Middle to Late Miocene terrestrial biota and climate

by

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Declaration of Authorship

The candidate confirms that the work submitted is his/her own, except where work which has formed part of jointly-authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

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Abstract

The Middle to Late Miocene (15.97 – 5.33 Ma) is considered a time interval that was warmer than today. It is also a time interval of significant cooling. The aim of this study is to provide a new global view of this 10 Ma interval of global warmth and climate change, through the use of vegetation, mammals and modelling. The study begins in the UK and uses palynology to assign, the previously poorly constrained, Brassington Formation to the Tortonian. The pollen of the Brassington Formation shows the existence of a warm-temperate mixed forest in the UK with a mean annual temperature of 16°C – roughly twice the modern mean annual temperature. Using this fossil site, as well as 633 others, the global biome distributions are determined for the Langhian, Seravallian, Tortonian and Messinian stages. The data show that the Langhian represents a world significantly warmer than today. Cooling occurred through the Seravallian and Tortonian and by the Messinian, this cooling trend had eliminated warm – temperate mixed forests from the western USA and Australia and had formed mid – latitude deserts. Using the palaeobotanical data for the Tortonian age a data – model hybrid vegetation map has been made, suitable for use in palaeoclimate modelling studies. This is then used as a boundary condition in the HadAM3 climate model to show influence of vegetation on the Tortonian climate. Finally the palaeoecology of Late Miocene mammals is investigated to develop a new proxy for vegetation. The co–occurrence technique uses the biome tolerances of Late Miocene mammals to reconstruct regional vegetation. This has been successfully used to add further details to the vegetation maps from palaeobotanical data. This study presents a new approach to exploring vegetation and climate during the Miocene and provides novel details on this dynamic epoch.

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Chapter 1

Introduction

"Everything is related to everything else," – Waldo Tobler

1.1 Project rational

As a result of anthropogenic emissions of greenhouse gases it has been predicted that by the end of the 21st Century average global surface temperatures would have increased by 1.8 to 4°C (Meehl et al., 2007). This increase in surface temperature will lead to a global climate that has not been experienced by modern civilisation. Predicting the wider implications of these higher surface temperatures is in the realm of General Circulation Models (GCMs). These numerical representations of the many systems and feedbacks of the planet are a primary source of climate change information. Understanding the full implications of this future warming is vital for providing policy makers with the evidence that they need to make society wide decisions (Füssel, 2007). However there is inherent uncertainty in many GCM predictions, which limits how useful they are to adaptation planning (Füssel, 2007; Gagnon-Lebrun and Agrawala, 2006).

Preserved within the geological record are a myriad of climates and transitional events. These events offer a unique view on the wider implications of different climates; especially relevant are those described as "warmer worlds". The Miocene (23.03 – 5.33 Ma) reflects one such warmer world. The Miocene was not only a warmer world but has been described as the "making of the modern world" (Potter and Szatmari, 2009). During the 17.7 million years of the Miocene there was: major uplift of modern mountain chains, the initiation of bipolar glaciations, the origin of modern ocean currents, the aridification of the continental interiors, an overall cooling trend of the global climate and a reduction in atmospheric CO_2 levels (Beerling and Royer, 2011; Potter and Szatmari, 2009; Zachos et al., 2008). This interplay of elements of the Earth system has created a complex story of evolving global climate. This makes the Miocene an ideal epoch for observing climates significantly different from modern and changes in climate. This thesis will provide evidence about the warmer-than-modern Miocene climates through a global study of the terrestrial biota. This will provide an improved understanding of this warmer world that is becoming more commonly used to test the predictive ability of GCMs (Herold et al., 2010; Micheels et al., 2007). In order to gauge the extent and nature of the Miocene warmth, global vegetation will be used as a proxy for climate. Today, the global distribution of vegetation is mainly controlled by temperature and precipitation, as well as, soil type, seasonality, fire and biogeographic history (Schulze et al., 2010). Vegetation is also an important component of the Earth System, mainly impacting on surface albedo (Bonan et al., 1992; de Noblet et al., 1996; Hoffmann and Jackson, 2000) and regional precipitation patterns (Shukla et al., 1990). The understanding of global vegetation, for a geological time interval, provides a view of global climate (Salzmann et al., 2008; Wolfe, 1985), a method to assess GCMs (Bradshaw et al., 2010; Herold et al., 2010; Micheels et al., 2007; Salzmann et al., 2009) and an important boundary condition for palaeoclimate modelling (Herold et al., 2010; Salzmann et al., 2008). These three main palaeoclimate uses for global vegetation will be explored within this thesis.

1.2. The Earth as a system and its dynamics during the Miocene

The idea of the Earth as a system and that all its components and processes are interrelated developed from a growing awareness that historically distinct scientific disciplines overlapped (Committee on Earth System Science, 1988). To look at the modern Earth system there are three possible techniques: 1) a macroscopic view; leaving the planet and observing it, 2) Digital mimicry; mathematically modelling the Earth using computers and 3) the Lilliput process; the construction of a fully working mini Earth (Schellnhuber, 1999). The third technique proved to be unsuccessful when attempted (Beardsley, 1995; Cohen and Tilman, 1996; Schellnhuber, 1999) and so the best options are to combine a macroscopic view with advanced computer simulations (Schellnhuber, 1999). This combination of a macroscopic view (typically from satellites) and GCM simulations is now common practice to explore the modern Earth system (e.g. Quaas et al., 2009). Applying this combination technique to Earth systems of the geological record is more challenging. Firstly, there is the trouble of getting a macroscopic view of a temporally distant planet and secondly, there is the difficulty of successfully simulating an Earth system we cannot observe! These two obstacles would seem to suggest that to investigate the Earth system in geological time would be a fruitless endeavour, but there are valuable objectives in palaeoclimate research. These include providing evidence about climates significantly different from modern, providing a longer term view of the Earth System and the evaluation of GCMs.

It is possible to argue that the evaluation of a GCM's performance of simulating modern climate using datasets that were used in model development may not be the strictest assessment (Haywood et al., 2011). A more rigorous evaluation would be to use GCMs developed with modern datasets and attempt to simulate climates of the geological past (Haywood et al., 2011; Valdes, 2011). These can then be assessed with data from the geological record and areas of data – model inconsistency should promote better model development (e.g. Lunt et al., 2008; Salzmann et al., 2009). In reality this in itself is a monumental task, comparing data with models requires first that the data are comparable to the model (e.g. Salzmann et al., 2008) and then that all the uncertainty (in both data and models) is understood (Haywood et al., 2011).

The geological record also provides an opportunity to potentially identify an "analogue" to future anthropogenic climate change (Haywood et al., 2011; Zeebe, 2011). This would be of great societal benefit as it could provide information on regional changes in climate and environment, which could be used to direct adaptation policy in the future (Haywood et al., 2011). However, the likelihood of identifying a true analogue is unlikely due to the nature of our dynamic planet; ever changing components that modify processes in the Earth system (Haywood et al., 2011). Possibly more relevant to palaeoclimates is the concept of Earth system sensitivity (Haywood et al., 2011; Lunt et al., 2010). Earth system sensitivity looks at the changes in mean surface temperature, from a forcing of CO_2, with long time scale feedbacks (Lunt et al., 2010). This differs from Charney sensitivity which looks at the change in surface temperature, from a forcing of CO_2, with only short timescale feedbacks (Haywood et al., 2011; Lunt et al., 2010; Meehl et al., 2007). Many of these long term feedbacks are not considered in understanding anthropogenic climate change, as most studies are only concerned with the coming century (Meehl et al., 2007). But the effects of these long term feedbacks do not suddenly occur after a preconceived amount of time and there are observations that some are already in operation (Sturm et al., 2001). One of these "long term feedbacks", in Earth system sensitivity, is vegetation (Cox et al., 2000; Salzmann et al., 2009).

I will fully introduce vegetation as a component of the Earth system in Section 1.4, for now I would like to start off with a general introduction to the other components of the Miocene Earth system before focussing on the theme of this thesis. In the following sub-sections I will introduce what is known about some of the more important components of the Earth system during the Miocene.

