightly rounded, whereas RGM 232138 is pale grey to white, angular, and as noted above, has a ‘rusty’ haematitic rind (Fig. 6.7B). Furthermore, in thin section, specimens show dark organic-rich cell walls, whereas sections of RGM 232138 are extremely pale, showing almost no contrast between the cell wall and the silicic lumen infill, except in peripheral areas in the haematitic rind. However, a few specimens in the University of Utrecht collections from the Pliocene of the South Merangin River, Province of Jambi, western Sumatra (Posthumus, 1929) are near-identical to RGM 232138, in their pale colour, presence of a haematitic rind (Fig. 6.7A), and cellular preservation. The four near-identical specimens are numbered Utrecht 04480, 04482, 04529 and 04710 and correspond to thin sections 1909 – 1911, 1915 – 1917, 1993 – 1994 (slide 1995 is missing), and 2001 – 2003, respectively, with the closest petrographic match being Utrecht 04529 (slides 1993 – 1994).

There are two further lines of evidence, which also point to an identity with the Jambi material. (1) RGM 232138 belongs to exactly the same species (*Dryobalanoxylon bangkoense* Schweitzer) as the comparable Jambi material. While *D. bangkoense* is known from six localities from across Java and Sumatra in Indonesia (Schweitzer, 1958) it is unlikely that petrographically identical specimens would belong to the same species unless they derived from the same site. (2) Both RGM 232138 and Utrecht 04482 contain minute borings, 700 µm in diameter, showing a concave back-fill (Fig. 6.8). These borings are larval feeding galleries produced by scolytid bark beetles (Radek Mikulas and Leif Tapanila, pers. comm., 2012). Although scolytid beetles originated in Mesozoic times (Labandeira et al., 2001), they especially diversified in the Neogene times. Scolytid beetle traces are only seen in the Jambi material and RGM 232138, but not seen in thin sections of fossil wood from other localities examined.

Therefore, this study concludes that RGM 232138 was originated from Jambi. Although the matching Jambi material (Posthumus, 1929) is accessioned in Utrecht, and RGM 232138 is accessioned in Naturalis, Leiden, this is easily accounted for by the fact that Posthumus's collection was split between these two institutions (see section

4.3.3.2). In making this inference of provenance, it is stressed that the RGM 232138 lacks correct accession information, and therefore provenance can never be proven, and there will always be a degree of doubt.

Kräusel's material from the Pliocene of Java (part of the same back-arc basin deposits in which Jambi material occurs; Barber and Crow, 2005) bears a passing similarity to RGM 232138 (although it lacks the distinctive borings). The pale preservation and haematitic rind characteristic of RGM 232138 may be a superficial tropical weathering feature and therefore not indicative of a particular site. These caveats aside, in terms of petrography, wood anatomy, and trace fossils, the late Pliocene Jambi material is the closest match to RGM 232138, and therefore the most likely source based on currently available information.

6.5.4. Probable provenance: Jambi area, western Sumatra, Indonesia

The Merangin River of the Jambi region, from which Posthumus (1929) obtained his dipterocarpoid woods, dissects a complex geological terrain (Fig. 6.9). Its headwaters are located in Jurassic and Cretaceous deposits of the Woyla nappe, which are not reported to contain any silicified wood. Further downstream, the South Merangin River crosses a Triassic granodioritic unit (Air Batu Batholith) near the town of Dusunbaru, before flowing through Permian (Asselian) volcaniclastic sediments and extrusive lavas (Mengkarang and Telukwang Formations), which contain *Dadoxylon* trees in growth position. It finally dissects the Middle Palembang Formation, which is late Miocene in age (Zwierzycki, 1935) and is known to hold tuffs and carbonaceous shales, before flowing onto the town of Bangko (Fig. 6.9). Overlying this complex bedrock succession, and widespread across the entire area, is a late Pliocene volcaniclastic unit (Kasai Formation), which also contains silicified wood (Suwarna et al., 1994, 1998; Zwierzycki, 1935).

All the fossil wood specimens described from the Posthumus 1925 expedition were found rolling as loose float in the river valley of the South Merangin River. Some of those fossil woods (*Dadoxylon*) presumably eroded out of the Permian strata because later surveys have found trees in growth position in these strata (van Waveren, unpublished observations, 2012). However, Permian strata are extremely unlikely to be the source of any angiosperm wood and can reasonably be excluded as a source of dipterocarpoid wood, which is very similar to that of an extant genus. According to Schweitzer (1958), Posthumus collected the dipterocarpoid woods in areas where the Miocene is absent, but where Pliocene strata is present; therefore, the most reasonable inference is that the woods had eroded from the late Pliocene Kasai Formation.

The holotype of *Dryobalanoxylon bangkoense* (Utrecht 04527), which is not petrographically similar to RGM 232138, was collected from Posthumus's Point 201 on the South Merangin River (Schweitzer, 1958). However, the specimen (Utrecht 04529), which is near-identical to RGM 232138 in thin section, and other closely similar specimens, was obtained from Posthumus's field collection number 92, which may represent the same general area on the South Merangin River where Utrecht 04527 was obtained (I am uncertain because information associated with Posthumus's field numbering system has been lost). Therefore, I conclude that RGM 232138 originated in the late Pliocene Kasai Formation near Bangko in the Jambi region of western Sumatra, Indonesia. The reason that RGM 232138 was incorrectly accessioned in Naturalis Biodiversity Center may be because it was a very pale (almost white) specimen (Fig. 6.7B), superficially somewhat similar to Cretaceous specimens associated with the chalk facies of northern Europe.

6.6. SIGNIFICANCE FOR MARIE STOPES'S CONTROVERSIAL *WOBURNIA POROSA*

The discovery that a Neogene specimen of dipterocarpoid wood from Indonesia was, for nearly a century, incorrectly accessioned in the collections of Naturalis Biodiversity Center, Leiden, as a Cretaceous specimen may have wider ramifications for a century-long controversy. Stopes (1912, 1915) famously reported a similar-looking wood reputed to be from the Cretaceous (Aptian-Albian) of the Woburn Sands, Bedfordshire, England (*Woburnia porosa* Stopes), which attracted considerable interest because, at the time, it was the oldest known angiosperm wood. However, doubts about the age and provenance of *Woburnia* began to surface after Kräusel (1922a) confirmed it to be of dipterocarp affinity, and transferred the specimen to *Dipterocarpoxylon*. Harris (1956) and Hughes (1961), in particular, expressed their doubts about its provenance, and encouraged Casey (1961) to resolve the provenance issue by conducting a petrographic study of any adhering sediment; however, no matrix could be detected on the *Woburnia* type specimen. Crawley (2001) therefore concluded that *Woburnia* was probably not of Cretaceous age. This is supported by the fact that the holotype differs from fossil wood confirmed to be from the Woburn Sands (e.g. *Podocarpoxylon woburnense* Stopes 1915), the former being dark grey to black, the latter being pale grey.

Nothing is known of the collection history of the holotype of *Woburnia* except that it was transferred unnumbered, in 1898, from the Botany to the Geology Department of the British Museum of Natural History (Hughes, 1976), and the record in the catalogue book at NHM only mentions the collection transfer and "Woburn Sands" as its locality of origin. Consequently, the uncertainty about *Woburnia*'s genuine provenance remains. In order to shed light on provenance, the holotype is described and illustrated in full detail for the first time, and compared with dipterocarp fossil woods of known provenance.

6.6.1. Description of Woburnia porosa

The holotype of *Woburnia porosa* (Natural History Museum, London; NHM V.5254) is very small (25 x 18 mm diameter), rather poorly preserved in thin section (slides V.5254a–i), and somewhat compressed. Consequently it is impossible to give a full anatomical description of the wood from the existing material, and the size of the hand specimen means that new thin sections cannot be obtained. This partial description augments that of Stopes (1915) as follows:

Growth rings absent; vessels diffuse-porous, exclusively solitary (Plate VI, 1); perforation plates simple (Plate VI, 2); intervessel pitting not observed; vessel – ray pitting not observed; mean tangential vessel diameter 224 – 337 µm (mean: 248 ± 31, n = 50); vessels per mm^2 4 – 8 (mean: 6, n = 25) (Plate VI, 1); mean vessel element length 522 – 658 µm (mean: 547 ± 16 µm, n = 35) (Plate VI, 2); vasicentric tracheids abundant (Plate VI, 4); vessel – tracheid pitting 2 – 4-seriate showing alternate, circular pits, 4 – 7 µm diameter (mean: 5.6 ± 2 µm, n = 40) (Plate VI, 6).

Fibres, 29 – 35 µm diameter (mean: 32 ± 2 µm, n = 25) thin to thick and very thick walled (Plate VI, 5, arrow C); non-septate fibres present, no pit observed.

Axial parenchyma thin walled surrounding axial canals (Plate VI, 5, A), elsewhere diffuse (Plate VI, 5, arrow B); axial parenchyma strand length 3 – 8 cells, cell length 90 – 113 µm (mean: 97 ± 5 µm, n = 20) (Plate VI, 3, arrow E).

Rays 1 – 7 cell wide (mean: 4, n = 22) (Plate VI, 3, arrow A); ray height 983 – 1545 µm (mean: 1256 ± 243 µm, n = 19); long tails of uniseriate cells (Plate VI, 3, arrow D). Sheath cells present especially in largest rays (Plate VI, 3, arrows B and C).

Axial canals, 52 – 129 µm diameter (mean: 92 µm ± 13, n = 25), in mostly long, but locally short tangential lines (Plate VI, 7).

6.6.2. Comparison with woods of extant dipterocarps

Woburnia shows vasicentric tracheids (IAWA character 60) and axial canals in long tangential lines (IAWA character 127), a combination that is almost exclusive to extant Dipterocarpaceae. However, it is difficult to establish a more precise affinity with extant taxa due to the relatively poor preservation quality, which rules out observation of key characters such as ray cell composition in RLS, intervessel pitting, vestured pits, silica crystals, and tyloses. In addition, the compression of the fossil means that measuring some quantitative features is also challenging. Nonetheless, comparison of *Woburnia* with extant dipterocarp genera using Principal Component Analysis and Cluster Analysis (a) suggests an affinity with *Dryobalanops* (Fig. 6.3a) – although the utility of the PCA is somewhat compromised due to the incomplete anatomical dataset for *Woburnia*. This is also the case for the cluster analysis (6.3b) in which *Woburnia* shows little similarity to the genus *Dryobalanops.* The key characters that *Woburnia* shares with *Dryobalanops* include the presence of vasicentric tracheids, thick-walled fibres and axial canals in long tangential lines (IAWA characters 60, 70 and 127 respectively), as well as quantitative features such as tangential vessel diameter, vessel density, ray height and ray width. As such *Woburnia* is somewhat similar to RGM 232138 in the collections of NCB Naturalis.

6.6.3. Comparison with fossil dipterocarp wood

Prior to 1898 – the date that the *Woburnia* holotype was already present in the Natural History Museum, London (NHM) collections – there was one Dutch expedition to Indonesia, which obtained dipterocarp fossil woods (Crié, 1888). It is intriguing, therefore, that among all the collections containing dipterocarp fossil woods examined in the Naturalis Biodiversity Center and Utrecht University, the specimens that show the closest petrologic similarity with the *Woburnia* holotype are samples of *Dryobalanoxylon spectabile* (Crié) Den Bergen, 1927 collected, in the course of the Crié (1888) expedition, from several localities in Java and Sumatra, Indonesia. It is known that some of Crié's material was donated to various academic institutions in Germany and Britain, and Crié exchanged material with London colleagues (Edwards, 1921). It is conceivable, though not supported by any evidence, that a dipterocarp fossil wood from Crié's 1888 expedition could have been sent to the NHM and then a decade later, in 1898, mislabelled during its transfer from the Botany to the Geology Department, later to fall into Stopes' hands in 1912. Some of Crié's holotypes are in the collections of Naturalis, Leiden (van Konijnenburg-van Cittert et al., 2004).

I conclude that the most likely provenance of *Woburnia*, like that of RGM 232138 in the collections of NCB Naturalis, is the Neogene of Indonesia and not the Cretaceous of England. This is based on (1) the holotype's close affinity with *Dryobalanops*, an extant taxon in Indonesia, (2) its affinity to *Dryobalanoxylon*, a fossil wood genus restricted to Neogene and younger rocks in southeast Asia and India, and (3) its similarity with fossil dipterocarp woods collected from Indonesia at about the same time that the holotype of *Woburnia* entered the NHM collections.

6.7. CONCLUSIONS

1. A new specimen of dipterocarpoid fossil wood, *Dryobalanoxylon bangkoense* Schweitzer is described from the collection in the Netherlands Centre for Biodiversity (NCB) Naturalis, Leiden, The Netherlands. The species diagnosis is emended.

2. Although accession details for this specimen are incorrect, a detailed analysis of the taxonomy and preservation of the specimen, and comparison with material of known provenance enables the inference that the genuine provenance is the Neogene of Indonesia, possibly the late Pliocene Kasai Formation of the Jambi area, western Sumatra.

3. Comparison with an anatomical database of 81 extant dipterocarpoid woods (76 species), including a Principal Component Analysis, suggests a close affinity, or possible identity, with the extant genus *Dryobanalops*, which today is distributed through parts of western Sumatra, Kalimantan and the Malay Peninsula.

4. The fact that a fossil dipterocarpoid wood from the Neogene of Indonesia was wrongly accessioned as a Cretaceous specimen for nearly a century is significant for interpreting Stopes' controversial *Woburnia porosa*. Examination of the holotype of *Woburnia porosa* suggests that this specimen may have also originated from the Neogene of Indonesia.

FIGURES CHAPTER 6

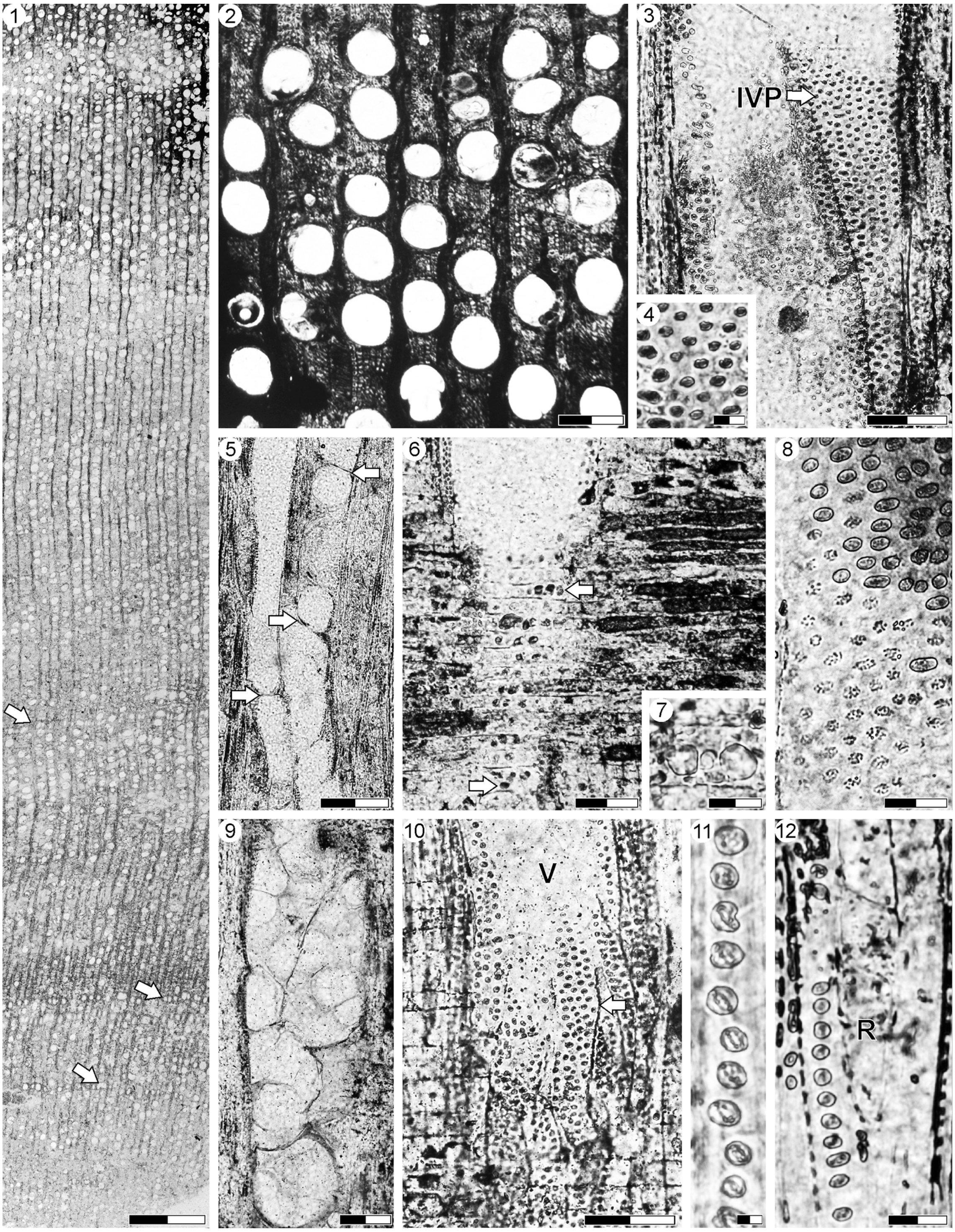


Plate I. *Dryobalanoxylon bangkoense*, Naturalis Biodiversity Center, Leiden, The Netherlands, accession number RGM 232138.

Plate I. *Dryobalanoxylon bangkoense*, Naturalis Biodiversity Center, Leiden, The Netherlands, accession number RGM 232138.

1. Growth ring boundaries indistinct or absent; vessel arrangement, diffuse-porous; arrows highlight lines of axial canals. TS. Scale bar: 2 mm.
2. Vessels, circular outline and exclusively solitary, TS. Scale bar: 250 µm.
3. Intervessel pits (IVP) alternate, RLS. Scale bar: 100 µm.
4. Intervessel pits, alternate arrangement, polygonal, RLS. Scale bar: 10 µm.
5. Individual vessel elements with simple perforation plates (arrows), TLS. Scale bar: 200 µm.
6. Vessel – ray pits (arrows) large with reduced borders, RLS. Scale bar: 80 µm.