1.2.1. Miocene chronology

Before introducing the components of the Miocene world it would be sensible to define the Miocene chronologically. The Miocene Epoch (meaning “less recent” in Greek) begins at the Paleogene – Neogene boundary (23.03 Ma) and continues until the start of the Pliocene at 5.33 Ma (Fig. 1.1). It originated as one of Sir Charles Lyell’s three divisions of the “Tertiary” based on his travels through southern France and Italy (Lyell, 1833). In current chronology the Miocene is the second longest epoch of the Cenozoic and is composed of six ages (Gradstein et al., 2004).The first age in the Miocene is the Aquitanian (23.03 – 20.43 Ma) and was named for the Aquitaine region of France (Mayer-Eymar, 1858). Following the Aquitanian is the Burdigalian (20.43 – 15.97 Ma) named after the Latin for the city of Bourdeux, France (Depéret, 1892). The Aquitanian and Burdigalian can be combined to form the Early Miocene (Gradstein et al., 2004). Following the end of the Burdigalian is the Langhian (15.97 – 13.65 Ma), which was named for the Langhe area of northern Italy (Pareto, 1864). The Seravallian (13.65 – 11.61 Ma) follows the Langhian and was named for the town of Serravalle Scrivia, also in northern Italy (Pareto, 1864). Together the Langhian and Seravallian form the Middle Miocene (Gradstein et al., 2004).The Tortonian age (11.61 – 7.25 Ma), named after the Italian city of Tortona, follows the Seravallian (Mayer-Eymar, 1858). The final age of the Miocene is the Messinian (7.25 – 5.33 Ma) and was named for the city of Messina, Italy (Mayer-Eymar, 1858). Together the Tortonian and Messinian constitute the Late Miocene (Gradstein et al., 2004). The Global Boundary Stratotype Sections (GSSP) for the Aquitanian, Seravallian, Tortonian and Messinian are all well established and defined from the Mediterranean region (Hilgen et al., 2000; 2005; 2009; Steininger et al., 1997). Whilst the Burdigalian and Langhian GSSPs still need to be ratified, they are likely to be from the Mediterranean as well (Turco et al., 2011). In oceanic settings the defined boundaries fall on or near to first or last occurrence datums of plankton, boundaries of polarity chronozones or oxygen isotope events (Hilgen et al., 2000; 2005; 2009; Steininger et al., 1997; Turco et al., 2011). Miocene terrestrial deposits are commonly dated using regional mammal stratigraphy (Agusti et al., 2001; Flynn and Swisher, 1995; Qiu and Qiu, 1995; Woodburne, 1987) or palynology (e.g. Partridge, 2006). These regional stratigraphies are tied to the international ages through correlation with more complete marine sections, magnetostratigraphy and radiometric dating. For consistency in this thesis I will refer only to the timescale of Gradstein et al. (2004).

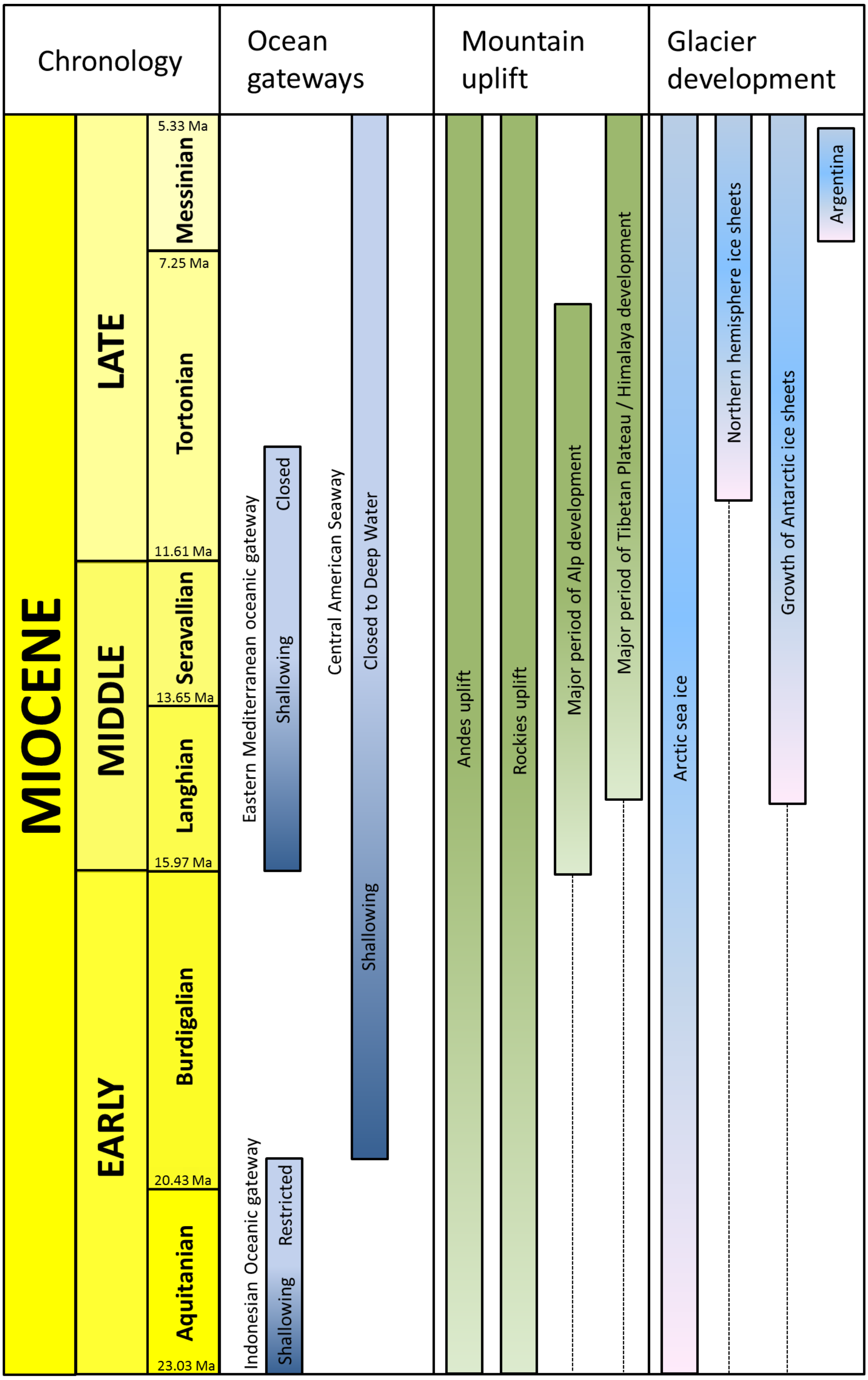


Figure 1.1. Key events in the evolution of the Miocene Earth System. References for specific events are presented in Section 1.2.

1.2.2 Tectonics and ocean circulation

During the Miocene the distribution of the continents is similiar to the modern configuration, with some exceptions: There was more land in the high northern latitudes and a series of large lakes and seaways in South America (Aceñolaza and Sprechmann, 2002; Markwick, 2007). The collision of the African, Anatolian and Arabian plates with the Eurasian plate closed the remnant Tethys Ocean creating the modern Aral, Azoz, Black, Caspian, Marmara and Mediterranean Seas (Harzhauser and Piller, 2007; Potter and Szatmari, 2009). During the Early Miocene the Western Tethys Ocean connected the Atlantic and Indian Oceans, but by the Middle Miocene this had been closed to the Indian Ocean and became the Mediterranean Sea (Harzhauser and Piller, 2007). Parallel to the Western Tethys Ocean there existed the Central and Eastern Paratethys, covering most of Europe during the Early Miocene. These gradually became more restricted through the Miocene and by the Late Miocene the Central Paratethys became isolated and referred to as Lake Pannon (Harzhauser and Piller, 2007; Kern et al., 2011). During the Miocene land bridges linked Southeast Asia with Indonesia and an intermittent land bridge in the Bering straits linked North America and Eurasia (Johnson et al., 2006; Markwick, 2007; Scotese, 2004).

The Miocene bore witness to the onset of modern oceanic currents through the collision of tectonic plates and the closure of oceanic gateways (Fig. 1.1). During the Paleogene, a circum – equatorial current dominated global water movement (Potter and Szatmari, 2009). This form of ocean circulation started to lose dominance before the Miocene, between 41 – 33 Ma the Drake Passage (South America – Antarctica ocean gateway) and the Tasmanian Gateway (Australia – Antarctica ocean gateway) opened (Kennett and Exon, 2004; Potter and Szatmari, 2009; Scher and Martin, 2006). This isolated Antarctica through the formation of the Antarctic Circumpolar Current (ACC) and may represent the onset of deep water formation around this continent (Potter and Szatmari, 2009; Strugnell et al., 2008). By the latest Oligocene (ca. 25 Ma) the Australian tectonic plate had collided with the Eurasian plate, by the late Early Miocene this had blocked deep water exchange between the Pacific and Indian Oceans and restricted deep water movement along the circum – equatorial current (Kuhnt et al., 2004; Potter and Szatmari, 2009). By the Middle Miocene the Arabian plate - Eurasian plate collision had closed this Early Paleogene seaway to such an extent, allowing only intermittent water exchange until a complete closure at 11 – 10 Ma (Allen and Armstrong, 2008; Potter and Szatmari, 2009; Rögl, 1999). The final seal on the circum – equatorial current was the collision of North and South America at 12.8 Ma (Coates et al., 2004). Before 12.8 Ma, deep water could exchange between the Pacific and Atlantic Oceans. After 12.8 Ma the Central American Seaway gradually shallowed, until its final closure at 3.5 –

2.7 Ma (Coates et al., 2004; Webb, 2006). From the late Middle Miocene the Greenland – Scotland Ridge gradually subsided, bringing cold Arctic water into contact with the North Atlantic Ocean (Wright, 1998). The Messinian witnessed a temporary ocean gateway closure when, between 5.95 – 5.70 Ma, the Straits of Gibraltar sealed (Clauzon et al., 1996; Londeix et al., 2007). This isolated the Mediterranean Sea and allowed the deposition of thick successions of evaporates (Krijsman et al., 1999).

The closure and opening of these oceanic gateways established a more modern circulation pattern, associated with Antarctic ice sheet expansion from ca. 15 Ma (Flower and Kennet, 1994; Lewis et al., 2008; Shevenhell et al., 2004) and northern hemisphere ice sheet expansion in the Late Miocene (Thiede and Myhre, 1996; Warnke and Hansen, 1977) intensified deepwater circulation and oceanic turnover (Diekmann et al., 2004; Flower and Kennett, 1994; Potter and Szatmari, 2009). As well as completely reorganising ocean circulation, Miocene tectonics also uplifted global mountain chains.

1.2.3. Mountains

The Miocene was a key interval for mountain construction with all the world's major orographic regions uplifting (Fig. 1.1), not only altering topography but reorganising global river directions and forming biogeographic boundaries (Potter and Hamblin, 2005; Potter and Szatmari, 2009). The Rocky Mountains of western North America are a product of several orogenic events, the most recent of which was the Laramide Orogeny which is dated to the Late Cretaceous to Paleogene (English and Johnston, 2004). Subsequent to this major event there has been considerable dynamics in topography but this is poorly constrained (Aslan et al., 2010). It is known that the Colorado Plateau has been uplifted by nearly 2 km since the Cretaceous (Spencer, 1996). Estimates on the exact timing of the uplift and the rate are still unresolved but recent work suggests a change in the dynamic topography of 400-1100 m has occurred in the last 30 Ma (Flowers et al., 2008; Moucha et al., 2009; Wolfe et al., 1997).

The Andes may have been at half their modern height by 10.7 Ma (ca. 1800 m) and have since been uplifting at 0.2-0.3 mm per year (Gregory-Wodzicki, 2000). Erosional surfaces in the Western Andes show that considerable uplift occurred during the Middle and Late Miocene (Tosdal et al., 1984), whilst isotopic studies of Bolivian caliches show strong uplift in the Late Miocene (Ghosh et al., 2006; Grazione et al., 2008; Poage and Chamberlin, 2006). The changing topography of South America altered river direction and wetland terrains (Diaz de Gamero, 1996; Parnaud et al., 1995; Wesselingh and Salo, 2006).

On Eurasia the main development of the Alps occurred in the Early and Middle Miocene and the Carpathians have not been uplifted since 11 Ma (Frisch et al., 2000; Kuhlemann et al., 2001; Potter and Szatmari, 2009). Though the Alps have been raised steadily since the Middle Miocene from 1600 to 3000m above sea level at 16 – 14 Ma, to 2500 – 3500m at around 8 Ma (Jiménez-Moreno et al., 2008; Kuhlemann, 2007). The Tibetan Plateau and the Himalayas uplifted at an increased rate during the Middle and Late Miocene as suggested by a rise in sediment flux into the Indian Ocean after 15 Ma (Potter and Szatmari, 2009; Rea, 1992). At 15 Ma the mean maximum altitude of the region was between 3775m and 6570m (Currie et al., 2005; Spicer et al., 2003), at 11 – 9 Ma the mean maximum altitude for the region is estimated to have been between 3200m and 6630m (Garzione et al., 2000a; Garzione et al., 2000b; Harrison and Yin, 2004) and areas over 7000m existed by 5 Ma (Molnar et al., 2010; Rowley et al., 2001).

1.2.4. Ice sheets

During the Miocene ice sheets expanded in both hemispheres (Fig. 1.1). In the northern hemisphere perennial sea ice has been present in the Arctic Ocean since the start of the Miocene (Moran et al., 2006). Evidence for the Greenland ice sheet comes from Ice Rafted Debris (IRD), which appears in the Greenland Sea between 10.8 - 5.5 Ma (Thiede and Myhre, 1996; Warnke and Hansen, 1977) and the Norwegian Sea between 7 - 5 Ma (Talwani et al., 1976). In Alaska tillites are found in the Wrangell Mountains at 1200m. These are interbedded with lava flows dated to around 10 Ma (Denton and Armstrong, 1969).

In Prydz Bay, East Antarctica ODP Site 1165 records four intervals of glacial advance and retreat during the Miocene (Hannah, 2006). At 22-19 Ma there was a minimum Amery ice shelf and thriving *Leiosphaeridia* (acritarch cyst), the ice shelf expanded between 19–17 Ma and the climate is suggested to be colder due to a reduced biota in the bay. The warmest interval is recorded between 17-15 Ma with an inferred minimum of the ice shelf and maximum planktonic and benthic biota. After 15 Ma the only preserved biota are reworked palynomorphs; representing a major climatic deterioration and large growth of ice (Hannah, 2006). The absence of in-situ palynomorphs has also been recorded from the Olympus Range, Antarctica and the Antarctic Peninsula, but after 14-12 Ma (Anderson et al., 2011; Lewis et al., 2008). This disappearance of biological evidence coincides with Mg/Ca ratios from the Southwest Pacific (55°S), which show a drop in temperature of six or seven degrees Celsius between 14.2 and 13.8 Ma (Flower and Kennett, 1994; Shevenhell et al., 2004). Whilst, relic tundra may have survived on the James Ross Peninsula until 12.8 Ma, showing that the Antarctic glaciers were not at their present extent (Anderson et al., 2011). By 12 Ma glacial sediments were being deposited on the James Ross Peninsula showing further growth of ice sheets (Dingle and Lavelle, 1998; Marenssi et al., 2010).

In Argentina glacial till is present layered between lavas K/Ar dated to 7.14 – 5.56 Ma (Mercer and Sutter, 1982). These sediments suggest the Neogene glacier had a greater extent than today and the local climate may have been colder (Mercer and Sutter, 1982).

1.2.5. Climate of the Miocene

The Miocene is classically thought of as a transitional epoch from the greenhouse climate of the Paleogene, to the icehouse conditions of the Quaternary (Steppuhn et al., 2006; Zachos et al., 2008). Our present understanding of the Miocene climate comes from two distinct sources: climate proxies and GCM experiments. One of the most complete views of one aspect of the Miocene climate system comes from the compilation of bottom water oxygen isotope studies (Zachos et al., 2001; 2008). This compilation shows the evolution of bottom water temperatures and global ice volume (Zachos et al., 2001). Overall there is a downward trend towards colder temperatures and more ice through the Miocene (Fig. 1.2). This is punctuated by the Middle Miocene Climatic Optimum (MMCO) roughly between 17 and 14 Ma (Fig. 1.2), which represents a significantly warmer interval than the preceding Early Miocene and the remainder of the Miocene (Zachos et al., 2008). Following the MMCO is a steady reduction of temperature and/or increase in ice volume known as the Middle Miocene Climate Transition (MMCT) (Flower and Kennett, 1994; Zachos et al., 2001). The MMCT is a period of rapid climate cooling shown by a Ca. 1‰ $^{\delta 18}$O increase, IRD deposition in the Southern Ocean and eustatic sea level drop, all of which reflects a significant growth in the Antarctic ice sheet (Shevenhell et al., 2004; Zachos et al., 2001). By the Late Miocene the rate of cooling and/or ice growth had slowed (Fig. 1.2) creating a more modest downward trend than during the MMCT (Zachos et al., 2001; 2008). Numerous other studies have also shown this same change in the global climate; a general cooling trend punctuated by the MMCO (e.g. Donders et al., 2009). These proxy based studies have provided a view of the changes in the Miocene climate. But to look at the global pattern of climate (for example the distribution of precipitation) it is necessary to utilise GCMs.