7 Detail of vessel – ray pits, large with reduced borders, RLS. Scale bar: 20 µm.

8. Vestured pits in vasicentric tracheids, RLS. Scale bar: 25 µm.
9. Tyloses common, RLS. Scale bar: 100 µm.
10. Vasicentric tracheids (arrow) with several rows of alternate pitting adjacent to vessel (V), RLS. Scale bar: 100 µm.
11. Bordered fibre pits with oblique apertures, common on radial walls, RLS. Scale bar: 10 µm.
12. Bordered fibre pits with oblique apertures common on tangential walls, adjacent to ray (R), TLS. Scale bar: 22 µm.

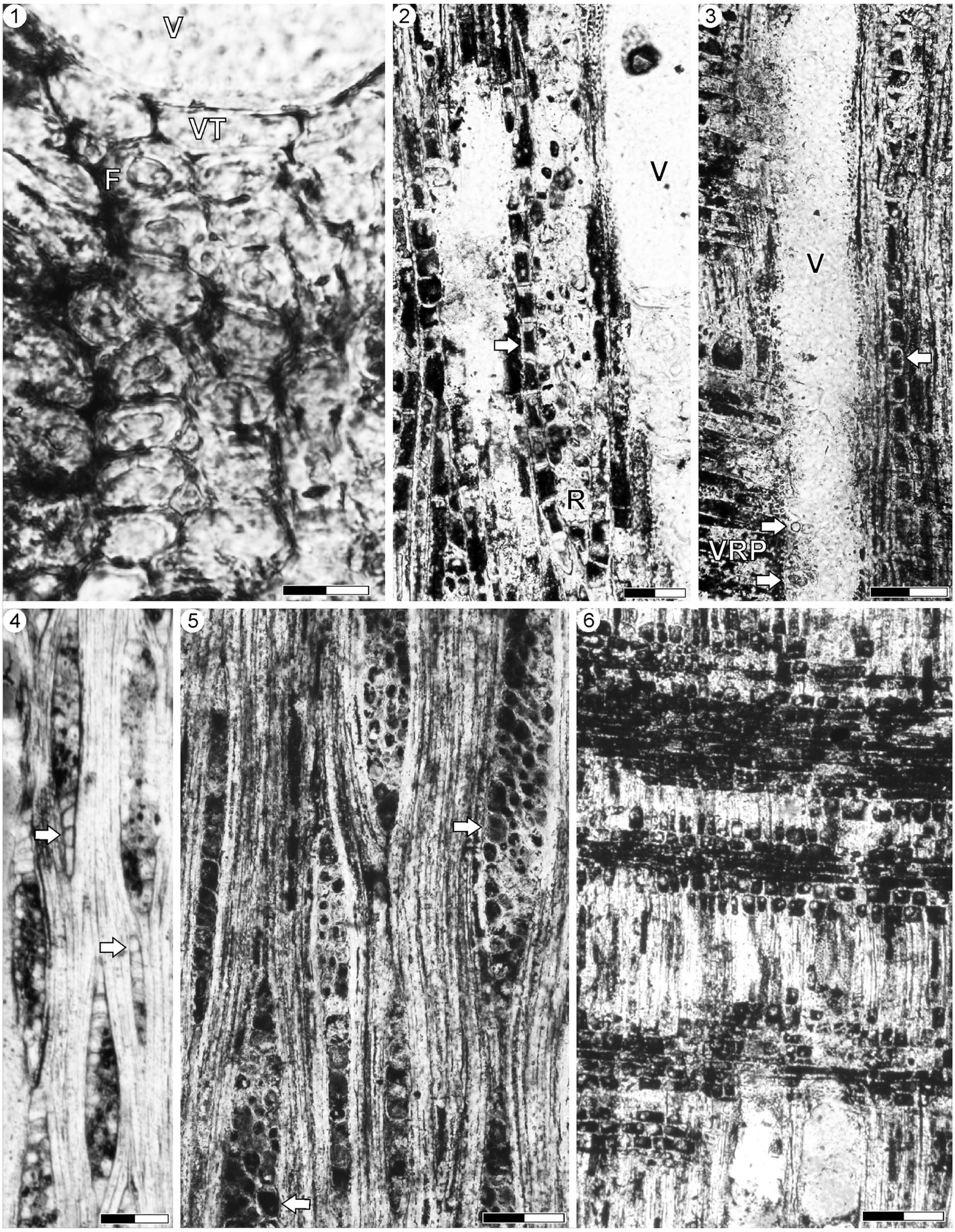


Plate II. *Dyobalanoxylon bangkoense*, Netherlands Centre for Biodiversity (NCB Naturalis), Leiden, The Netherlands, accession number RGM 232138.

Plate II. *Dyobalanoxylon bangkoense*, Netherlands Centre for Biodiversity (NCB Naturalis), Leiden, The Netherlands, accession number RGM 232138.

1. Fibres, very thick-walled (F), fibre-tracheids, vasicentric tracheids (VT) and a vessel (V), TS. Scale bar: 10 µm.
2. Axial parenchyma strand, > 8 cells high (arrow), vessel (V), ray (R), TLS. Scale bar: 100 µm.
3. Axial parenchyma strand, > 8 cells high (top arrow) near vessel (V) showing vessel – ray pits (VRP) (bottom arrows), RLS. Scale bar: 175 µm.
4. Rays with uniseriate tails (top arrow) and uniseriate rays (bottom arrow), TLS. Scale bar: 130 µm.
5. Uniseriate rays and multiseriate rays, up to 4-seriate; weakly developed sheath cells (arrows), TLS. Scale bar: 100 µm.
6. Body ray cells procumbent with 2 – 4 rows of square to upright marginal cells, RLS. Scale bar: 450 µm.

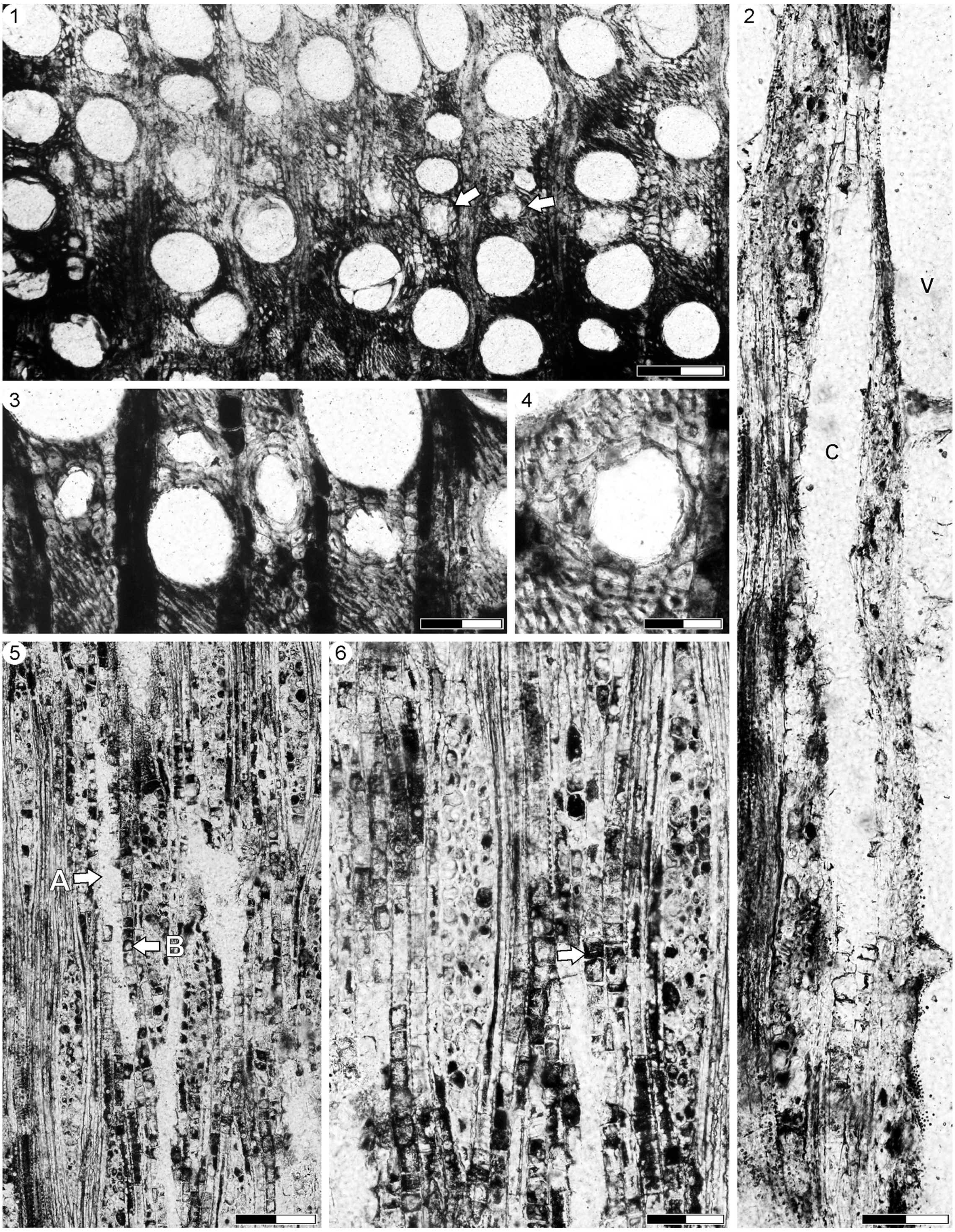


Plate III. *Dryobalanoxylon bangkoense*, Netherlands Centre for Biodiversity (NCB Naturalis), Leiden, The Netherlands, accession number RGM 232138.

Plate III. *Dryobalanoxylon bangkoense*, Netherlands Centre for Biodiversity (NCB Naturalis), Leiden, The Netherlands, accession number RGM 232138.

1. Axial canals in long tangential lines (arrows) surrounded by parenchyma cells (thin-walled cells in light grey), TS. Scale bar: 270 µm.
2. Longitudinal view of an axial canal (C) adjacent to a vessel (V), TLS. Scale bar: 130 µm.
3. Axial canals surrounded by parenchyma cells, TS. Scale bar: 125 µm.
4. Detail of axial canal epithelial cells, TS. Scale bar: 70 µm.
5. Longitudinal view of axial canal (arrow A) showing the abundance of axial parenchyma cells (arrow B), TLS. Scale bar: 275 µm.
6. Detail of epithelial cells associated with axial canals (arrow), TLS. Scale bar: 260 µm.

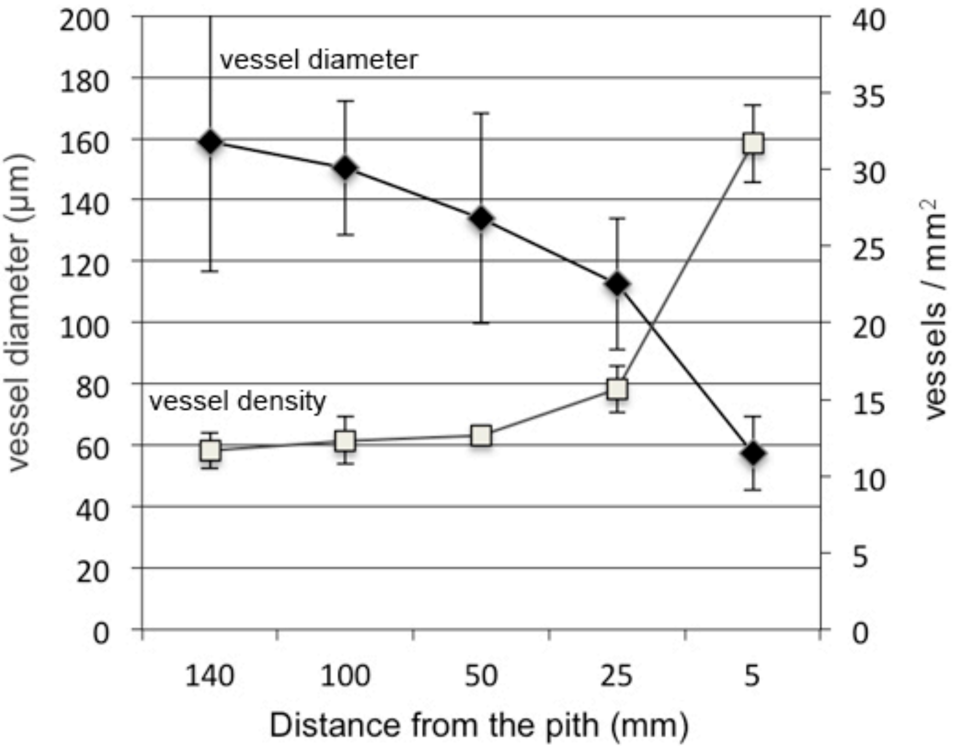


Figure 6.1. Ontogenetic trends in mean tangential vessel diameter and vessel density from the pith to the preserved exterior of the specimen. Anatomical properties are variable within 50 mm of the pith (juvenile wood) but become relatively constant at a distance > 100 mm from the pith (inferred to be mature wood).

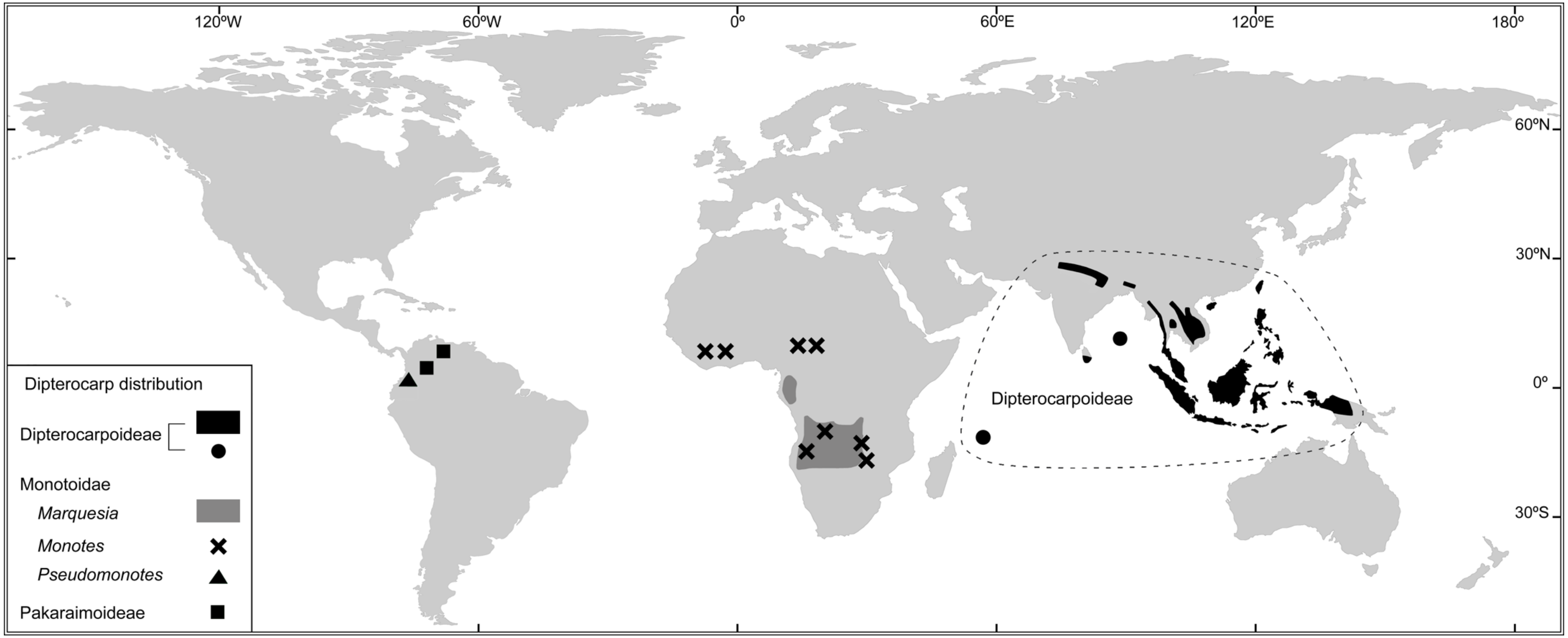


Figure 6.2. Distribution of extant species of Dipterocarpaceae (after Maguire and Ashton, 1977; Meher-Homji, 1979; Whitmore, 1998; Maury-Lechnon and Curtet, 1998).

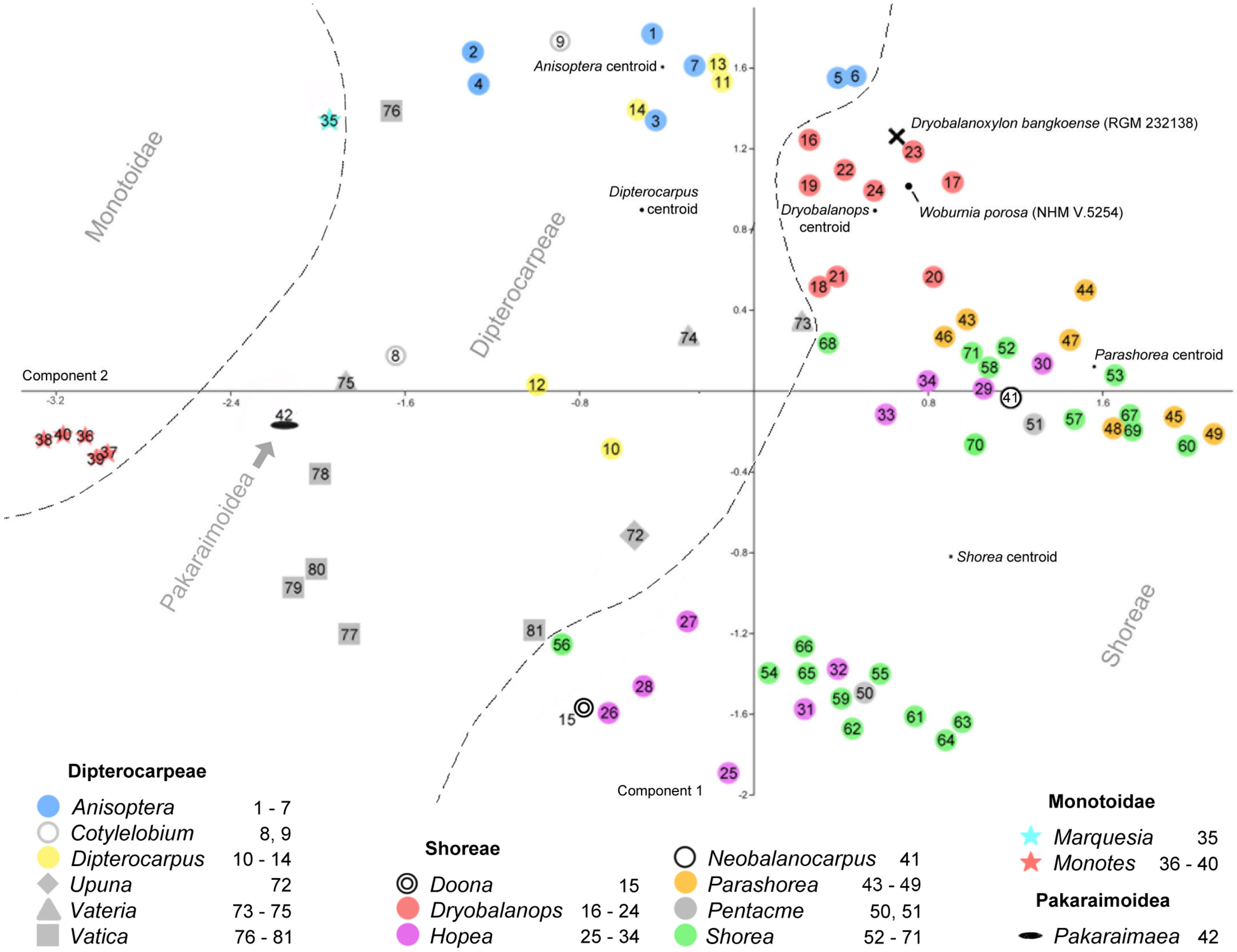


Figure 6.3. Principal Component Analysis of extant dipterocarp woods utilizing 66 anatomical characters. PC1 represents 20.7% of the original variance of the dataset while PC2 represents 13.1% of the original variance of the dataset (see Appendix 4).