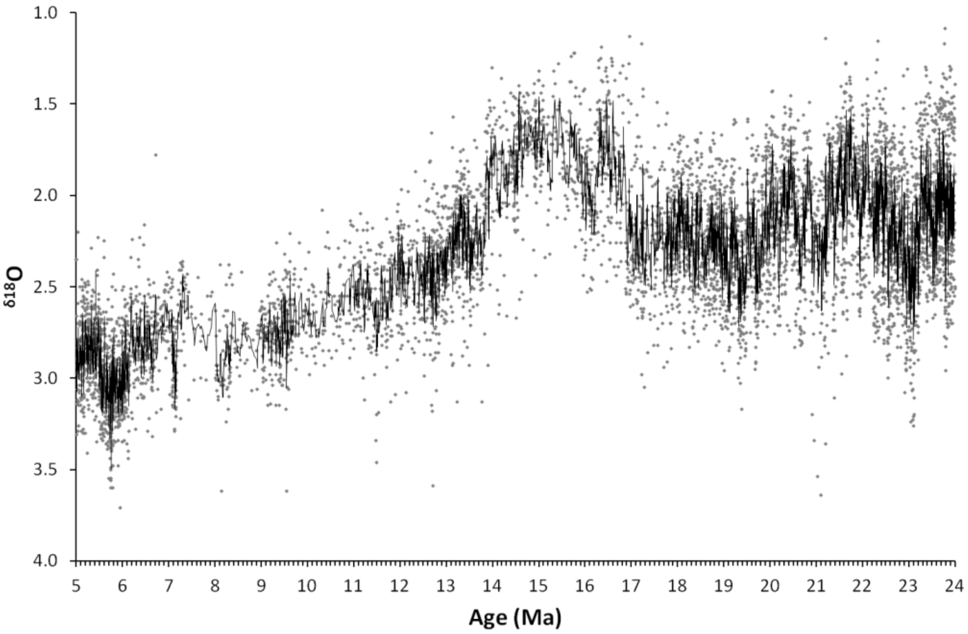


Figure 1.2. The benthic $^{\delta18}$O curve for the Miocene. The grey dots represent individual data points whilst the black line is a 5 point running average (replotted from Zachos et al., 2008).

Modelling experiments on Miocene time slabs indicate a world that is both warmer and wetter than the pre-industrial (Lunt et al., 2008; Micheels et al., 2007; Steppuhn et al., 2007). The degree of warming, relative to the pre – industrial is largely dependent on CO_2 concentration (Bradshaw et al., 2010; Micheels et al., 2009a; Tong et al., 2009), topographic changes (Micheels et al., 2011), palaeogeography (Barron, 1985; Fluteau et al., 1999) and vegetation (Dutton and Barron, 1997). The increase in precipitation, within each modelling experiment, appears to be directly related to the change in Mean Annual Temperature (MAT), relative to the pre-industrial (Fig. 1.3). This would be related to increased evaporation due to higher temperatures, an intensification of the Hadley Cell and a reduced latitudinal temperature gradient due to more heat being exported from the tropics to the poles by greater Hadley Cell activity (Micheels et al., 2011; Rind, 1998). Changes in the atmospheric Hadley Cell have also been shown to displace subtropical jet streams and storm tracks in Miocene GCM experiments (Herold et al., 2011).

Overall proxy evidence and GCM experiments show that Miocene climate was warmer and wetter than the pre-industrial. In the following section I will introduce some of the ideas behind the cause of this warmth.

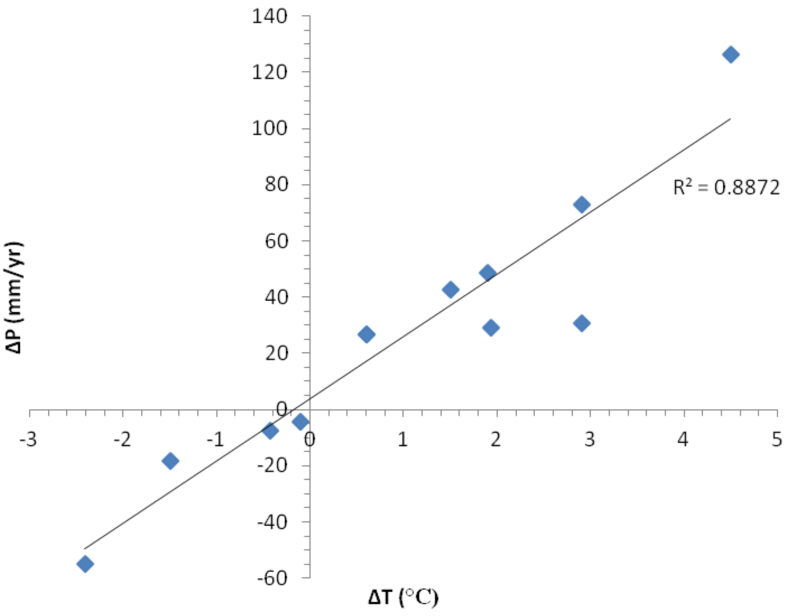


Figure 1.3. A compilation of Miocene modelling studies showing the change in temperature (ΔT) and precipitation (ΔP) relative to today. The graph shows a near linear relationship between changing temperature and precipitation (Data from: Bradshaw et al., 2010; 2012; Lunt et al., 2008; Micheels et al., 2007; 2009b; 2011; Steppuhn et al., 2006; 2007; Tong et al., 2009).

1.3. Driving forces and evolution of Miocene climate

It has proven difficult for an agreement to be reached in the literature about the driving forces of Miocene climate (Knorr et al., 2011; Kürschner et al., 2008; Mosbrugger et al., 2005; Pagani et al., 2005; Shevenell et al., 2004). This uncertainty in the driving force of Miocene climate stems from the inconsistency of reconstructed atmospheric CO_2 records (Fig. 1.4). This has promoted the search for other factors that may be behind Miocene warmth (Pagani et al., 2005; Royer et al., 2001). In this section I will present what is known about Miocene CO_2 levels and the other ideas responsible for forcing Miocene climate.

1.3.1. Atmospheric concentrations of CO_2 during the Miocene

Despite recent claims that Cenozoic CO_2 levels are coming into agreement (Beerling and Royer, 2011) this does not appear to be the case for the Miocene (Fig. 1.4). Miocene CO_2 levels have been reconstructed using numerous techniques and each differs in both atmospheric concentration and in trend through time (Fig. 1.4). Reconstructions are based on alkenones (Pagani et al., 2005; 2010), boron isotopes (Pearson and Palmer, 2000), B/Ca ratio (Tripati et al., 2009), pedogenic carbonates (Ekart et al., 1999; Retallack, 2009) and stomatal indices (Beerling et al., 2009b; Kürschner et al., 1996; 2008; Stults et al., 2011). Through the Middle Miocene to the end of the Miocene the alkenone based reconstructions place atmospheric CO_2 levels between 190 – 360 ppmv reaching a peak at around 6 - 7 Ma of ca. 360 ppmv (Pagani et al., 2005; 2010). The reconstructed atmospheric CO_2 concentrations from boron isotopes show a range from 137 – 305 ppmv with a peak in CO_2 at ca. 16 Ma and ca. 6 Ma (Pearson and Palmer, 2000). The stomatal indices reconstructions are very different to those based on boron isotopes and alkenones. A range over the Middle to end Miocene of 270 – 564 ppmv has been reconstructed, with a peak at ca. 16 Ma of between 460 – 564 ppmv (Beerling et al., 2009b; Kürschner et al., 2008). These records then show a fall in atmospheric CO_2 concentration to between 270 – 370 ppmv for the rest of the Miocene (Beerling et al., 2009b; Kürschner et al., 1996; 2008; Stults et al., 2011). The B/Ca ratio shows a peak of 433 ppmv at 15 Ma and then drops to concentrations of between 206 – 304 ppmv by 10 Ma (Tripati et al., 2009). The pedogenic carbonate reconstructions could be described as more erratic, fluctuating from very low to as high as 1170 ppmv (Ekart et al., 1999). More recent work on pedogenic carbonates, across the Middle Miocene, has shown a peak in concentration at 15.6 Ma of 852 ppmv (Retallack, 2009). This then drops rapidly to 116 ppmv at 14.6 Ma and rises to 433 ppmv by 12.8 Ma (Retallack, 2009). Overall, the apparent low atmospheric levels of Miocene CO_2 have led to disagreements over how much Miocene climate was influenced by this greenhouse gas (Kürschner et al., 2008; Mosbrugger et al., 2005; Pagani et al., 2005; Shevenell et al., 2004).

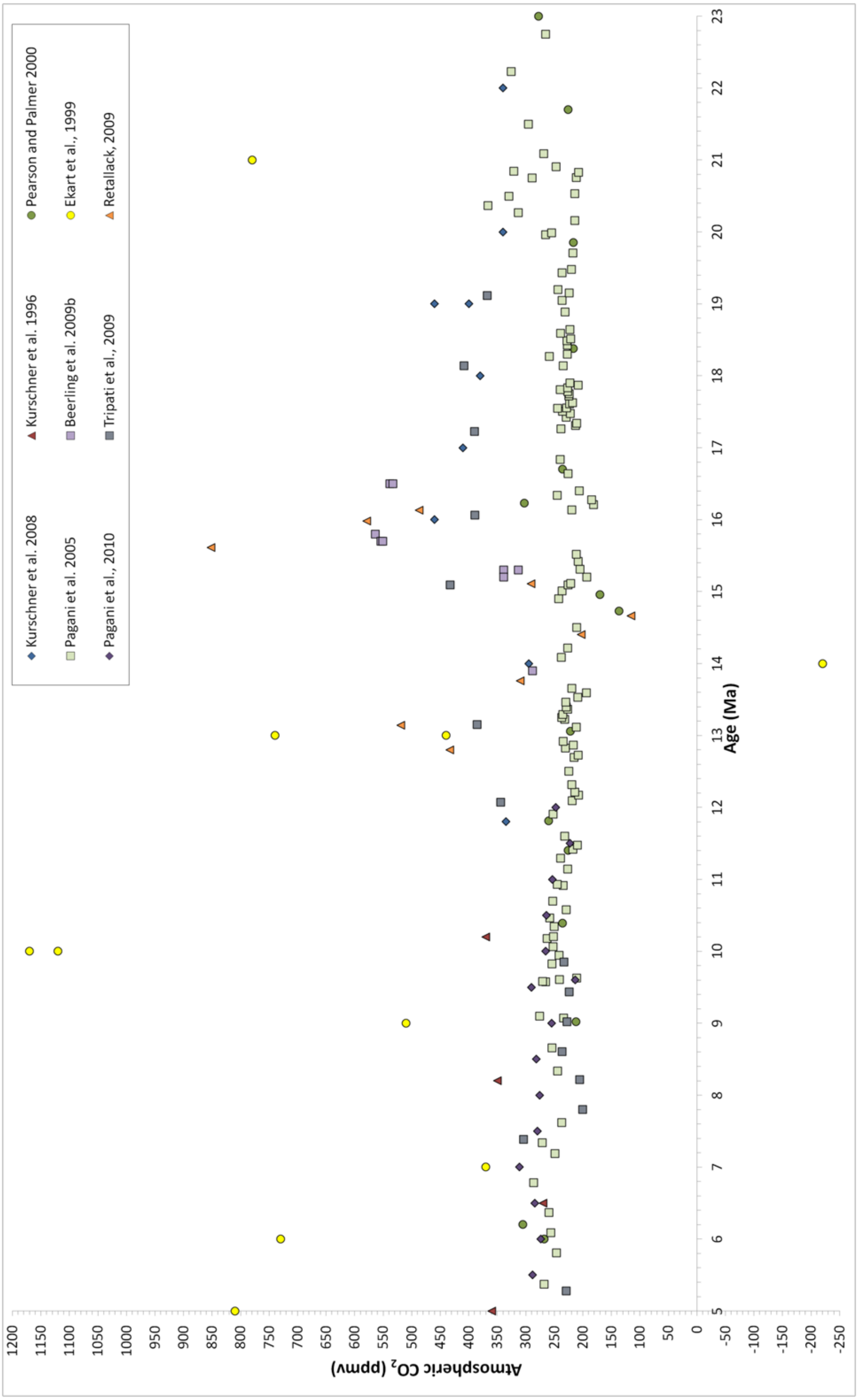


Figure 1.4. Miocene atmospheric CO2 reconstructions from various sources.

1.3.2. Other climate forcing agents and their importance in the Miocene

From the previous subsection it is easy to see how some authors have suggested that the Miocene was a warm period in Earth history, where climate was decoupled from CO_2 (e.g. Pagani et al., 2005). This has led to studies focussing on why Miocene CO_2 was low and what else could be contributing to the warmth and climate changes seen in the fossil proxy record.

Mountains affect climate by altering atmospheric circulation, changing patterns of precipitation and seasonal heating and may increase rates of chemical weathering (Broccoli and Manabe, 1997; Hay, 1996; Raymo and Ruddiman, 1992; Ruddiman and Kutzbach, 1989). As the Miocene is a key period for mountain uplift an increase in chemical weathering, during Miocene uplift of Tibet, has been connected to some of the low CO_2 reconstructions (Fig. 1.4) as this would draw CO_2 out of the atmosphere, cooling global temperatures and causing ice sheet growth (Raymo and Ruddiman, 1992). Challenging this idea of increased silicate rock weathering driving Miocene climate is the $^{10}Be/^{9}Be$ proxy (Willenbring and von Blanckenburg, 2010). Using the $^{10}Be/^{9}Be$ proxy shows constant weathering rates from 12 Ma to today, suggesting elevated weathering was not responsible for later Neogene cooling (Willenbring and von Blanckenburg, 2010). But this disagrees with the strontium isotopes, which suggest continuous increases in weathering since 40 Ma (Raymo and Ruddiman, 1992).

The silicate weathering hypothesis raises an issue: as none of the CO_2 reconstructions show the atmosphere devoid of this important greenhouse gas. Yet mountain uplift has been continuous since ca. 15 Ma, so there must be a feedback which prevents CO_2 levels from dropping too low (Fig. 1.1; 1.4). This has been suggested to be a vegetation – weathering feedback, which occurs when CO_2 levels drop below a threshold (Beerling et al., 2012; Pagani et al., 2009). Below this unknown threshold level the productivity of forests fall allowing the expansion of grasslands (Pagani et al., 2009). Grasses have shallow roots and do not produce certain organic acids that facilitate rock weathering (Pagani et al., 2009). Theoretically, if during periods of very low reconstructed CO_2 levels (Fig. 1.4) there is an expansion of grasslands, then this feedback kicks in preventing atmospheric concentrations falling any further (Beerling et al., 2012; Pagani et al., 2009). Retallack (2001) considers grasslands a larger carbon sink than any other vegetation type and when grassland soils are eroded, they are unusually rich in organic matter. Grasslands also encourage export of bicarbonate and nutrient cations to lakes and oceans, where they stimulate productivity and C burial (Retallack, 2001). So in the view of Retallack (2001) grasslands should actually contribute to a draw-down of CO_2, rather than preventing it. From a global study of paleosols, their carbon isotopes and the evolution of grazing mammals Retallack (2001) concludes that the evolution of climate is more related to grasslands and grazers than to tectonics.

The Monterey Excursion is a broad increase in $\delta^{13}C$ with several distinct maxima between 17 and 13.5 Ma, showing a large scale increase in organic carbon deposition around the Pacific Ocean rim (Flower and Kennett, 1994; Vincent and Berger, 1985; Woodruff and Savin, 1991). This increased carbon burial was thought to have been made possible through global cooling increasing upwelling and zones of productivity (Kender et al., 2009; Vincent and Berger, 1985). This original hypothesis does not take into account two recent observations; 1) the increasing $\delta^{13}C$ with increasing global temperatures, prior to 16 Ma (Kender et al., 2009; Zachos et al., 2001) and 2) the deposition of C would require the drawdown of large amounts of CO_2, which according to some proxies were not present in the atmosphere at this time (Kender et al., 2009; Pagani et al., 2005). The Monterey Excursion has recently been linked with the Columbia River Flood Basalts (CRFB), these eruptions mostly took place between 16.1 and 15 Ma (Kender et al., 2009). They are estimated to have emitted 672 Gt of CO_2 (Kender et al., 2009) and more than 1000 Gt of SO_2 (Blake et al., 2010). This would have not only increased atmospheric CO_2 concentrations by ca. 80 ppmv, but also induced periods of volcanic winter that could have enhanced offshore winds and oceanic productivity (Blake et al., 2010; Kender et al., 2009). Therefore, the CRFB could have provided the necessary conditions for the Monterey Excursion (Kender et al., 2009).