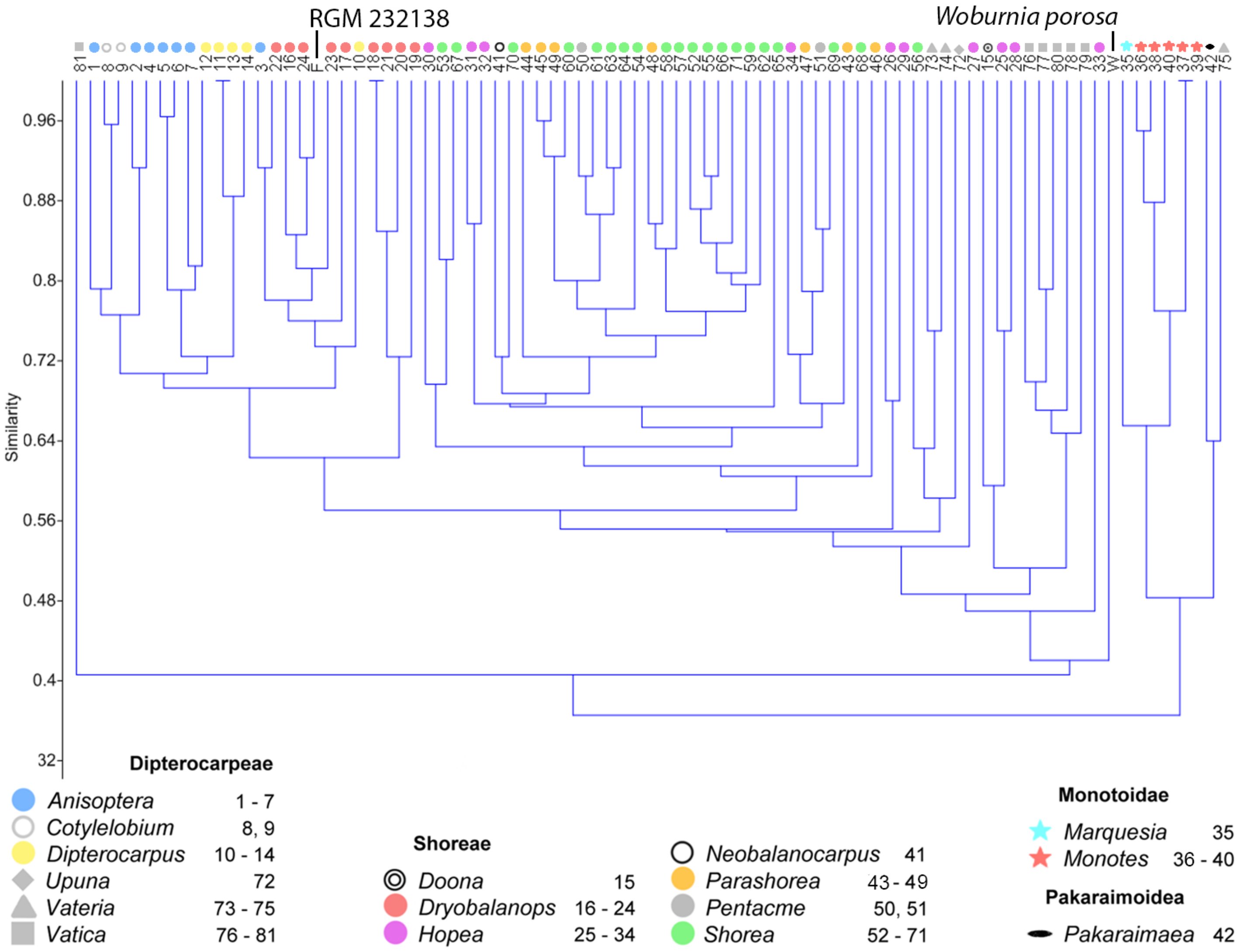


Figure 6.3b Cluster Analysis of extant dipterocarp woods utilizing a presence/absence matrix of 66 anatomical characters (see Appendix 4). Jaccard similarity measure, Min Y: 0.302, Coph. corr.: 0.8418

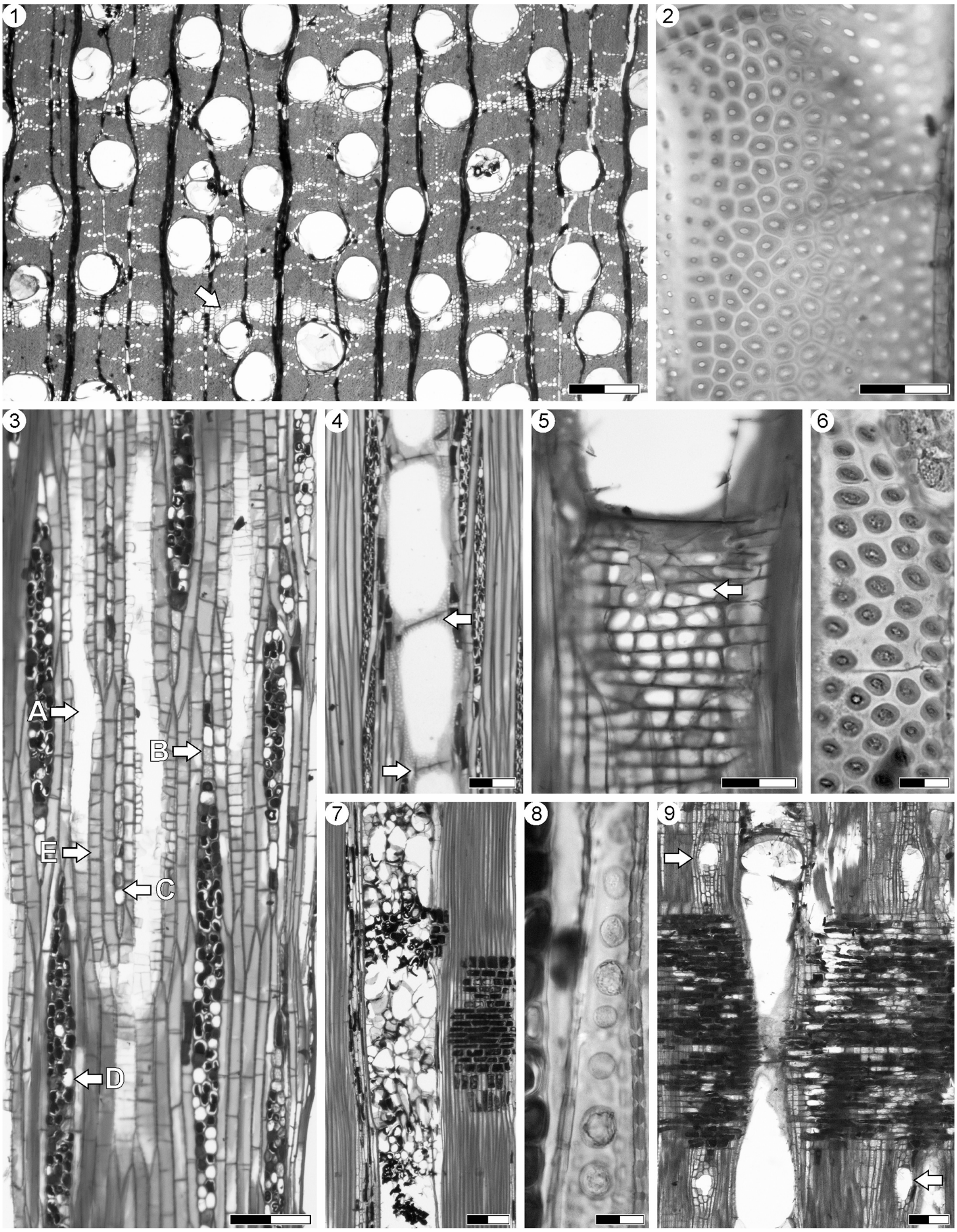


Plate IV. Various extant Dipterocarpoideae for comparative purposes. All specimens accessioned in the Jodrell Laboratory, Royal Botanic Gardens Kew.

Plate IV. Various extant Dipterocarpoidae for comparative purposes. All specimens accessioned in the Jodrell Laboratory, Royal Botanic Gardens Kew.

1. *Shorea albida* Symington (accession number Kjw 17058), Wood diffuse porous, fibres thick walled, axial canals in long tangential lines embedded in a band of axial parenchyma (arrow), axial parenchyma also scanty paratracheal and diffuse in aggregates, TS. Scale bar: 400 µm.
2. *Shorea albida* Symington (accession number Kjw 17058), Alternate, polygonal pits in a vessel, TLS. Scale bar: 100 µm.
3. *Shorea albida* Symington (accession number Kjw 17058), Axial canal (arrow A), uniseriate ray tail (arrow B), uniseriate ray (arrow C), multiseriate ray 3 cells wide, sheath cells (arrow D), parenchyma strand more than 8 cells long (arrow E), TLS. Scale bar: 500 µm.
4. *Shorea acuminata* Dyer (accession number Kjw 17057), Vessel with simple perforation plates (arrows), RLS. Scale bar: 125 µm.
5. *Shorea albida* Symington (accession number Kjw 17058), Vessel – ray pits of varied shape with reduced borders (arrow), RLS. Scale bar: 200 µm.
6. *Shorea rubra* P.S. Ashton (accession number Kjw 40509), Vestured pits, TLS. Scale bar: 50 µm.
7. *Shorea curtisii* Dyer ex King (accession number Kjw 40486), Abundant tyloses in a vessel, ray with two rows of square marginal cells, RLS. Scale bar: 500 µm.
8. *Shorea albida* Symington (accession number Kjw 17058), Bordered pits in a fibre, TLS. Scale bar: 20µm.
9. *Shorea albida* Symington (accession number Kjw 17058), Body ray cells procumbent and square marginal cells, axial canal (arrows), vessel with simple perforation plate, RLS. Scale bar: 200 µm.

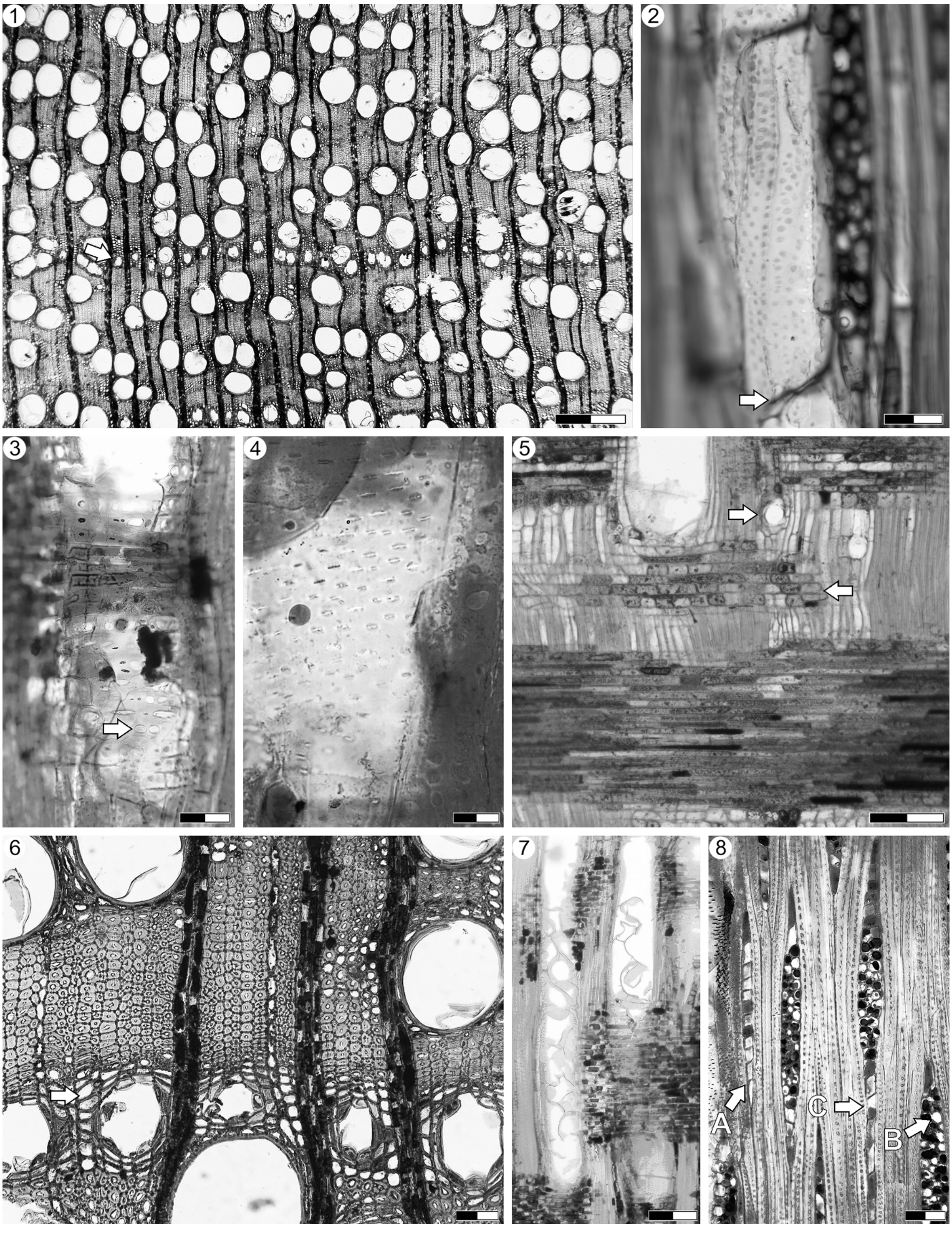


Plate V. Extant *Dryobalanops lanceolatum* Burck, for comparative purposes. All specimens accessioned in the Jodrell Laboratory, Royal Botanic Gardens Kew, accession number Kjw 17023.

Plate V. Extant *Dryobalanops lanceolatum* Burck, for comparative purposes. All specimens accessioned in the Jodrell Laboratory, Royal Botanic Gardens Kew, accession number Kjw 17023.

1. Wood diffuse porous, axial canals in long tangential lines (arrow) embedded in a band of axial parenchyma, axial parenchyma also scanty paratracheal and diffuse in aggregates, TS. Scale bar: 600 µm
2. Simple perforation plates (arrow), vasicentric tracheids present, pits present, TLS. Scale bar: 100 µm.
3. Vessel-ray pits with reduced borders (arrow), RLS. Scale bar: 180 µm.
4. Vestured pits present, TLS. Scale bar: 30 µm.
5. Body ray cells procumbent with mostly 2-4 rows of square marginal cells (bottom arrow), axial canals (top arrow), RLS. Scale bar: 200 µm.
6. Parenchyma vasicentric and surrounding canals in long tangential lines (arrow), TS. Scale bar: 100 µm.
7. Tyloses common, RLS. Scale bar: 200 µm.
8. Uniseriate rays present (arrow A), multiseriate ray 3 cells wide, sheath cells (arrow B), ray tails present (arrow C), TLS. Scale bar: 100 µm.

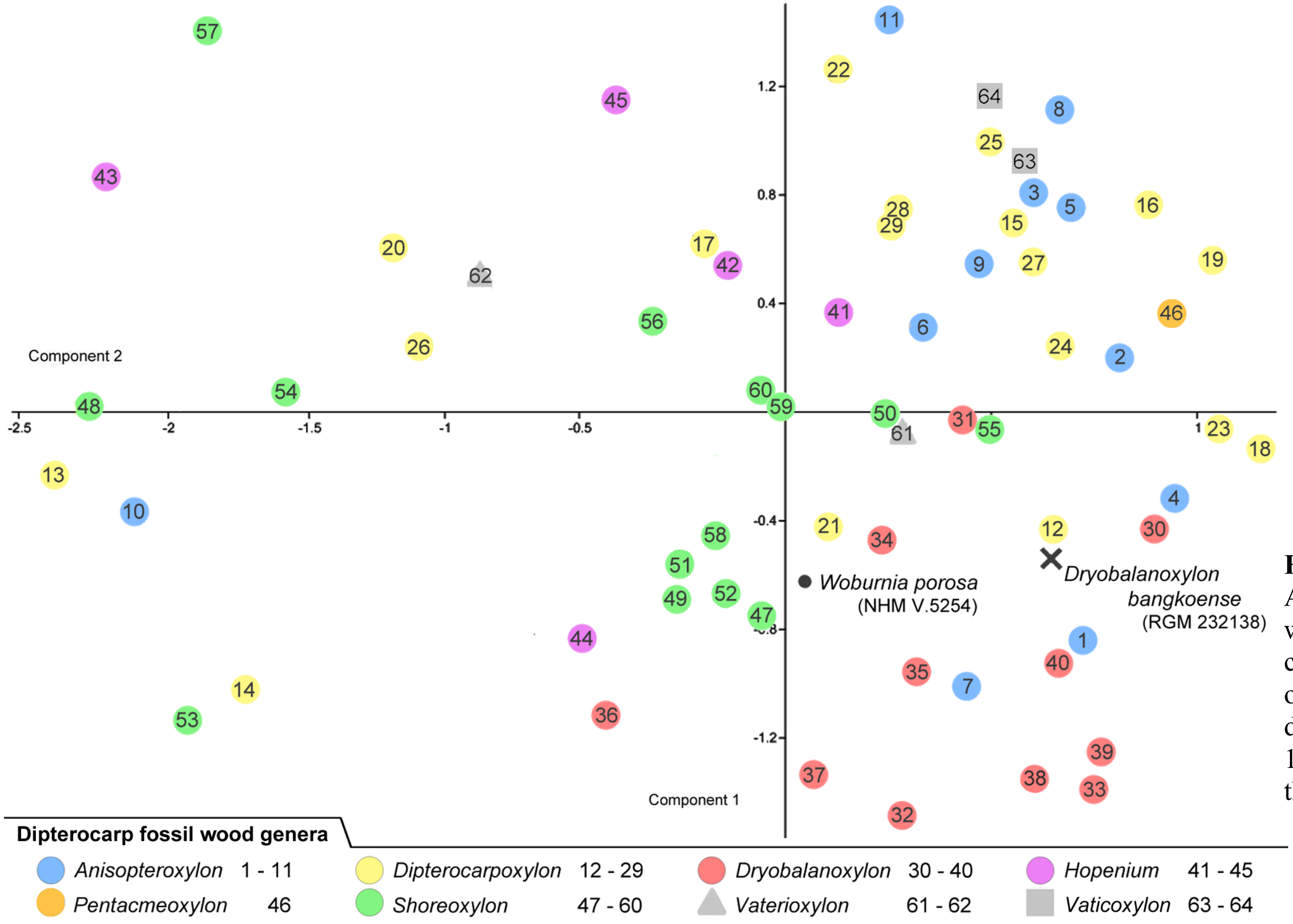


Figure 6.4. Principal Component Analysis of fossil dipterocarp woods utilizing 44 anatomical characters. PC1 represents 14.9% of the original variance of the dataset while PC2 represents 10.9% of the original variance of the dataset (see Appendix 5).

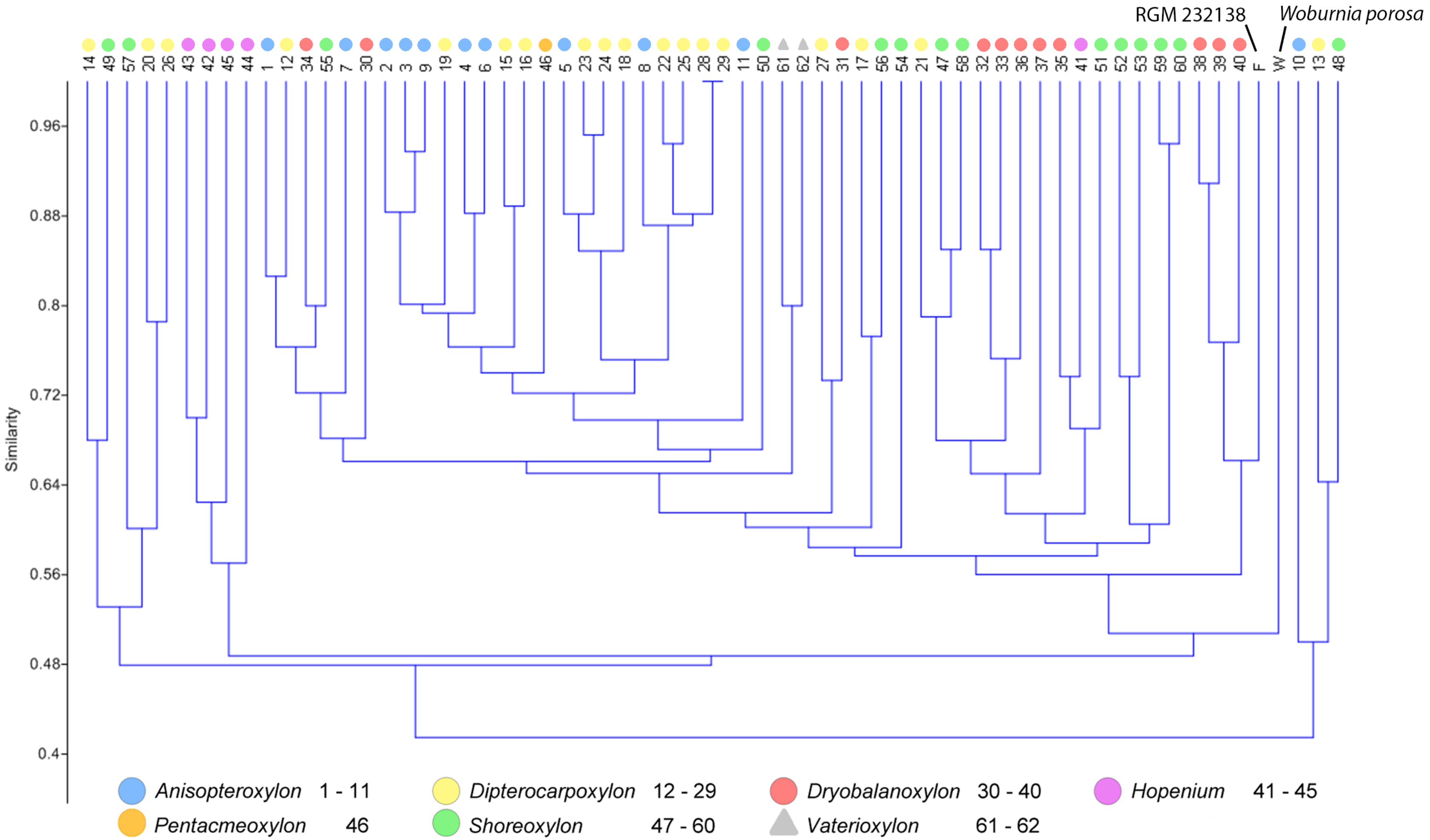


Figure 6.4b Cluster Analysis of fossil dipterocarp woods utilizing a presence/absence matrix of 44 anatomical characters (see Appendix 5). Jaccard similarity measure, Min Y: -5, Coph. corr.: 0.8205

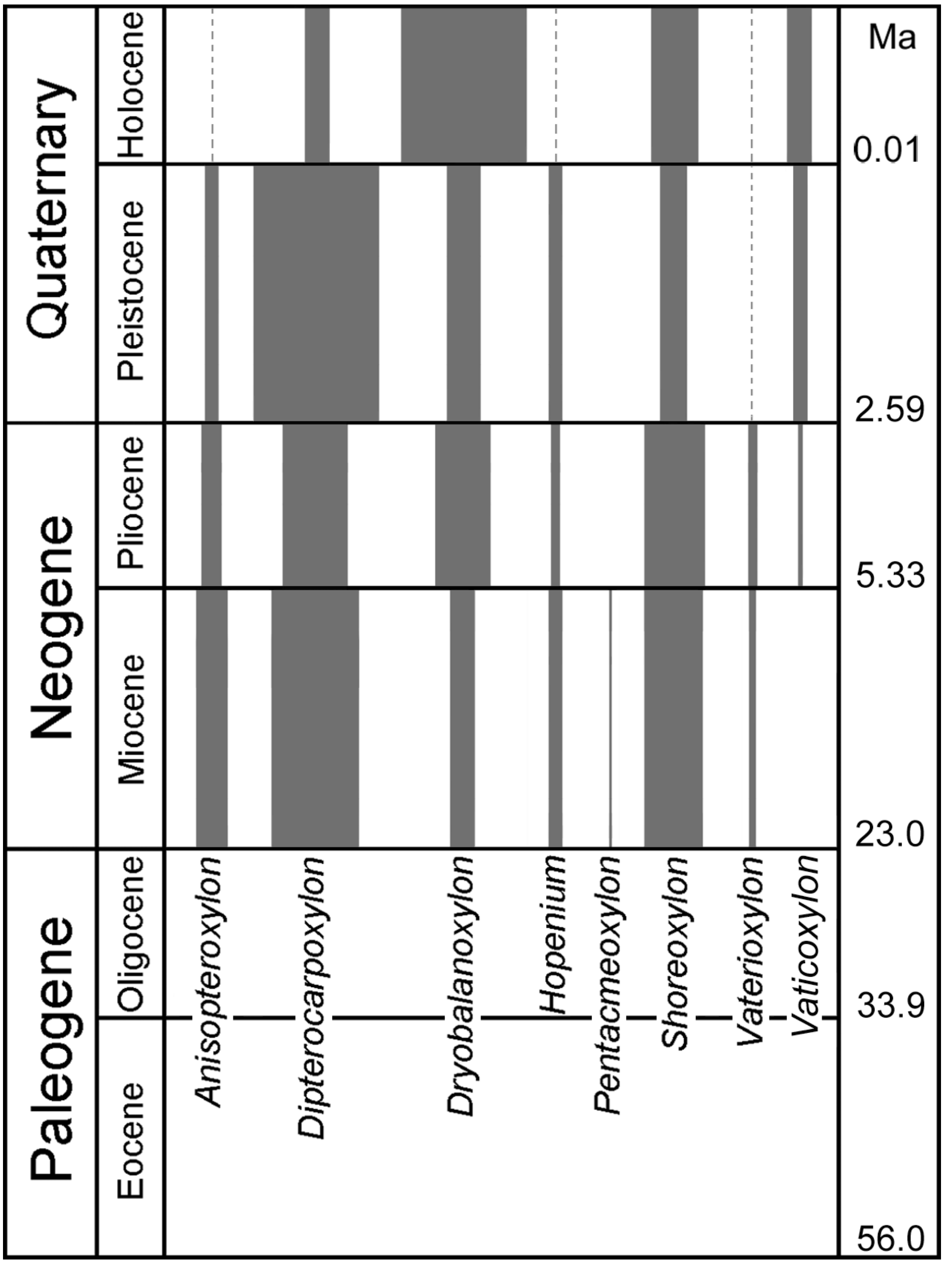


Figure 6.5. Stratigraphic distribution of all fossil taxa of dipterocarp wood described in the literature using the timescale of Gradstein et al. (2012). Width of the grey line is proportional to the percentage of specimens reported for each epoch (see Appendix 6).

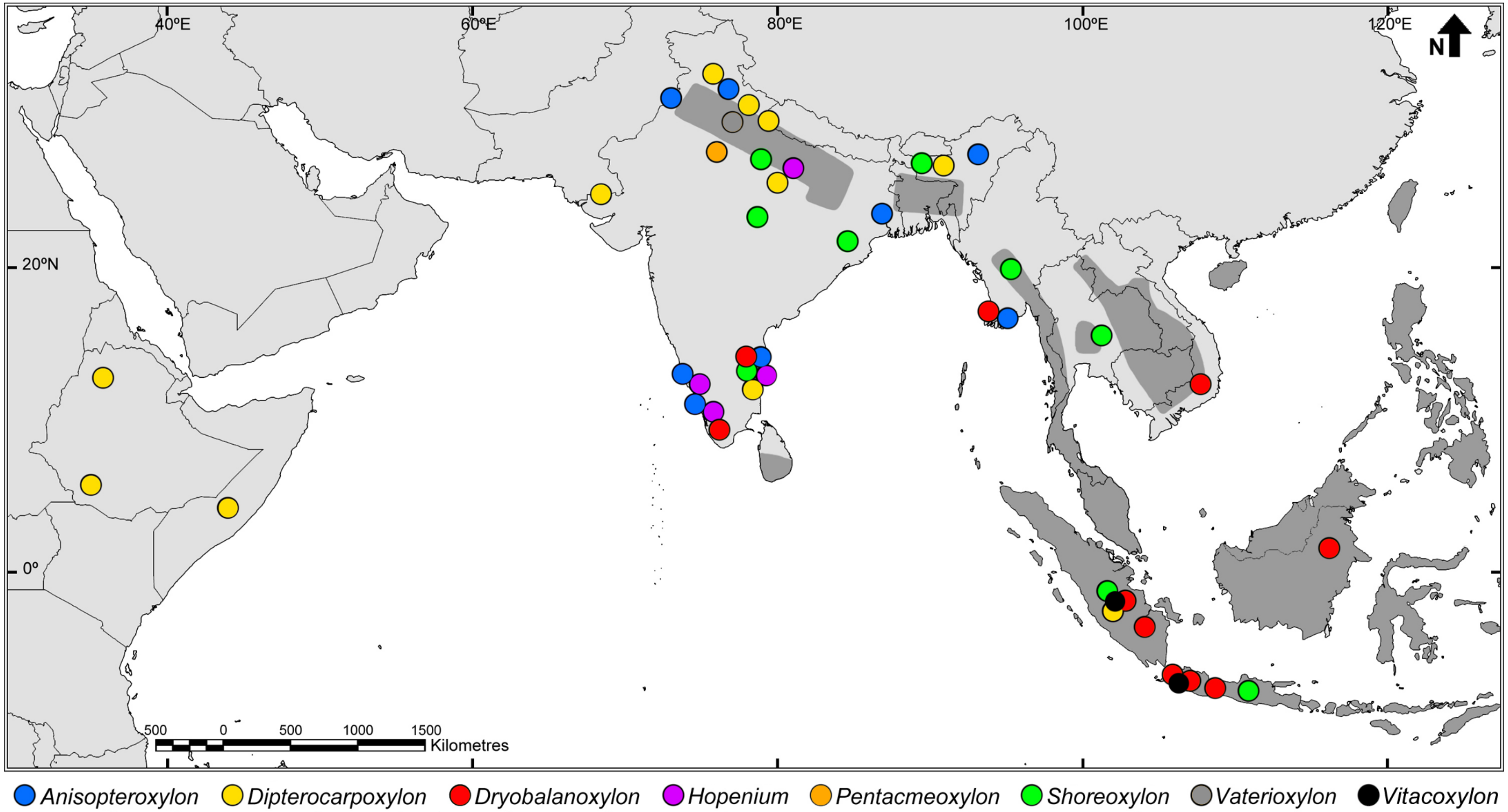


Figure 6.6. Geographic distribution of dipterocarpoid fossil wood specimens reported in the literature (see Appendix 6), and the present-day distribution of the subfamily Dipterocarpoideae (dark grey; cf. Fig. 4.1).

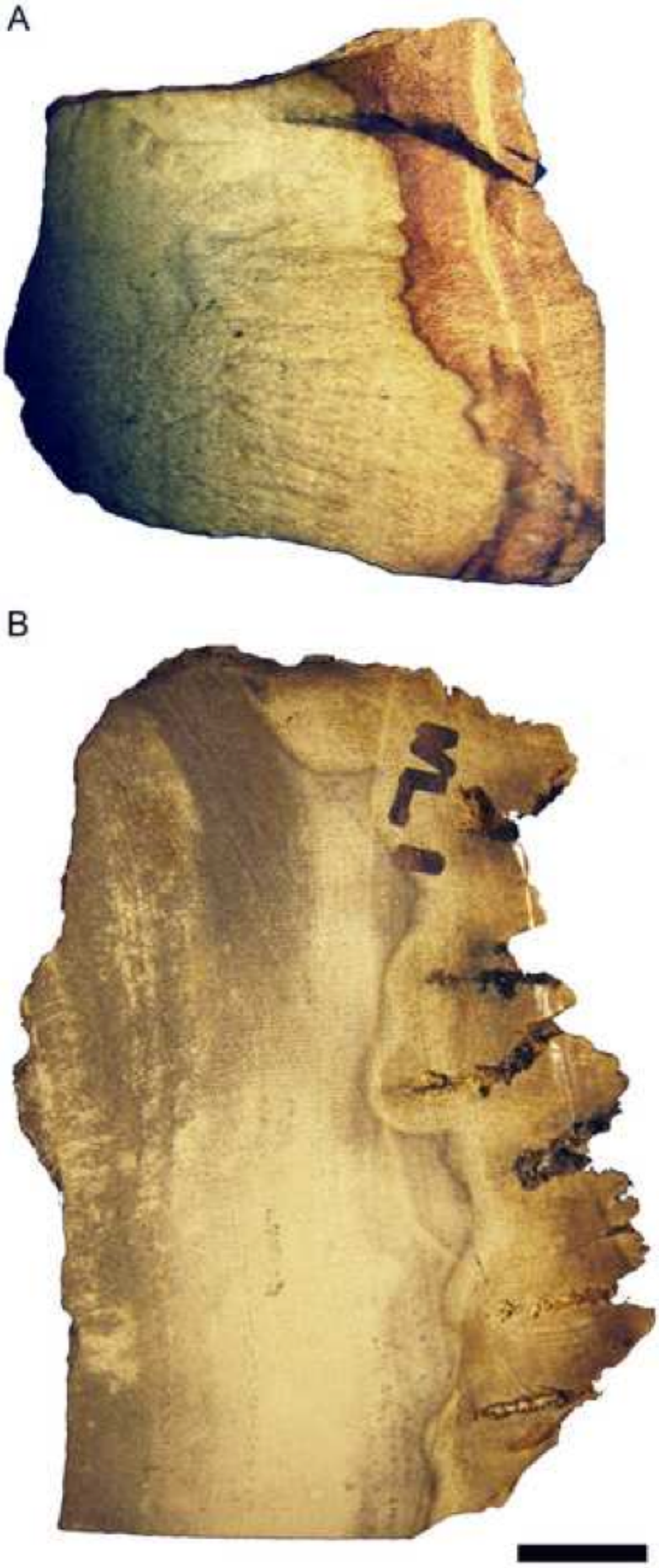


Figure 6.7. Comparison of haematitic rind in RGM232138 (Fig. 4.7B) and dipterocarp wood from Jambi (Fig. 4.7A), western Sumatra, Indonesia in collections of Utrecht University. Scale: 15 mm