A reorganisation of ocean circulation has been suggested as another potential mechanism that could have driven Miocene climate (Shevenhell et al., 2004; Tian et al., 2009). The closure of key equatorial gateways, as introduced in section 1.2.1, would have segmented the oceanic area that could absorb solar radiation (Potter and Szatmari, 2009; Smith and Pickering, 2003). Analysis of foraminifera Mg/Ca values has led to the idea that orbitally paced intensification of the ACC, perhaps by increasing circumpolar winds may have driven Antarctic ice sheet growth and global climate evolution through the MMCT (Shevenhell et al., 2004). This theory has been expanded by carbon isotope results from the South China Sea (Tian et al., 2009). An observed reversal in benthic foraminifera $\delta^{13}C$ values indicates a reorganisation of bottom water currents which may have reduced the sensitivity of Antarctica to lower latitude derived heat (Tian et al., 2009).

Linked to both the idea of mountain uplift and the reorganisation of oceanic currents, is the concept that plate tectonics drove Miocene cooling (Potter and Szatmari, 2009). The Miocene contains numerous tectonic scale events that in combination could have influenced Miocene climate (Potter and Szatmari, 2009). The positioning of Eurasia and North America within the high northern latitudes would have enhanced global cooling (Smith and Pickering, 2003). Though it could be said that these continents have occupied the high northern latitudes since at least the Cretaceous (Markwick, 2007). Behind the mountain uplift and oceanic gateway closure is a larger driving force; superplumes (Potter and Szatmari, 2009). A superplume is a broad area of mantle upwelling, typically thousands of kms in extent (Larson, 1991). There were two such superplumes in the Miocene; the African and the Pacific and their acceleration of plate tectonics, causing palaeogeographic changes may have driven global climate evolution (Potter and Szatmari, 2009).

The ideas around the evolution of Miocene climate are complex. Part of this complexity revolves around the idea of having lower than modern atmospheric CO_2 levels with warmer than modern climate (Pagani et al., 2005; Shevenhell et al., 2004). However, the greatest assumption in all of this argument is that the global CO_2 reconstructions are accurate. Ruddiman (2010) recently suggested that one of the possibilities for apparent low CO_2 levels during the Miocene, whilst climate has fluctuated considerably, could be the incorrect calculation of CO_2 from proxies. Further proof of the inaccuracies in some CO_2 proxy records comes from seemingly ignoring the CRFB and the emissions that would have come with it (Kender et al., 2009).

1.4. Vegetation in the Earth system and our present understanding of Miocene global vegetation

Vegetation is an important part of the Earth System. The global distribution of vegetation is a product of the ambient climate, but vegetation can also influence climate (Fig. 1.5). Vegetation is readily preserved in the geological record and its role both as a climate observer and as a climate controller makes it an ideal proxy to study in palaeoclimates. In this section I will first introduce vegetation in the Earth System, then the distribution of modern vegetation. Finally, introducing what is currently known on the global scale about Miocene vegetation.

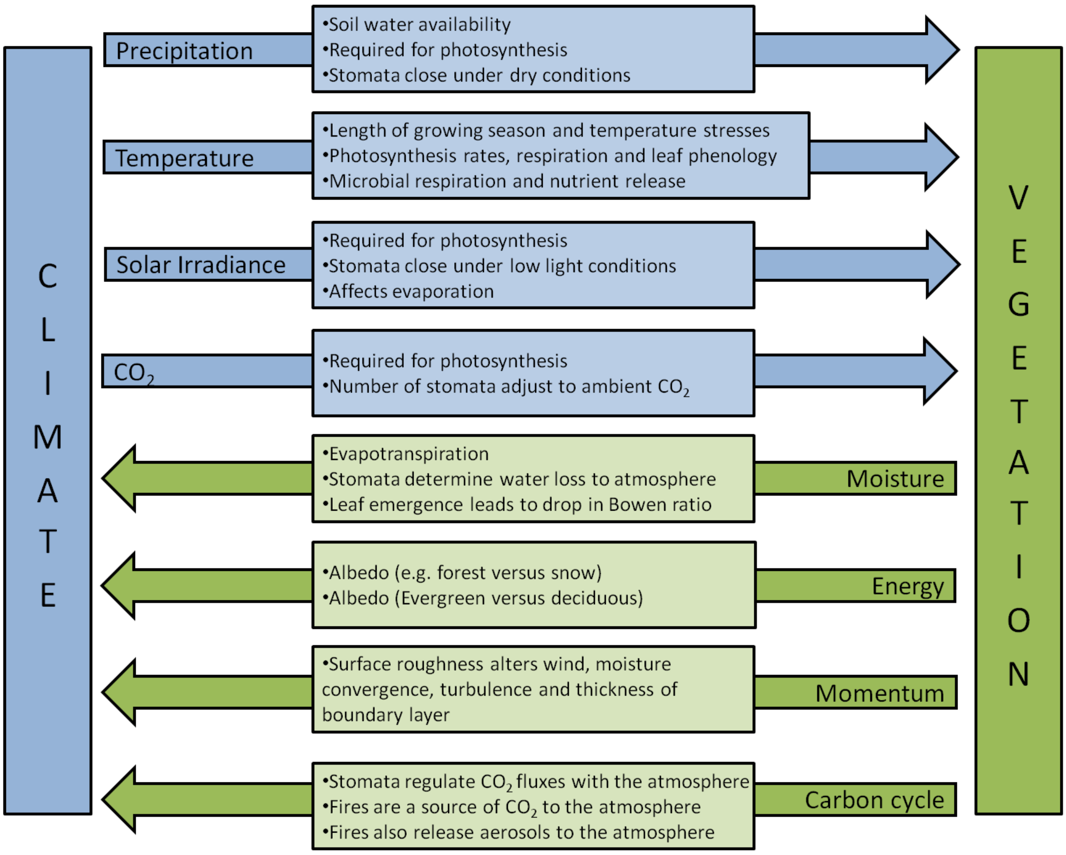


Figure 1.5. Summary of climate – vegetation feedbacks (redrawn from Notaro et al., 2006).

1.4.1. Vegetation in the Earth system

Climate ultimately controls the global distribution of vegetation (Fig. 1.6), but the distribution of vegetation also feedbacks to climate (Fig. 1.5). One of the largest vegetation to climate feedbacks is altering surface albedo (Notaro et al., 2006). This alteration of surface albedo (the amount of solar radiation absorbed or reflected) is most pronounced when changing white or pale coloured land covers to darker colours (Bonan, 2002; Bonan et al., 1992; Notaro et al., 2006). For example current anthropogenic warming is allowing forests to expand northwards (Sturm et al., 2001). This replaces snow (high albedo, low solar radiation absorption) with boreal forests (low albedo, high solar radiation absorption), which in turn forces more warming allowing further forest expansion; a positive feedback (Notaro et al., 2006). Changing one biome type to another and the impact on climate has been further explored in modelling studies. Using the fully coupled atmosphere – ocean – land model FOAM-LPJ the feedbacks of changing boreal forest into grassland across Asiatic Russia was assessed (Notaro and Liu, 2008). In an ensemble of simulations the boreal forest was initially reduced and replaced with grassland. As a Dynamic Global Vegetation Model (DGVM) was used the forests were capable of growing back should the climate be suitable. It was found that the replacement of forests by grassland created a positive feedback on climate; lowering MAT and Mean Annual Precipitation (MAP), which favoured the grassland biome. The change in biome caused an increase in surface albedo, prolonged the snow season, reduced surface air temperature, increased atmospheric stability and enhanced low cloud cover. Changes to the hydrological cycle included a diminished rate of evapotranspiration and moisture recycling (Notaro et al., 2008).

Vegetation – climate interactions are currently not fully understood (Notaro et al., 2006), but a summary of known interactions are presented in Figure 1.5. From what we understand about the feedbacks from vegetation to climate it is obviously an important component in the Earth System. This has been applied previously to palaeoclimates with aspects of past warmth related to the differences in global vegetation and its feedback on global climate (e.g. Knorr et al., 2011; Salzmann et al., 2009).

1.4.2. Present day distribution of vegetation

Present day vegetation (without anthropogenic alteration) is predominantly controlled by temperature, precipitation, seasonality, solar irradiance, soil conditions, CO_2 concentrations and biogeographical history (Notaro et al., 2006; Woodward, 1987; Woodward et al., 2004). At a global scale the easiest way to visualise the distribution of vegetation is through biomes (Fig. 1.6). Terrestrial biomes are the world's major biological communities, classified by their vegetation and defined by their ambient climate (Cramer, 2002). Today most biomes have very limited extent due to being converted to "*anthromes*" (anthropogenic biomes) and so we rely on what is termed the "present day potential natural vegetation" (Fig. 1.6), or what would grow if all of human society were removed from the planet (Ellis, 2011; Kaplan, 2001). As biomes are climatically controlled, the present day potential natural vegetation shows a pattern comparable to the distribution of MAT, MAP and seasonality (the variation in temperature and precipitation through the year). In fact biomes are so intricately linked to the macroclimatic regime, that before the advent of widespread weather stations the type of vegetation was used to infer the local climatic character (Darwin 1845; Köppen, 1884).