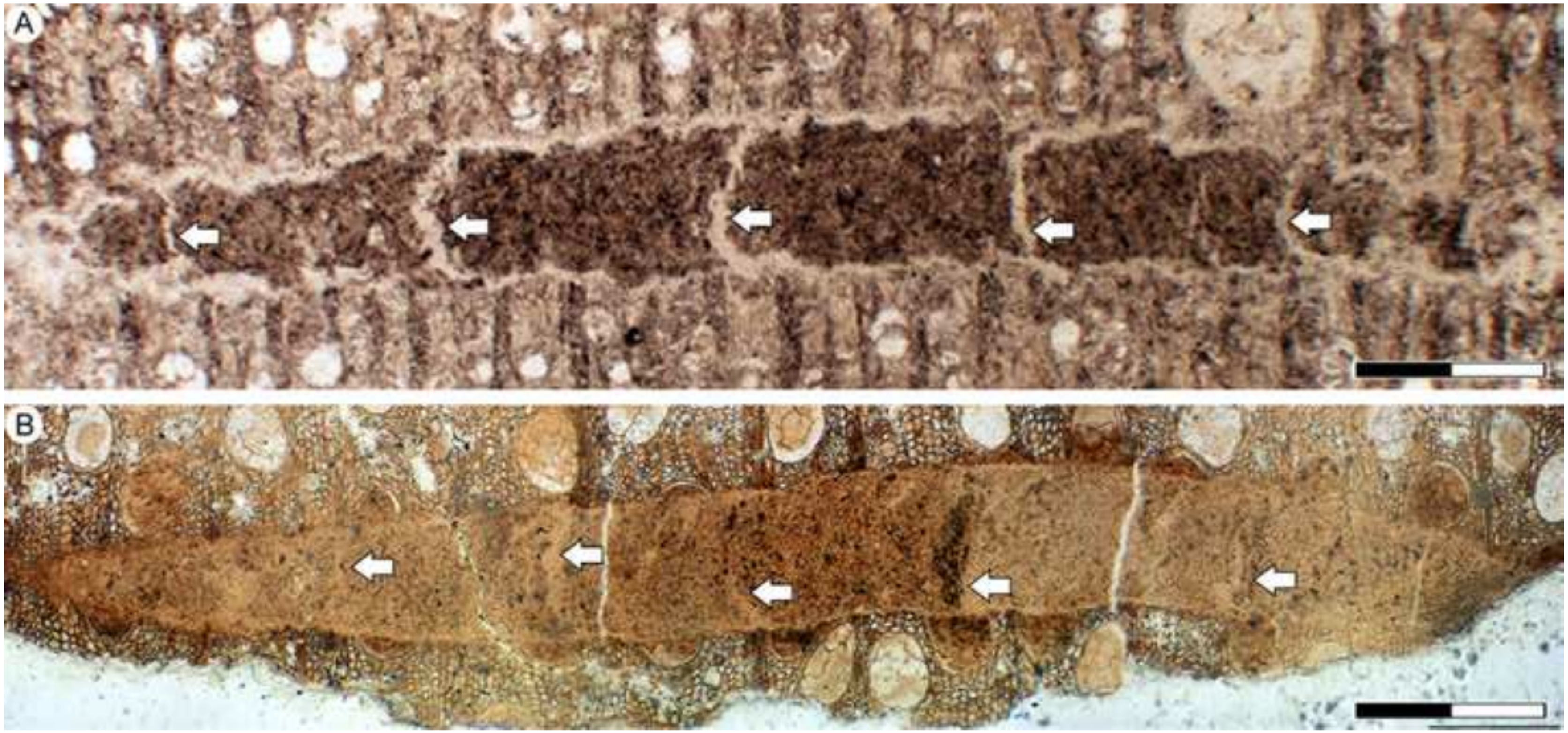


Figure 6.8. Borings in wood. A, Small concave back-filled boring in the wood of RGM 232138, TS, Scale: 750 µm, arrows point to back-fills. B, Boring in *Dryobalanoxylon bangkoense* Schweitzer from Jambi area, western Sumatra, TS, Utrecht 04482, Scale: 750 µm, arrows point to back-fills

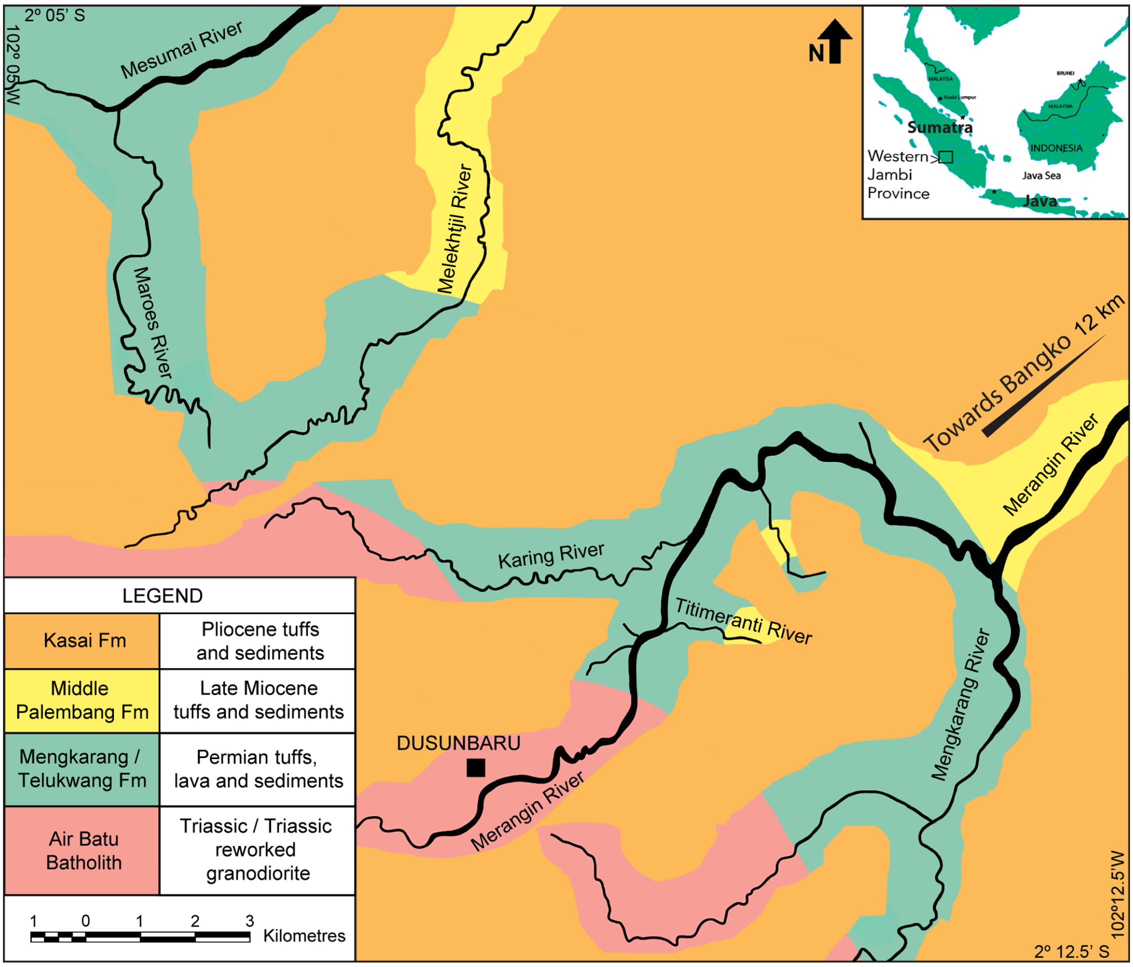


Figure 6.9. Geological map of the South Merangin River area (based on Suwarna et al., 1998; Zwierzycki, 1935) showing the distribution of the principle rock units in the area where Posthumus (1929) made his collections in 1925. The probability is that RGM 232138 came from this area (after Suwarna, 1994, 1998).

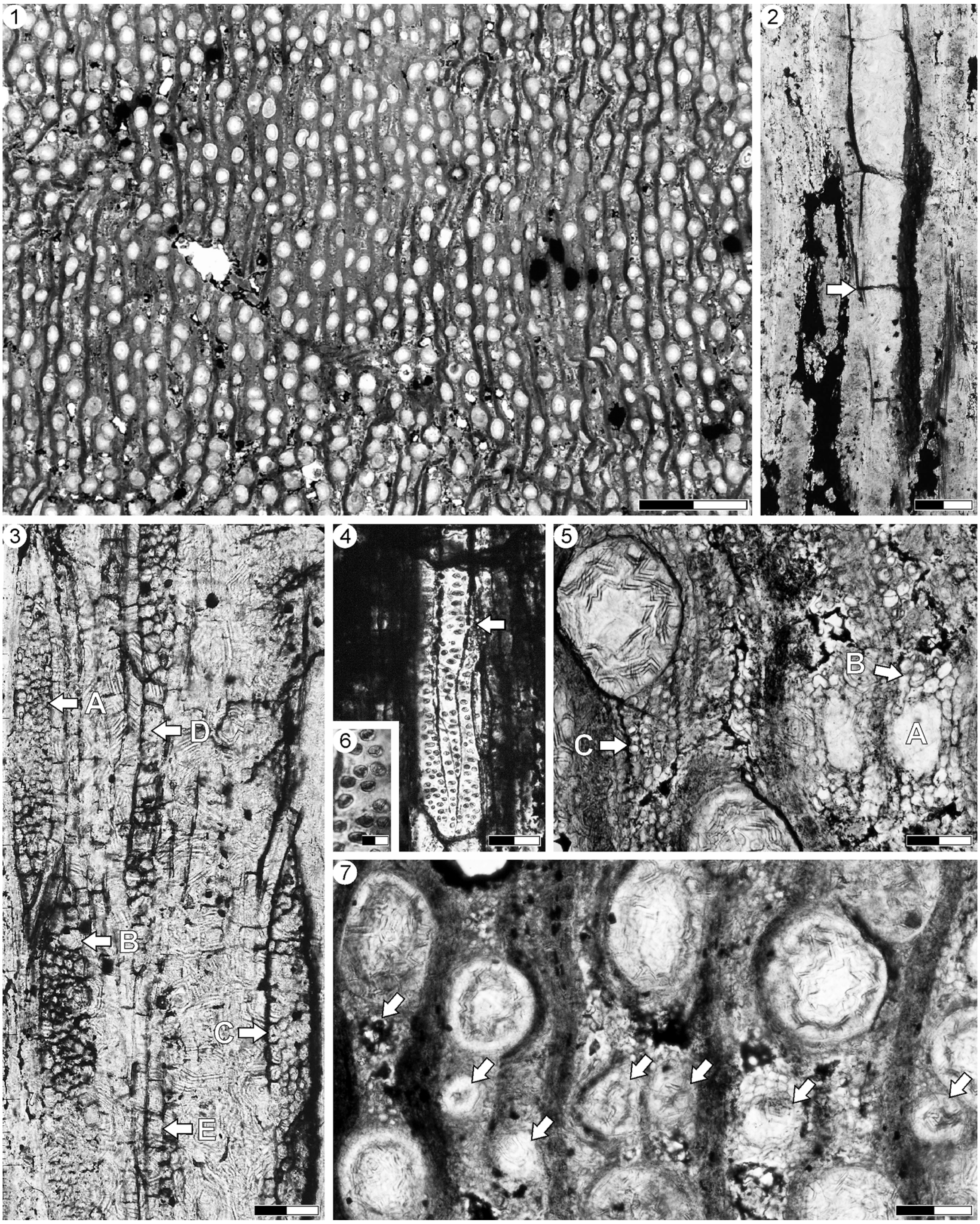


Plate VI. *Woburnia porosa* Stopes 1912 supposedly from the Cretaceous (Aptian) Lower Greensand Group near Woburn Sands, southern England, but its age and provenance have long been disputed (Crawley, 2001); Natural History Museum (London), accession number NHM V.5254a–i.

Plate VI. *Woburnia porosa* Stopes 1912 supposedly from the Cretaceous (Aptian) Lower Greensand Group near Woburn Sands, southern England, but its age and provenance have long been disputed (Crawley, 2001); Natural History Museum (London), accession number NHM V.5254a–i.

1. Growth rings absent, vessel arrangement diffuse-porous, TS. Scale bar: 2 mm
2. Simple perforation plates (arrow) and short vessels, TLS. Scale bar: 280 µm
3. Rays mostly 5-seriate (arrow A) with sheath cells present (arrows B and C); long ray tails of uniseriate cells (arrow D); axial parenchyma strands > 8 cells high (arrow E), TLS. Scale bar: 110 µm
4. Vasicentric tracheids present (arrow), showing multiseriate, alternate pitting, TLS. Scale bar: µm
5. Axial canal (A); epithelial cells and thin-walled parenchyma cells surrounding axial canal (arrow B); thick-walled fibres (arrow C), TS. Scale bar: 140 µm
6. Vessel – tracheid pitting, TLS. Scale bar: 10 µm
7. Axial canals (arrows) present in long tangential lines, TS. Scale bar: 100 µm

CHAPTER 7: DISCUSSION

7.1. INTRODUCTION

The present thesis has studied the global distribution of Cretaceous vegetation based on biogeographic analyses of the fossil record. The purpose of this final chapter is to discuss the possible effects of paleogeography, climate and evolution on the distribution and composition of Cretaceous vegetation biomes. In this context, three major subjects are herein discussed, (1) the Cretaceous biome distribution, (2) the impact of angiosperm diversification in vegetation composition, (3) biogeographic analyses and the interpretation of Cretaceous biomes.

7.2. CRETACEOUS BIOME DISTRIBUTION

The analyses of floras from high latitude sites of the Northern (e.g. Herman and Spicer, 1996) and Southern Hemispheres (e.g. Cantrill and Poole, 2005; Francis, 1999) has provided extensive evidence for warm polar climates and global productivity centered at middle and high latitudes (Chapter 4; Spicer et al., 1993; Spicer and Herman, 2010).

During the Early Cretaceous high latitudes were dominated by warm-temperate (?subtropical) forest (Douglas and Williams, 1982; Falcon-Lang and Cantrill, 2001, 2002). Results of the global analysis of fossil wood suggest cupressoids and pinoids were more abundant at higher latitudes of the Northern Hemisphere, while araucarioid and podocarpoid dominated Southern Hemisphere where pinoids were completely absent and cupressoids were very few. In the latest Early Cretaceous no evidence of angiosperms wood is found at high latitudes; however, flowering plants were present as broad-leaved (Spicer et al., 1993) probably as elements of the understorey vegetation.

Early Cretaceous forests located at the mid-latitude warm humid belt show a similar composition to the temperate forests, being araucarioid and podocarpoid slightly more dominant at mid latitudes in the Southern Hemisphere compared to cupressoid and pinoid, while the occurrence of conifer superfamilies at mid latitudes in the Northern Hemisphere is more balanced. The presence of angiosperm wood at mid-latitudes starts to become stronger during the Albian–Cenomanian forming part of a dry-tropical (seasonal) mixed forest found in fossil floras from North America (Tidwell and Thayn, 1985), Portugal (Mendes et al., 2011), and China (Takahashi and Suzuki, 2003). The increasing abundance of angiosperm pollen during the late Barremian–Albian interval also reflects the initial radiation of flowering plants into mid-latitude floras (Heimhofer et al., 2005).

During the Early Cretaceous a successful arid ecosystem, that probably has no modern analogue, populated the dry subtropical equatorial belt (Chumakov et al., 1995; PALEOMAP project, 2001-present). Several records of araucarioid and podocarpoid wood and many occurrences of meso- and megafossils of cheirolepid conifers, as well as the presence of evaporites and calcretes (Hay and Floegel, 2012) suggest the existence of open semiarid woodlands. The few records of angiosperm wood in the equatorial region during the Early Cretaceous, as well as low pollen percentages (Heimhofer and Hochuli, 2010) suggest they were not abundant.

In contrast with the Early Cretaceous biome configuration, the Late Cretaceous wood distribution suggest an important expansion of the warm humid belt towards the equator and the appearance of a humid tropical biome supported by the presence of bauxite, laterite and coals (PALEOMAP project, 2001-present) as well as the record of anoxic events (Arthur and Schlanger, 1979; Jenkyns, 1980). This major shift from dry-arid seasonality to humid tropical is supported by the near-complete disappearance of cheirolepid conifers from low latitude and their occurrence in humid lacustrine environments at mid-latitudes (Gomez et al., 2002; Mendes et al., 2012). The higher efficiency of water transport from the substrate to the atmosphere by angiosperms was possibly related to the marked change of seasonality and the ecological shift in equatorial latitudes (Boyce et al., 2010). This is also observed in the withdrawal of cupressoid and pinoid conifers to middle and high latitudes. Likewise, araucarioid and podocarpoid previously codominant in equatorial regions were replaced by angiosperms indicated by a significant increase of fossil wood occurrences during the latest Cretaceous.

On the other hand, angiosperm wood distribution reaches highest latitudes of both hemispheres while they become dominant in terms of diversity and abundance at tropical low- and mid-latitudes during the Turonian–Santonian. Subsequently, Bennettitales, Caytoniales, and Cheirolepidiaceae all became extinct in the Campanian–Maastrichtian following a long decline (Knoll, 1986; Lupia et al., 1999; Van der Ham et al., 2003) probably replacement by angiosperms and their better ability to adapt to the changing temperatures and/or atmospheric changes (de Boer et al., 2012; McElwain et al., 2005). Although a gradual decline in terrestrial MAT occurred during the latest Cretaceous (Prince and Grimes, 2007) productivity remained centered at high polar latitudes occupied by a mixed conifer forest under a regime of high precipitation and humidity (Spicer and Herman, 2010).

7.3. THE IMPACT OF ANGIOSPERM DIVERSIFICATION IN VEGETATION COMPOSITION

Evidence suggests early angiosperms were limited to disturbed and/or aquatic sites (Feild and Arens, 2007; Friis et al., 2011) showing low levels of diversity and biomass (Taggar and Cross, 1997) suggesting that they were suppressed by gymnosperms and ferns that still dominated most Cretaceous biomes (Berendse and Scheffer, 2009).

There is abundant research on the ecological, reproductive, anatomical and physiological advantages that facilitated angiosperms to outcompete and escape from their subordinate position. Key physiological advantages include, for example, leaves with more efficient gas exchange capabilities that increased angiosperm ability to adapt better to drastic changes in CO_2 atmospheric concentration (de Boer et al., 2012; McElwain et al., 2005; McKown et al., 2010) and higher photosynthetic efficiency (Feild et al., 2011). The development of hardwood played an essential role in nutrient transport and absorption, and thus allowing a significant increase in growth efficiency (Feild and Arens, 2007). New anatomical characters not only increased growth rates by improving hydraulic and physiological functions, in addition, the litter produced by flowering plants, which takes less time to decompose became an extra source of nutrient cycling (Berendse and Scheffer, 2009). Likewise, reproductive strategies such as the positioning of pollen and seed organs in close proximity of one another (cf. Bennettitales), the production of fleshy fruits, and coloured flowers induced further diversity and coevolution with insects (Dilcher, 2000; Doyle, 2008; Friis et al., 2011; Moreau et al., 2006) allowing more effective and faster rates of reproduction (Verdu, 2002).

These adaptations caused angiosperms to undergo a burst of diversification, which conceded an increased flexibility to adapt more effectively to global climate changes during the Cretaceous (Lloyd et al., 2008; Friis et al., 2011) probably caused by sea-level and temperature variations (Fluteau et al., 2007; Jenkyns et al., 2004), poor ocean circulation (Haq et al., 1987), effusive volcanism (Courtillot et al., 2010), which resulted in cooler episodes (Prince, 1999; Steuber et al., 2005).

Proof of this rapid expansion is evident in the higher abundance of angiosperm pollen (Lidgard and Crane, 1988; Lupia et al., 1999), as well as their ecological effect such as the change in abundance and composition of Cretaceous biomes (Chapter 4). The wider distribution of angiosperm fossil wood can be explained by a ecological turnover of previous conifer-dominated biomes at mid-latitude. For example, the biogeographic analysis of cheirolepid shows these conifers were especially abundant during the Early Cretaceous in equatorial arid regions. However, during the early Late Cretaceous, coincident with the angiosperm diversification, they nearly disappear from low latitudes and their distribution reduced to the temperate belt at mid-latitudes where later became extinct. Although it is difficult to link ecological replacement of taxa caused by direct angiosperm competition in detail, the extinction of cheirolepids could have been accentuated by the progress of angiosperm diversification and dominance of low- an mid-latitudes by the latest Cretaceous. The disappearance of the previous araucarioid-podocarpoid equatorial forest supports the idea of a major shift in the vegetation composition, probably also associated to more humid climate in this region during the Late Cretaceous (Chumakov et al., 1995). Complete dominance of flowering plants near the equator is further supported by an almost exclusive presence of angiosperm wood in Santonian–Maastrichtian localities. Moreover, the global analysis of fossil wood indicate angiosperms assumed dominance in most terrestrial biomes by the end of the Cretaceous (with exception of the polar forest) at the same time that conifers suffered a significant reduction in abundance and were relegated to more extreme climatic conditions at high elevations and polar latitudes, where they continue to dominate today (Taggart and Cross, 1997).

Accordingly, the global patterns of distribution of Cretaceous biomes show a rapid ecological diversification of flowering plants probably assisted by environmental opportunities. There is compelling evidence that angiosperm diversification strongly altered climate by accelerating the water cycle (Boyce et al., 2010). The further expansion of angiosperms during the Cretaceous represents a marked evolutionary turnover from gymnosperm to angiosperm-dominated biomes within a time span of about 30 Ma (Heimhofer and Hochuli, 2010).

7.4. BIOGEOGRAPHC ANALYSIS AND THE INTERPRETATION OF CRETACEOUS BIOMES

Palaeobiogeography is a tool derived from the original biogeography school developed by Alfred Russell Wallace in the 19th Century. It studies the physical environment and how it shaped the distribution of the world's species, that is to say, it analyses biomes and their changes across space and time using palaeogeographic reconstructions and fossil species to describe their interactions (Lieberman, 2000). Palaeobiogeographic studies also investigate climate variations as a result of the continents being in different places as another factor for the presence of different plants and animals (Brooks, 1985).

This thesis employed different biogeographic techniques to analyse the compilation of many years of publications and palaeontological research, combined with climate-sensitive sediment data, to determine biomes. Palaeoclimatic zones obtained by this analysis indicate that major changes in abundance and composition affected the configuration and distribution of Cretaceous biomes.

General patterns that emerge from the analysis of the fossil wood record and that of the cheirolepid conifers reveal an Early Cretaceous dominated by dense and abundant high-latitude conifer forest growing in seasonal, temperate cool climates. Tropical-humid mixed forest living at mid-latitudinal belts and a subtropical-arid equatorial region dominated by thermophilous conifers. Late Cretaceous middle and high latitudes remain similar to those during the Early Cretaceous but with an increasing presence of angiosperms, although still not dominant. While the equatorial region suffered a major shift from dry-arid to warm-humid biome possibly linked to global climatic events (e.g. Fluteau et al., 2007; Courtillot et al., 2010) and angiosperms radiation (Lupia et al., 1999).

It is well known global biome reconstructions tend to have limitations due to biases related to model precision, palaeogeographic inconsistencies and collection biases (Rees et al., 2000; Salzmann et al., 2008). Some authors consider the information obtained from the fossil record is limited because its fragmented nature does not represent the total organisms that actually lived (Peters and Foote, 2002) and might as well show a geological rather than a biological signal (Raup, 1972; Smith 2001). Therefore it is important to evaluate the completeness of the fossil record to understanding evolution over long timescales (Foote and Sepkoski, 1999). The overview of vegetation distribution here presented is subjected to possible biases such as the larger amount of researchers working in the Northern Hemisphere compared to the lesser research done in the Southern Hemisphere and the higher interest in studying early angiosperms compared to the difficult task of working with conifers, cycads, and pteridophytes (Eklund, 2003). In addition, there are large portion of Cretaceous sedimentary rocks in remote regions (e.g. the Amazon, the Northern Territories of Canada, and the Middle East) not sampled well enough due to difficult access (Fig. 4.1).

On the other hand, the influence of biases in the interpretation of paleontological evidence has been proved to depend on the approach, discernment and type of analyses applied to fossils (Benton and Harper, 2009). For example, phylogenetic–stratigraphic analyses suggest that studies approached at a genera/family taxonomic scale are adequate and capable of showing patterns of diversity, extinction or origination of life through time (Benton et al., 2000; Foote and Sepkoski, 1999).

Misidentification caused by synonymy and the presence of plesiomorphic characters in fossil wood is frequent in the taxonomy of Early Cretaceous gymnosperms (Bamford and Philippe, 2001). Consequently, the grouping of conifers as morphotypes (i.e. pinoid araucarioid, cupressoid, and podocarpoid) allows avoiding morphological variability problems that arise when applying a strict taxonomic approach (Zeigler et al., 1996). Although climatic signals given by certain fossil species tend to be less strong using this approach, it is still possible to reach reliable ecological conclusions. For example, the distribution of pinoid fossil wood, which is restricted to the northern hemisphere since Cretaceous times, agrees with the previous hypothesis of the origin of Pinaceae family at Arctic high latitudes (LePage, 1999). Hence supporting the idea of conifer families maintaining ecological preferences through geological time.

Although problematic samples are common in the literature and palaeobotanical collections, the use of biogeographic techniques combined with anatomical comparisons and taphonomic observations allow a clarification of their age, provenance and affinity. The case of *Woburnia porosa* Stopes, once considered the earliest evidence for angiosperm wood, represents a good example where the presence of modern characters as well as the geographic distribution of other fossils of very similar anatomy helped to resolve this taxonomical problem. The use of these tools allows us to further improve the quality of fossil data, which helps us to develop more accurate biome reconstructions.

The importance of global biogeographic analyses of fossil evidence therefore resides in the valuable information on general evolutionary trends that allow us to obtain a deeper understanding of the Earth System biologic and climatic processes at a geological time-scale.

CHAPTER 8: CONCLUSION AND FUTURE WORK

8.1. CONCLUSIONS

The global biogeographic analysis of Cretaceous fossil wood indicate that the loss of conifer abundance and the reduction of their distribution in the Late Cretaceous is parallelled by the rise of co-occurring angiosperms, which increased rapidly and expanded their distribution towards low and high latitudes. Angiosperm dominance in these regions is probably related to the increased (x2) biome productivity and to their various ecological adaptations and flexibility to adjust to climate variations during the Cretaceous.

The distribution of Cretaceous Cheirolepidiaceae fossils show these conifers were related to sediments indicative of dry-hot environments during the Early Cretaceous where they were abundant. In the Late Cretaceous they are often associated with humid environments suggested by their common occurrence in bauxite, kaolinite and coal. Although in lower abundance, they also inhabited humid tropics at mid-latitudes. The biogeography of cheirolepid conifers indicates they were not restricted to dry-hot environments as previously suggested, therefore, a cautious usage of cheirolepid fossils as indicators of aridity is recommended.

The implementation of anatomical and biogeographic analyses on fossil samples improves the quality of data offered by the fossil record of plants. They represent an essential tool for developing biome reconstructions with better taxonomic and geographic resolution. Hence, a re-examination of other problematic specimens of Cretaceous wood is recommended.

The biome reconstruction here presented offers a biogeographic frame of reference to contrast previous ideas and to integrate its new findings with computer climate models in order to develop more detailed global assessments of Cretaceous vegetation in the future.

8.2. FUTURE WORK

During the development of the present thesis it became evident that the task of a global inventory of Cretaceous wood was an immense goal probably more suitable if planned for a lifetime of research. The quality and validity of these types of analyses imply exhaustive investigations for each single record included in the dataset, which frequently implies a great amount of effort, time, logistics and resources that exceed those available for most doctorate candidates. Therefore, the final results of this thesis may leave many tasks still to be completed. The following pages explain some of the strategies, improvements and considerations that would improve the quality of biogeographic analyses of Cretaceous biomes as well as would offer new information on Cretaceous plants and palaeobotany in general.

8.2.1. Further research in targeted museums and collections

Biogeographic analysis carried on Cretaceous wood reveal that although there are a large number of studies on fossil wood that allow us to have a good general understanding of Cretaceous biomes, there is a significant amount of published literature that for accessibility issues has been left out of this study. Among these difficulties, for example, are the many journals (e.g. Palaeontographica) that their content has not been published online but there is also a vast amount of literature in other languages such as Chinese and Russian, that if carefully examined, may help to fill large gaps of data seen in the global map of fossil wood distribution (Fig. 4.1). Collaboration with colleagues from those and other countries would importantly contribute to develop a more comprehensive assessment of fossil woods at a global scale by completing existing resources such as InsideWood and paleodb.org with other important databases of difficult access (e.g. Chumakov et al., 1995).

Further targeted visits to museum and institutions such as the Natural History Museum in Paris, the Orlov Paleontological in Museum, Moscow, The Field Museum in Chicago, the Naturhistorisches Museum in Basel, and the Palaeobotanical Collection collection Rossmann in Bayreuth Germany. Although targeted collecting excursions would increase the amount of data, sometimes they involve more funding and human resources compared to visits to museums and collections, where large amounts of non-studied fossils are found. Most of the time non-classified fossils are available for lease upon request for students to take them back to their home university palaeontological lab for more detailed analyses.

Another possible bias is the limited amount of data reported from the equatorial region, possibly due to the infrequent exposure of Cretaceous rocks and poor fossil preservation in tropical regions. However, very little is known about the productivity Cretaceous equatorial ecosystems and fossil assemblages. Although tree-rings are not commonly found in wood of tropical species, the various techniques of paleoecology have not been applied to the few localities known in the equatorial region. New studies aimed to obtain climatic parameters from fossil plants found in low latitudes in order to assess the ecosystem productivity in the equatorial region would cover a large gap of knowledge in the current understanding of Cretaceous biomes.

New data of Cretaceous equatorial ecosystems would offer quantitative evidence of productivity levels of the equatorial province and thus allow a better assessment of biome distribution under greenhouse climate regimes.

8.2.2. Taxonomy of Cretaceous plants

The compilation of studies on Cretaceous woods reveals the need of taxonomical consensus among palaeobotanists when classifying fossil material, but at the same time when observing the variability of anatomic characters countless complications tend to arise. The study of small groups of wood morphotypes to document and quantify the variability based on the standard IAWA lists of characters (IAWA), PCA and Cluster Analysis seem a plausible solution to this problem.

New studies employing this approach could significantly improve data quality expand the record of fossil wood currently available in InsideWood Database. Pinaceous conifers, for example, represent an adequate morphologic group to test this idea since the numbers of Cretaceous fossils related to this group are small and relatively well defined by certain anatomic characters.

This system where new descriptions of fossil woods are standardized and incorporated to InsideWood database improve existing data and therefore its capabilities for wood identification, allowing a quantitative approach in the analysis of complex groups. Anatomical data generated in this research, such as dipterocarp woods, as well as some records of the fossil would database could be incorporated in IAWA and Palaeobiology databases to complement and update their current records.

8.2.3. Biome reconstructions

Further research on Cretaceous biomes including Chumakov's climate-sensitive sediment database and information of other museums, collections and missing publications in combination with the GIS analysis employed by Butler et al., (2009, 2010) would improve significantly biogeographic analyses. Their approach would implement 6 time bins for the Cretaceous allowing more accurate plant association assessments based on detailed maps and precise palaeocoordinate calculation. This would also produce sufficiently large sample sizes to allow meaningful statistical comparisons and analyses. Using this method, the correlation between climate-sensitive sediments and fossil wood, cheirolepid conifers and other Cretaceous plants would not only offer detailed biogeographic information to contrast with our current understanding of Cretaceous climate and vegetation, but it will also allow us to investigate possible correlations with geographic patterns reported for other organisms such as dinosaurs, mammals and insects.

In addition, detailed assessments of sampling biases such as the significance of the number of fossil plants recovered from marine sediments, as well as the problems of using very large time bins (~60 ma). Also, the association of fossil plant occurrences with climate-sensitive sediments needs to be addressed. For example, it is well known that large coal deposits tend to be overrepresented in the fossil record due to taphonomic megabias and rapid deposition rates (Falcon-Lang, 2009) and thus some considerations should be taken when compared to sediments of longer depositional time frame (e.g. evaporites). This is also de case for biome productivity assessment based on tree-ring that could also be improved by adding new measurements from the literature and museum visits, but more importantly is to test either if results are affected by ecological biases such as CO_2 fertilization raised by Brienen et al., (2012).

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APPENDIX

APPENDIX 1. Database of Cretaceous fossil wood

Database in PDF file (Appendix 1) to be found within the enclosed CD at the end of this thesis.

APPENDIX 2. Maps of Cretaceous wood distribution

The following maps show the distribution of conifers and angiosperm groups (Chapter 4) in more detail. Small black squares represent other localities within the same time-bin where the group is not present.

T1, Berriasian–Hauterivian (145.5–125 Ma); T2, Aptian–Albian (126–99 Ma); T3, Cenomanian–Santonian (99–83 Ma); T4, Campanian–Maastrichtian (84–65.5 Ma).

Angiosperm distribution T2

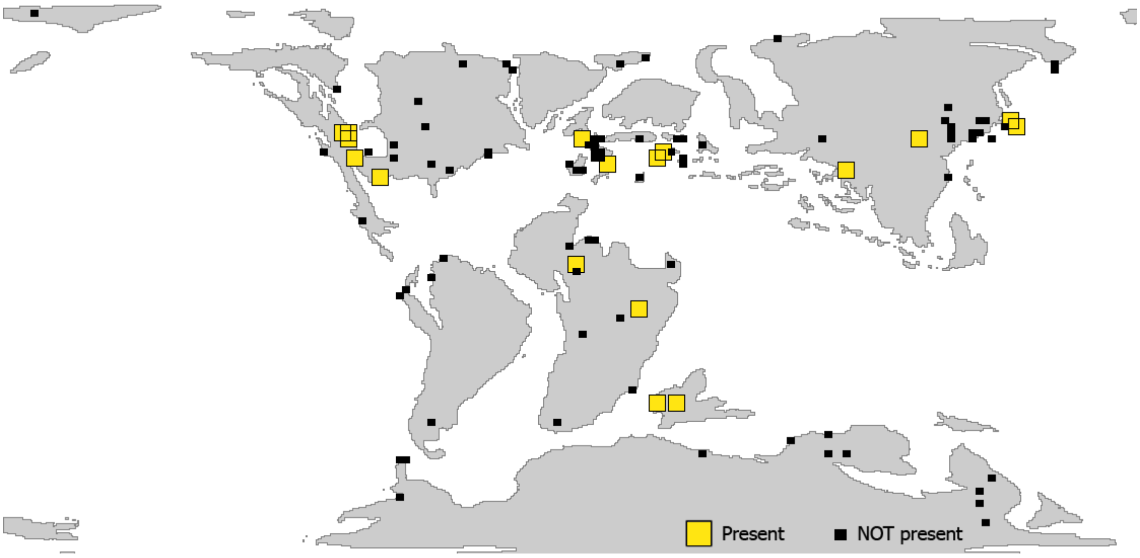

Figure 4.9. Angiosperm wood distribution for T2, Aptian–Albian (126–99 Ma).

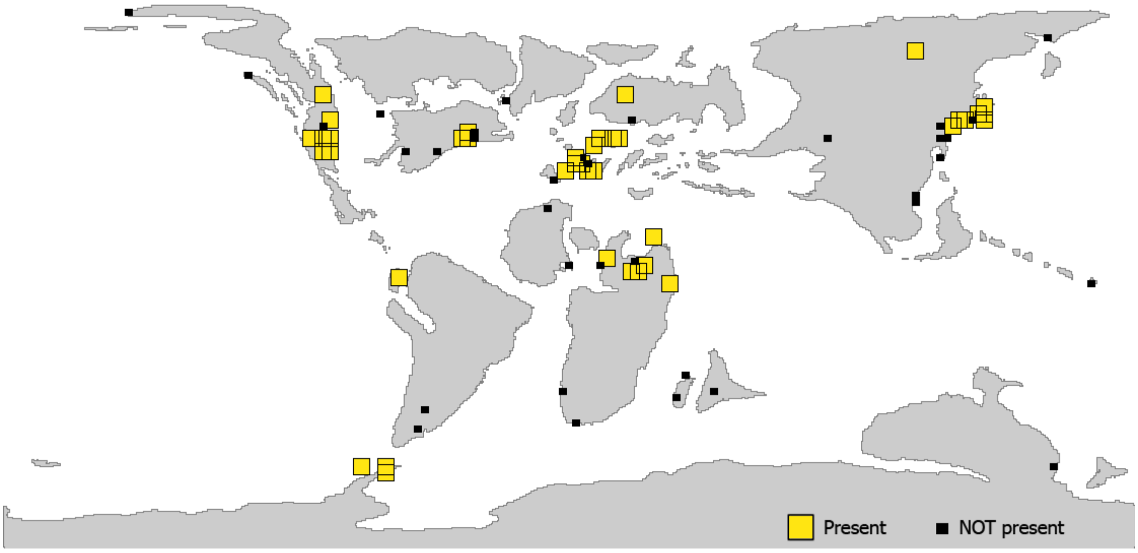

Figure 4.10. Angiosperm wood distribution for T3, Cenomanian–Santonian (99–83 Ma).