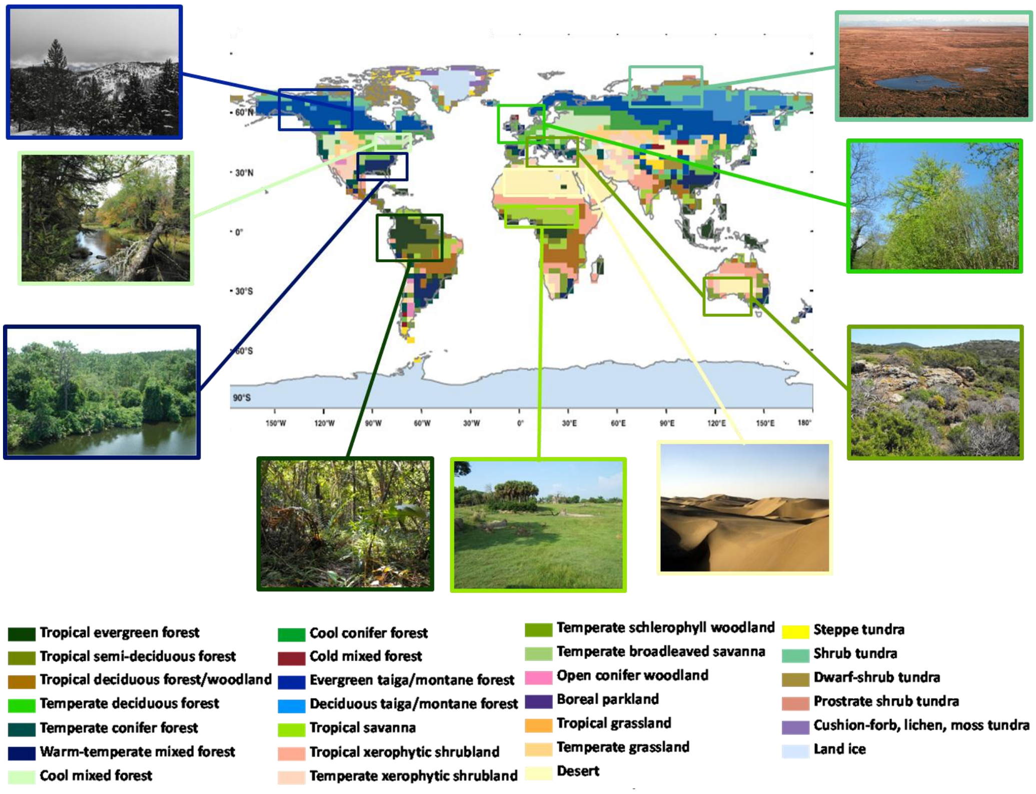


Figure 1.6. The present day potential natural vegetation simulated by the mechanistic vegetation model BIOME4 (Kaplan, 2001). This was simulated using the boundary conditions of the Palaeoclimate Modelling Intercomparison Project (PMIP) with present sea surface temperatures and a CO_2 concentration of 324 ppmv (Bonfils et al., 1998).

Today along the equator lies the tropical forests and moving poleward the forests change to warm – temperate, temperate, cool temperate, cool and cold, finally becoming tundra at the high latitudes (Fig. 1.6). This change in temperature type also occurs up mountains. This is further complicated by the non – uniform distribution of rainfall, both spatially and temporally. Meaning that as precipitation becomes less evenly distributed in the year, biomes change from evergreen forests, to deciduous forests, to woodlands, to savannas, to grasslands, to shrublands and finally deserts (Fig. 1.6). This change in biome type is ultimately related to the growing season; how long a plant can sustain adequate photosynthesis to facilitate growth and reproduction (Schulze et al., 2010). The growing season is further complicated at the high latitudes by the unusual light regime; periods of the year with no sunlight and times of continuous sunlight (Schulze et al., 2010).

Further studies have shown that although biomes are controlled by the macroclimate it is often specific bioclimatic controls of plant growth, development and survival that determines biome boundaries (Cramer, 2002). Examples of these include the absolute minimum temperature in the year, the length of the dry season or the number of growing days (Cramer, 2002). This is ultimately related to the idea that many biotic and abiotic factors form ecological gradients within the environment; these are n-dimensional ecological spaces where the axes are resources or environmental variables (Futuyma and Moreno, 1988; Hutchinson, 1957).

1.4.3. Current knowledge of Miocene vegetation

As the previous two subsections have introduced, modern day vegetation is intimately linked with ambient climate. This means that a good understanding of the distribution of past vegetation can provide a powerful view of past climate (e.g. Salzmann et al., 2008). Previous work on the Miocene vegetation has mainly been conducted on a regional (e.g. Favre et al., 2007) to continental scale (Utescher et al., 2011b). Global studies of vegetation have been based on small numbers of data sites either by extrapolation (Wolfe, 1985) or by combination with a vegetation model (Micheels, 2003; Micheels et al., 2007). Wolfe (1985) presented a broad overview of the evolution of global Miocene vegetation, based on the data available at the time. This study showed that the Miocene was warmer, particularly the first half of the time period where limited sites suggested cool mixed forests bordered the Arctic (Wolfe, 1985). More recently regional studies have provided improved insight into Africa (Jacobs et al., 2010), Asia (Wang, 1994; Yao et al., 2011), Australia (Macphail, 2007), Europe (Bruch et al., 2006; Favre et al., 2007; Jiménez-Moreno and Suc, 2007; Utescher et al., 2007), North America (Retallack, 2007; Yang et al., 2011) and South America (Barreda et al., 2007). All of these regional studies show the same general trend in climate induced vegetation changes through time. The Early Miocene had a vegetation pattern that was warmer and wetter than today (Wolfe, 1985). As the climate warmed into the MMCO the regional palaeobotanical studies show that the vegetation responded, creating the warmest and wettest interval of the Miocene (Macphail, 2007; Retallack, 2007; Wolfe, 1985). From the start of the MMCO to the end of the Miocene it appears, at the regional level that vegetation responded to a cooling and drying climate (Barreda et al., 2007; Favre et al., 2007; Jacobs et al., 2010; Wang, 1994). Despite the large amount of regional studies undertaken, especially in Europe, very little is known about the UK during the Miocene (e.g. Bruch et al., 2006; Utescher et al., 2007).

By 10 Ma all modern plant genera had evolved (Traverse, 1982). During the Miocene the key event in the evolution of plants was that of the C_4 photosynthetic pathway (Cerling et al., 1997; Osborne, 2008; Osborne and Sack, 2012; Vincentini et al., 2008). Plants using the C_4 photosynthetic pathway have a CO_2 pump that concentrates carbon dioxide around Rubisco, an enzyme that provides the first step in carbon fixation (Crawley, 1997; Kanai and Edwards, 1999; Sage, 2004). As CO_2 can be concentrated around Rubisco, plants with the C_4

photosynthetic pathway do not need to have their stomata open to the same degree as C_3 plants. This gives the plants using the C_4 photosynthetic pathway an advantage at high temperatures, arid conditions and saline habitats, where evapotranspiration is higher and opening stomata is a more costly exercise than in other habitats (Sage, 2001; Lunt et al., 2007). Recent phylogenetic work using molecular dating has revealed an Oligocene origin for the C_4 photosynthetic pathway apparently corresponding to a drop in carbon dioxide levels at around 30Ma (Christin et al., 2008; Vincentini et al., 2008). However it has been widely acknowledged that the expansion of the C_4 grasslands only came in the late Neogene (Cerling et al., 1997; Osbourne, 2008; Osborne and Sack, 2012). Plants using the C_4 photosynthetic pathway fractionate carbon isotopes differently, meaning they can be detected in the geological record (Cerling et al., 1997). Carbon isotope studies show that the C_4 pathway is first recorded between eight and six million years ago, but only becomes dominant in the isotopic signal during the Pliocene (Cerling et al., 1997; Fox and Koch, 2004; Latorre et al., 1997; Yang et al., 1999). It has been thought that the expansion of C_4 grasses was mainly linked to the apparent low levels of CO_2 (Fig. 1.4) in the Late Miocene (Cerling et al. 1997). However, this CO_2 hypothesis best explains competition between C_3 and C_4 grasses not competition with woodlands (Keeley and Rundel, 2005; Osborne, 2008; Osborne and Sack, 2012). As in time woodland would outgrow the grasses, creating a canopy and preventing savanna/ grassland development (Keeley and Rundel, 2005; Osbourne, 2008). For C_4 savannas/ grassland to gain dominance over woodland, disturbance is required. This is achieved in the modern world by fire, drought and animals (Fensham et al., 2009; Keeley and Rundel, 2005; Osbourne, 2008; Trollope et al., 1998). The levels of wildfire and drought are linked to the seasonality of rainfall and so the expansion of C_4 grasses is not only due to falling CO_2 levels, but also to the changing climate and the apparent increase in seasonality in the Late Miocene (Keeley and Rundel, 2005; Osbourne, 2008).