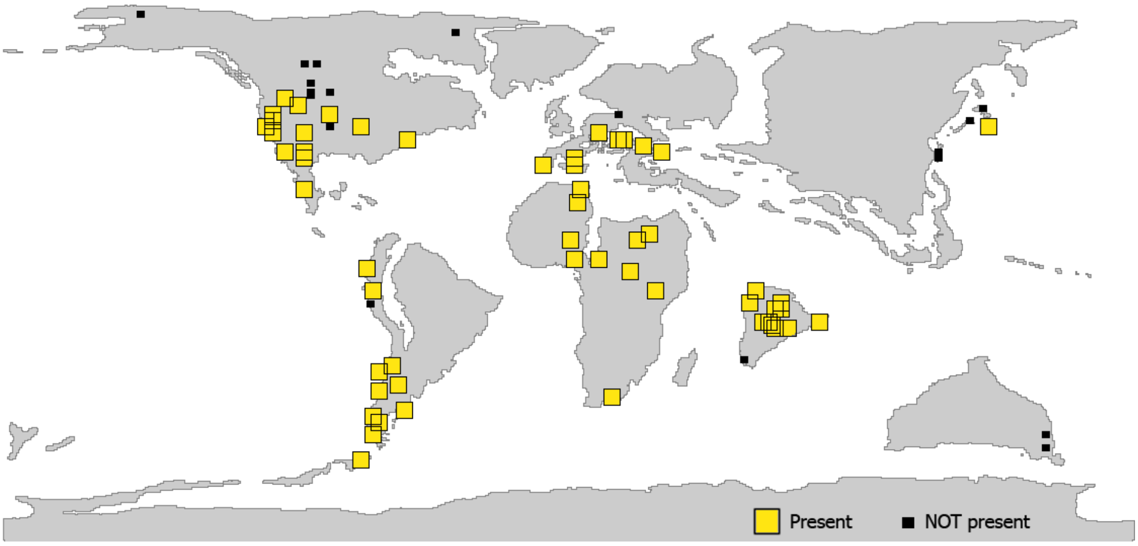

Figure 4.11. Angiosperm wood distribution for T4, Campanian–Maastrichtian (84–65.5 Ma).

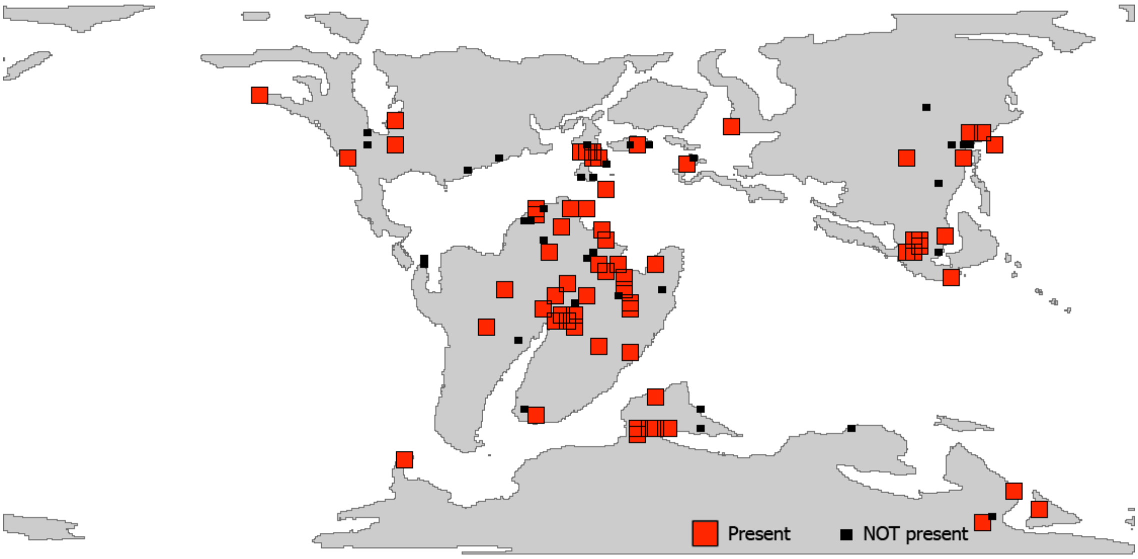

Figure 4.12. Araucarioid wood distribution for T1, Berriasian–Hauterivian (145.5–125 Ma).

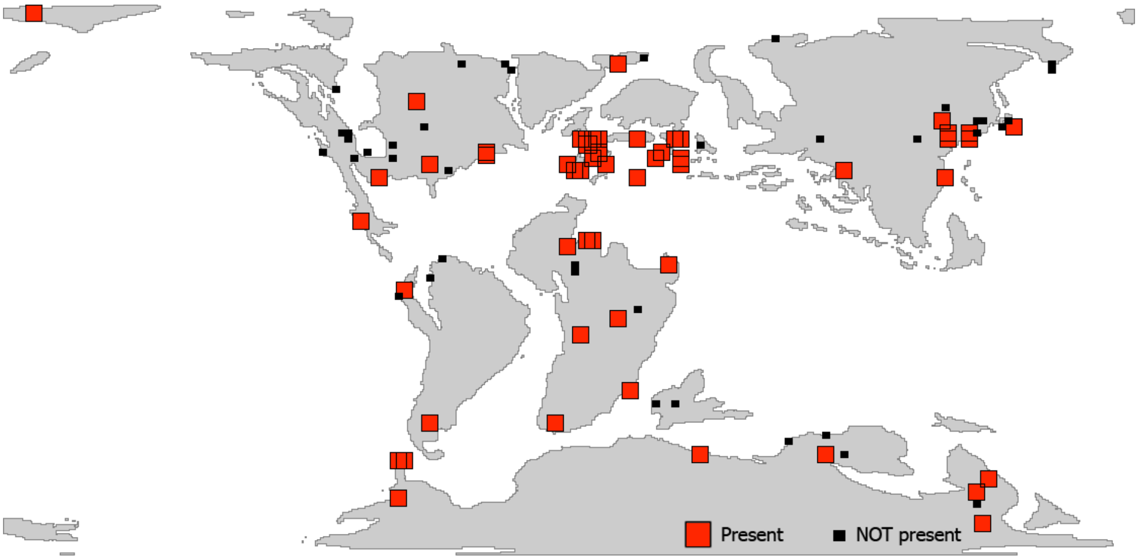

Figure 4.13. Araucarioid wood distribution for T2, Aptian–Albian (126–99 Ma).

Araucarioid wood T3 and T4

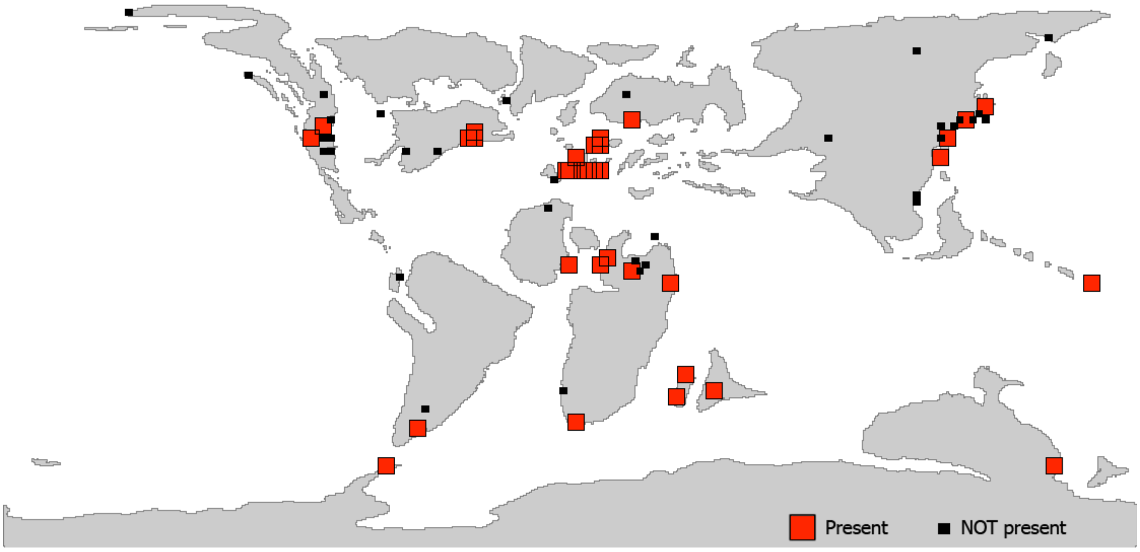

Figure 4.14. Araucarioid wood distribution for T3, Cenomanian–Santonian (99–83 Ma).

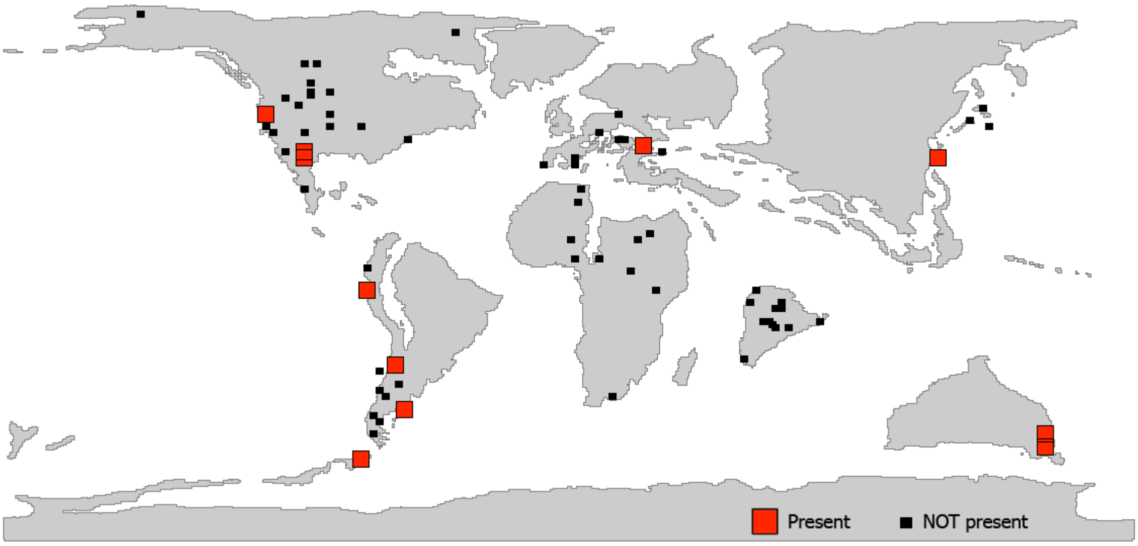

Figure 4.15. Araucarioid wood distribution for T4, Campanian–Maastrichtian (84–65.5 Ma).

Cupressoid wood T1 and T2

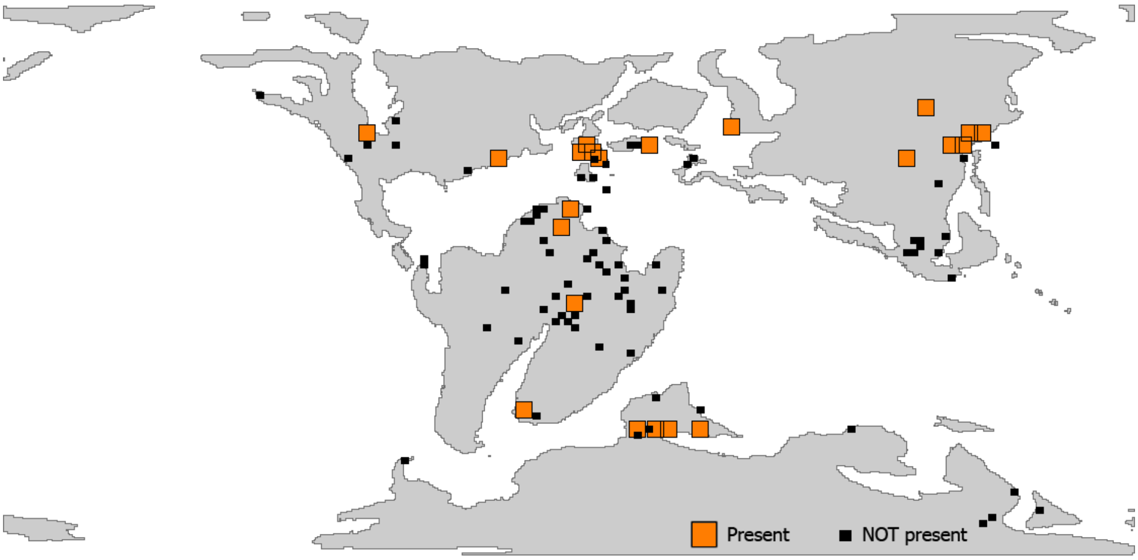

Figure 4.16. Cupressoid wood distribution for T1, Berriasian–Hauterivian (145.5–125 Ma).

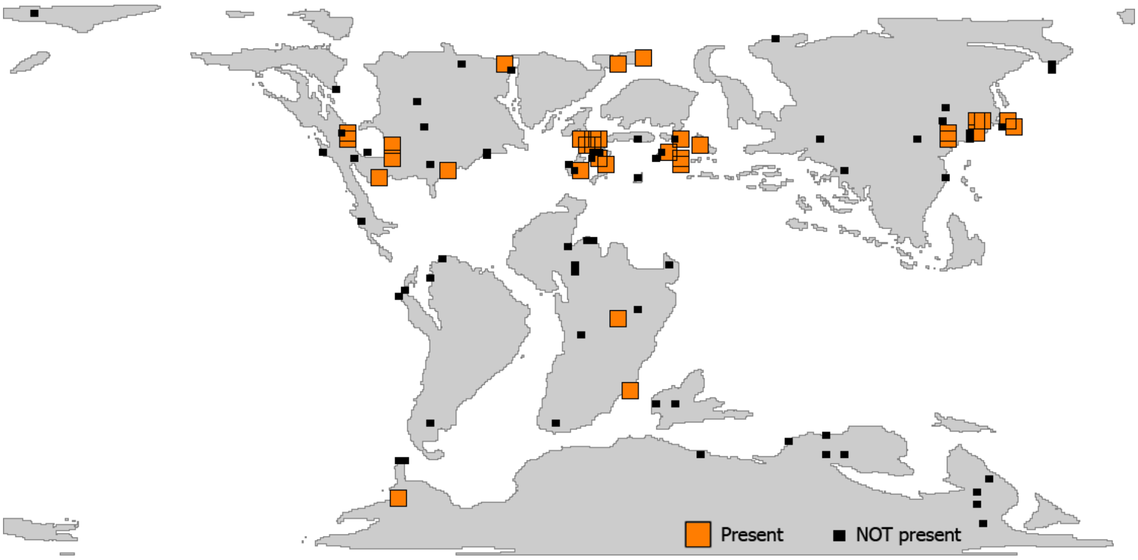

Figure 4.17. Cupressoid wood distribution for T2, Aptian–Albian (126–99 Ma).

Cupressoid wood T3 and T4

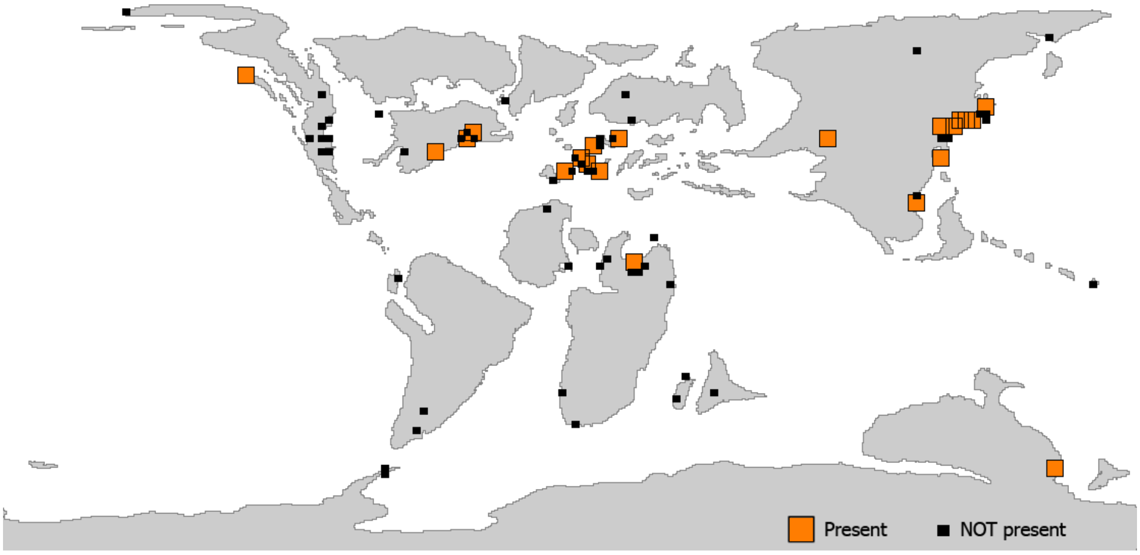

Figure 4.18. Cupressoid wood distribution for T3, Cenomanian–Santonian (99–83 Ma).

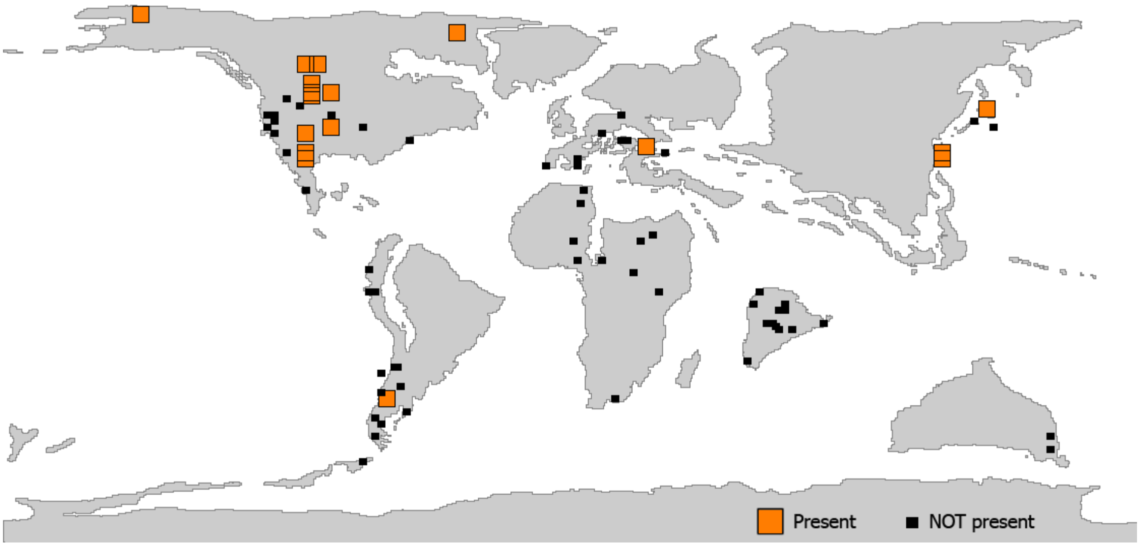

Figure 4.19. Cupressoid wood distribution for T4, Campanian–Maastrichtian (84–65.5 Ma).

Pinoid wood T1 and T2

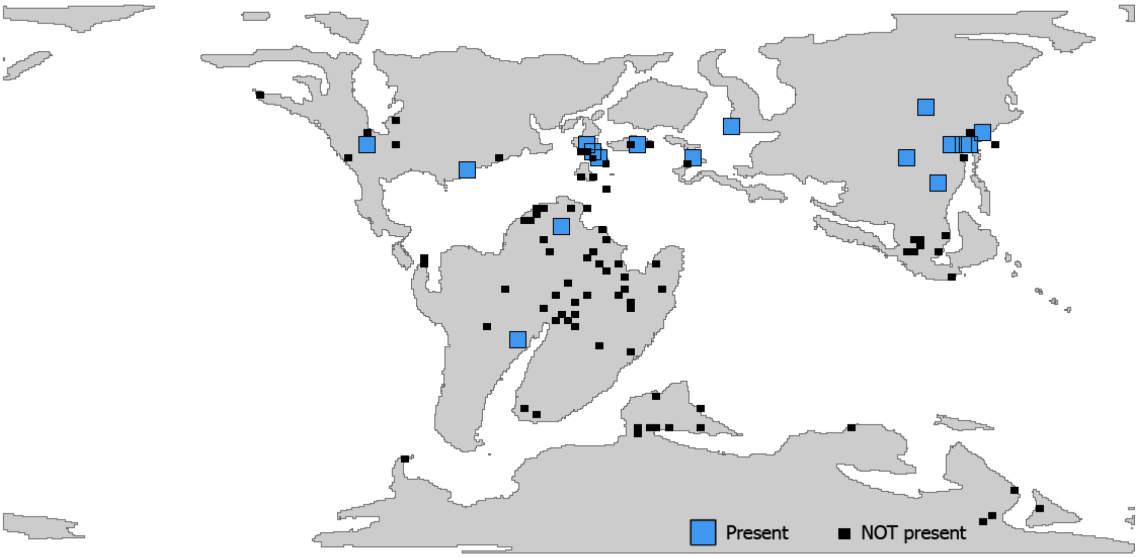

Figure 4.20. Pinoid wood distribution for T1, Berriasian–Hauterivian (145.5–125 Ma).

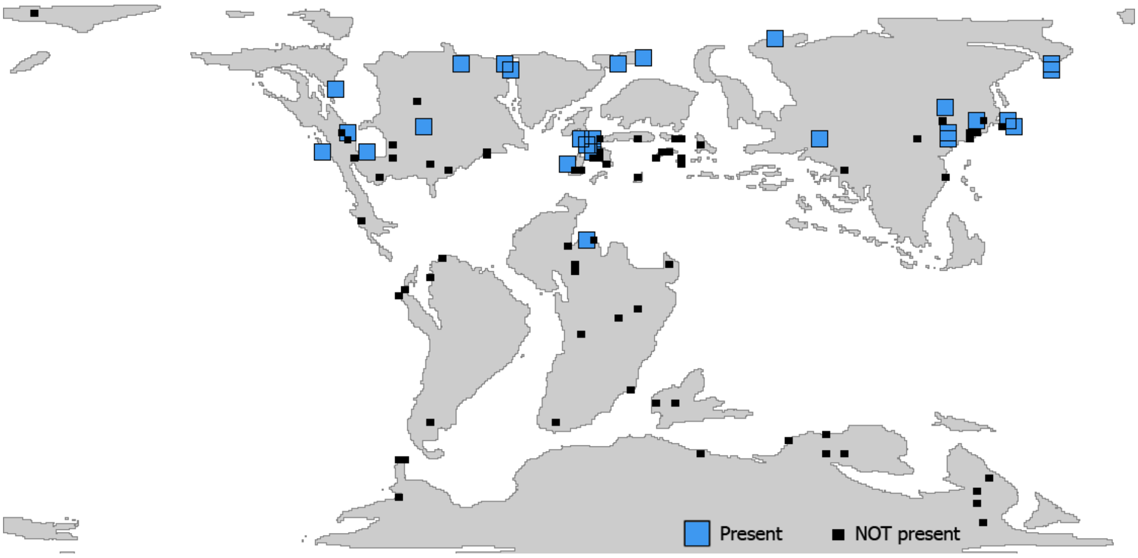

Figure 4.21. Pinoid wood distribution for T2, Aptian–Albian (126–99 Ma).

Pinoids wood T3 and T4

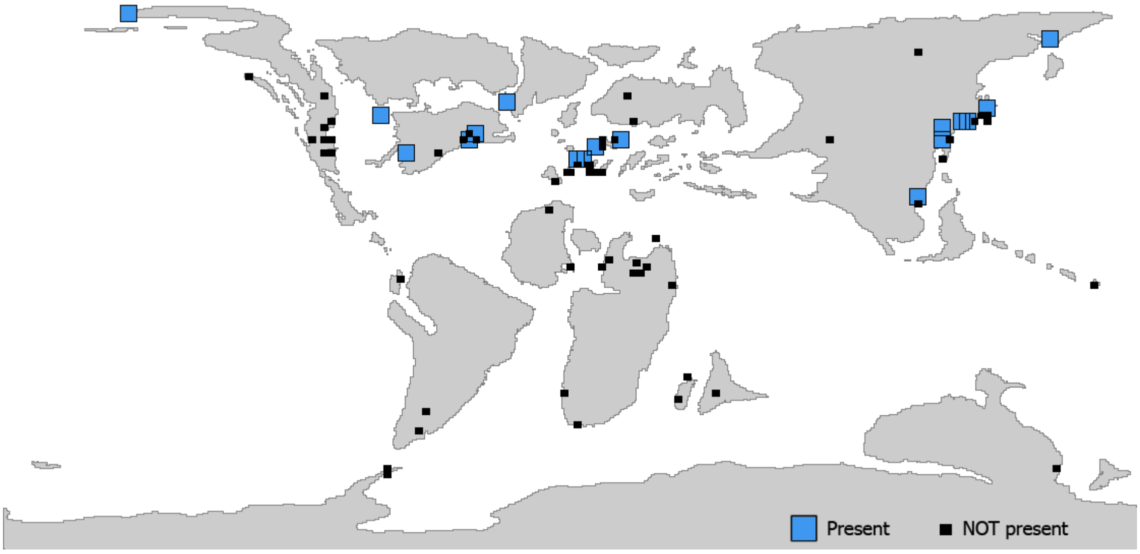

Figure 4.22. Pinoid wood distribution for T3, Cenomanian–Santonian (99–83 Ma).

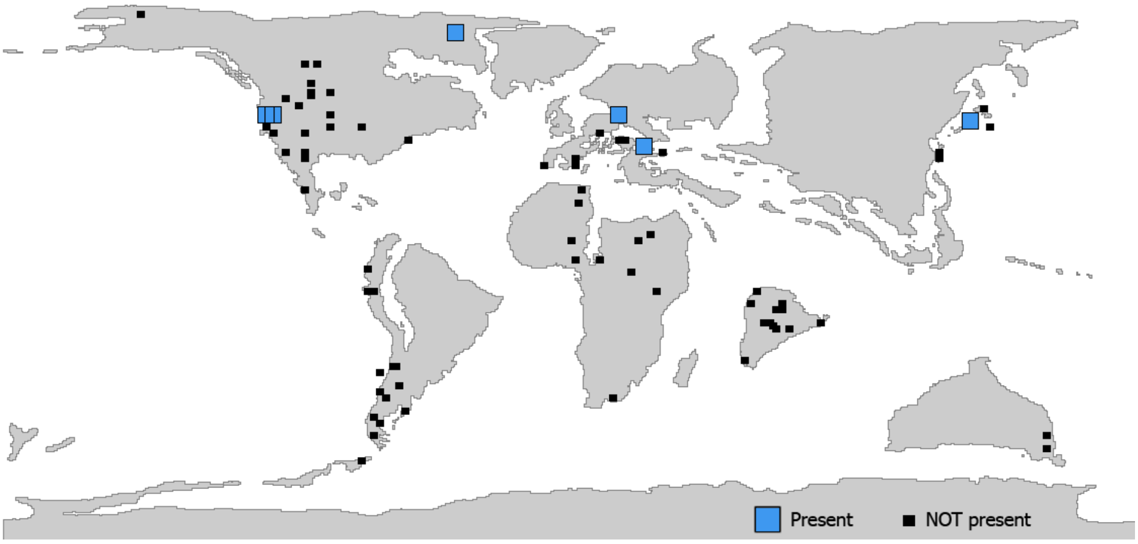

Figure 4.23. Pinoid wood distribution for T4, Campanian–Maastrichtian (84–65.5 Ma).

Podocarpoid wood T1 and T2

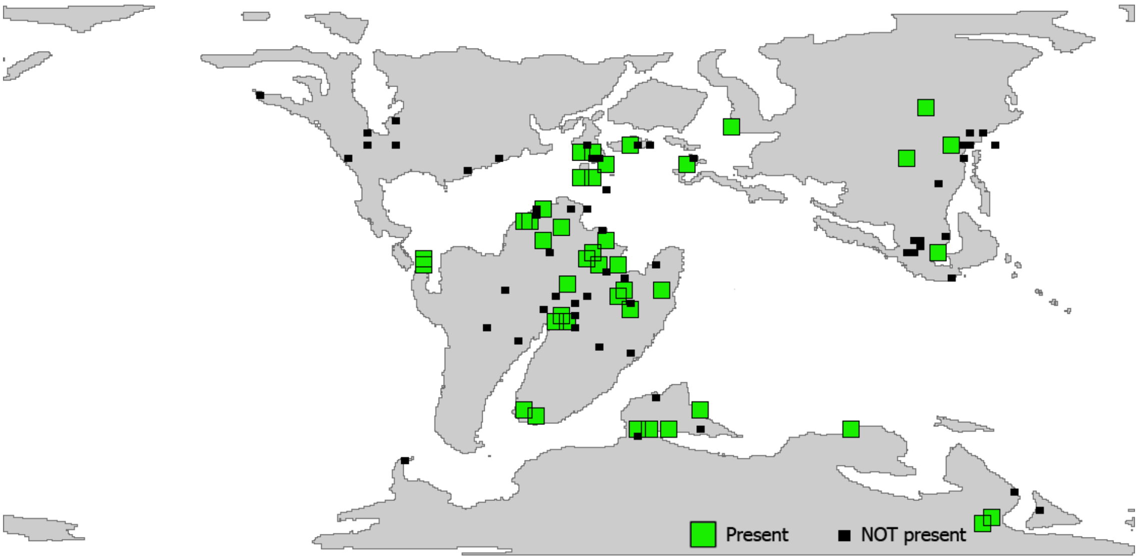

Figure 4.24. Podocarpoid wood distribution for T1, Berriasian–Hauterivian (145.5–125 Ma).

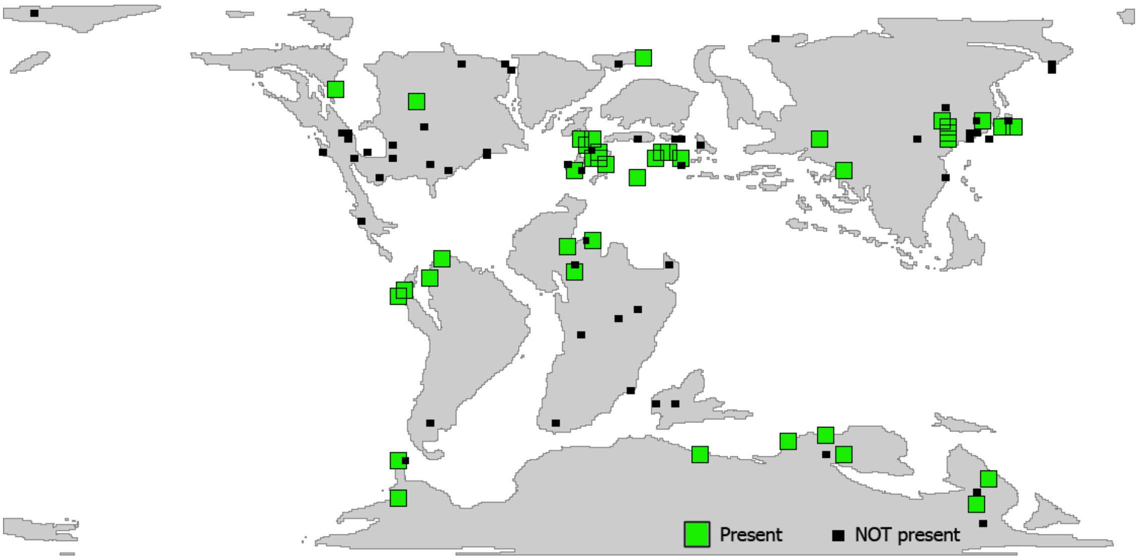

Figure 4.25. Podocarpoid wood distribution for T2, Aptian–Albian (126–99 Ma).

Podocarpoid wood T3 and T4

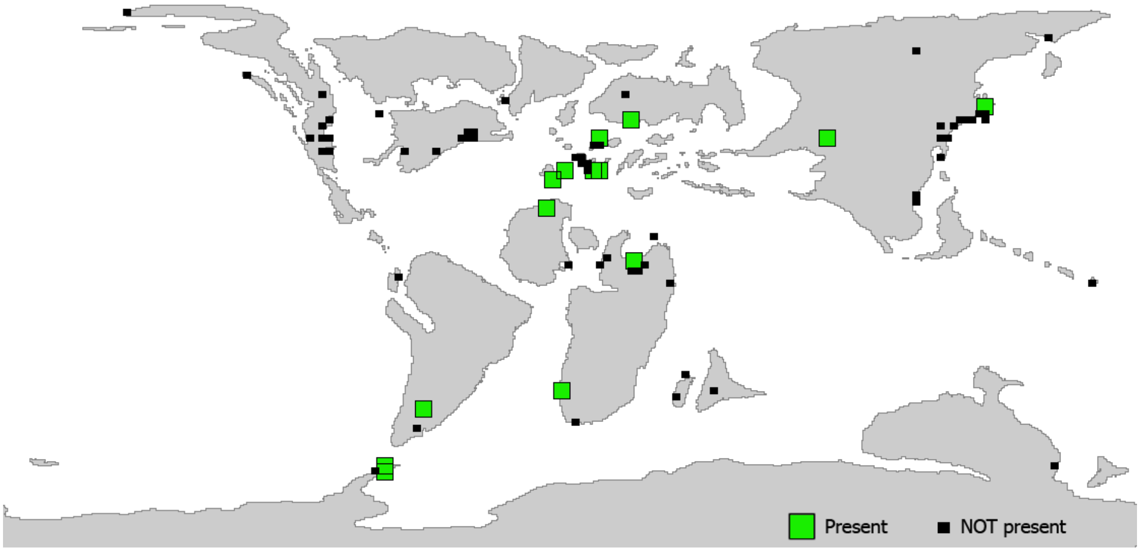

Figure 4.26. Podocarpoid wood distribution for T3, Cenomanian–Santonian (99–83 Ma).

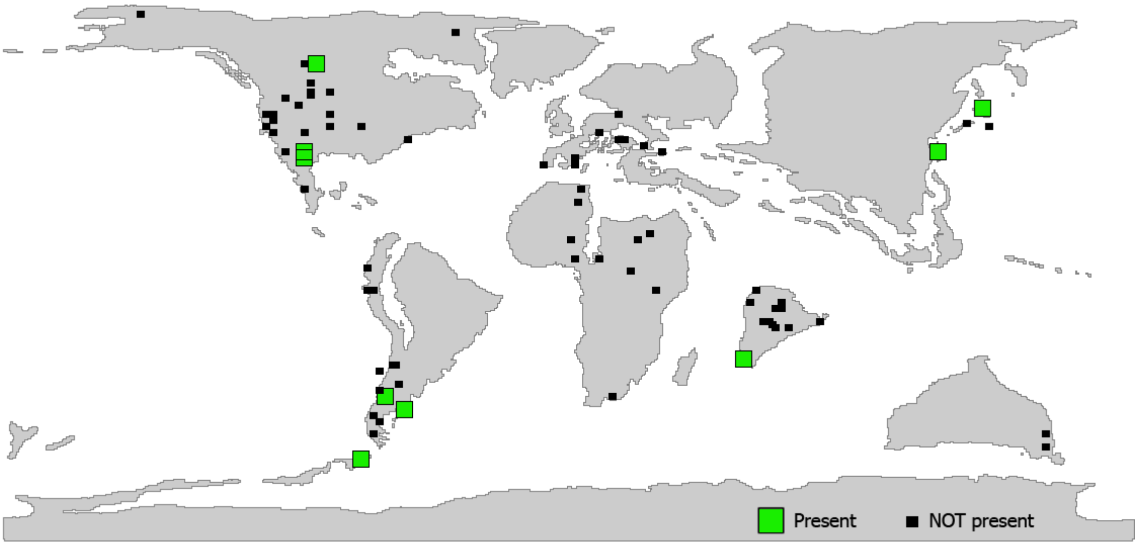

Figure 4.27. Podocarpoid wood distribution for T4, Campanian–Maastrichtian (84–65.5 Ma).

APPENDIX 3. Database of cheirolepid conifers

Database in PDF file (Appendix 3) to be found within the enclosed CD at the end of this thesis.

APPENDIX 4. Character matrix for the PCA analysis of extant dipterocarp woods

Character matrix in PDF file (Appendix 4) to be found within the enclosed CD at the end of this thesis.

APPENDIX 5. Character matrix for the PCA analysis of fossil dipterocarp woods

Character matrix in PDF file (Appendix 5) to be found within the enclosed CD at the end of this thesis.

APPENDIX 6. Database of the fossil wood record of Dipterocarpaceae

Database in PDF file (Appendix 6) to be found within the enclosed CD at the end of this thesis.