1.5. Vegetation as a proxy for climate

Vegetation is an excellent proxy for climate (Kohfield and Harrison, 2000; Valdes, 2000). It is readily and widely preserved in both marine and terrestrial environments (Traverse, 1982). In the form of wood, leaves, seeds, fruits, spores and pollen, making it an accessible and global source of climate information (e.g. Salzmann et al., 2008; Utescher et al., 2011b).

Quantitative estimates of temperature and precipitation can be reconstructed from palaeobotanical sites using techniques such as the co – existence approach (Mosbrugger and

Utescher, 1997) and Climate Leaf Analysis Multivariate Program (CLAMP) (Spicer et al., 2009; Wolfe, 1979), the estimates can then be compared directly to the climate produced by a GCM. The co – existence approach uses a Nearest Living Relative (NLR); the climate tolerance of a fossil taxon’s closest extant relative is likely to be comparable to that of the fossil (Mosbrugger and Utescher, 1997). From this idea an assemblage of fossils can be compared to find the overlapping climate space that all taxa could have survived in, based on the climate tolerances of each fossil’s nearest living relative (Mosbrugger and Utescher, 1997; Utescher and Mosbrugger, 2010). CLAMP is the latest iteration of the plant physiognomy that has been known for almost a century; plants vary their structure with climate, in a non – random way (Bailey and Sinnott, 1915; Holdridge, 1947). Growth rings in wood, drip tips on leaves and leaf margins can all provide important climate information (Holdridge, 1947; Wolfe, 1979). CLAMP uses leaf morphology to reconstruct quantitative climate information using “training sets” from undisturbed modern day floras (Spicer et al., 2009; Yang et al., 2011).

Both techniques provide quantitative climate information but both have limitations. Errors in the co – existence approach come from; the NLR may have a different climate tolerance to the fossil taxon, the NLR may be miss-identified, the NLR occupies only part of its climate range, the climate data taken for the NLR might be inaccurate (Mosbrugger and Utescher, 1997). However, errors in the coexistence approach can usually be identified as outliers when the technique is applied (Mosbrugger and Utescher 1997). Despite these four sources of error the co – existence approach can be applied to any palaeobotanical fossil, so long as it can be identified to a taxonomic level (Mosbrugger and Utescher, 1997). Conversely, CLAMP can only be applied to leaf floras (Wolfe, 1979). The quality of results from CLAMP can also be influenced by taphonomic processes (Burnham et al., 2001; Spicer et al., 2005) and the number of training sets available to evaluate a fossil flora against (Spicer et al., 2011). Despite these issues CLAMP benefits from not needing taxonomic information, which can be difficult to decipher in leaves to higher levels (e.g. genus or species) and limits the applicability of the co - existence approach to leaf floras (Mosbrugger and Utescher, 1997). Estimates from both these methods can then be compared directly to the climate produced by a GCM, providing clues on the pattern of global climate. However, the direct comparison of GCM climate parameters with those reconstructed from palaeobotanical sites need to take into account error margins. Both from the technique used to reconstruct the climate estimates from the fossil vegetation and from the boundary condition and physics uncertainties that are a challenge to fully explore with GCMs.

Alternatively, qualitative climate information can be gained by translating a fossil vegetation datum into a biome (Fig. 1.6). The fossil biomes can then be compared to a model predicted biome distribution using biome models, such as BIOME4, that are driven by the climate generated by a GCM (Kaplan, 2001; Prentice et al., 1992; 1998). By reconstructing a biome and comparing it to model generated biomes a simple and relatively quick comparison can be achieved (Haywood et al. 2009; Pope et al., 2011; Salzmann et al., 2008). However, biomes reconstructed from palaeobotanical sites need to be directly comparable to model output, this can be achieved by using the classification scheme of the chosen model. This raises the issue that biome models, such as BIOME4, have been developed using modern biomes and how comparable these are to fossil biomes has yet to be fully explored. Despite this the technique has been successfully applied to the Pleistocene (Prentice et al., 1998), the Pliocene (Pope et al., 2011; Salzmann et al., 2008) and the Miocene (Micheels et al., 2007).

All of this means that fossil vegetation can be used to examine climate from a single locality, providing a valuable pin – point view of the ambient conditions during deposition. To a regional or global view of climate using larger datasets of fossil vegetation distribution and finally, combining the data with GCMs to look at dynamic climate and vegetation patterns through time.

1.6. Aims and Objectives

The aim of this project is to provide a global view on Middle to Late Miocene vegetation and climate evolution through time. This period of the Cenozoic had a complex Earth System and would provide an ideal “significantly different world to modern” to test GCM experiments against. However, before the Miocene can be used as a period to test GCMs, the environments and climates need to be more thoroughly understood. Through the study of terrestrial biotas this thesis will provide this information. To achieve this aim the following objectives will be completed:

- To document climate and vegetation at a global scale, biomes will be reconstructed from the palaeobotanical literature. This will provide a uniform classification to the diverse palaeobotanical literature, allowing vegetation change through Miocene time to be analysed.

- To supplement the palaeobotanical literature, the Miocene vegetation of the UK will be investigated through the palynology of the Brassington Formation.
- Once a comprehensive dataset of Middle to Late Miocene biomes has been developed, it will be possible to compare and combine the data with GCM experiments. This will provide a broader view of Miocene climate, giving information on areas where palaeobotanical data are absent and allowing global differences to be presented.
- As vegetation is a component of the Earth System, the application of the global datasets of palaeobotanical biomes to GCM experiments will allow the impact on climate from the Miocene vegetation to be quantified.
- Regional studies on Miocene vegetation show that palaeobotanical data are not evenly distributed across the globe. Would it therefore be possible to improve global vegetation reconstructions by using fossil mammals? This will be investigating, firstly through the distribution of Miocene mammals and if they were controlled by vegetation. Then, if it has been shown that Miocene mammals were specialised for specific biomes, then it should be possible to reconstruct biomes based on the presence or absence of specialist taxa.

1.7. Structure of thesis

The rest of this thesis is divided into seven chapters. Chapter 2 explores the Miocene vegetation and climate of the UK geological record. Chapter 3 presents global vegetation for the Middle to Late Miocene and Chapter 4 uses some of this data to generate a data - model hybrid for the Tortonian age. Chapter 5 presents the impact of vegetation on the HadAM3 GCM using the hybrid global vegetation map produced in Chapter 4. Chapter 6 uses the data from Chapter 3 to explore the biome preferences of Late Miocene mammals .Whilst chapter 7 takes this mammal biome preference data and investigates the potential of Late Miocene mammals to be a proxy for vegetation. Chapter 8 will attempt to bring Chapters 2 – 7 all together, discuss what this thesis presents on *Middle to Late Miocene terrestrial biotas and climate* and how this fits into our understanding of Miocene palaeoclimates.

Chapter 2

The Miocene vegetation of the UK from the palynoflora of the Brassington Formation, Derbyshire.

Miocene formations, in the ordinary sense of the term, are almost entirely absent from the British Islands. – Encyclopaedia Britannica, 1889

2.1. Introduction

In Chapter 1, it was stated that the UK has not been previously used in Miocene regional vegetation or climate studies (e.g. Utescher et al., 2011b). In this chapter, this is remedied by Miocene climate information calculated using the coexistence approach (Mosbrugger and Utescher, 1997; Utescher and Mosbrugger, 2010) via new palynological data from the English Midlands.

Onshore Miocene deposits in the UK are extremely sparse and include the St. Agnes Outlier, Cornwall and the dissolution pipe fills at Trwyn y Parc, Anglesey, both of which are very small in extent and poorly dated (Walsh et al., 1987; 1996). Another possible onshore Miocene succession was discovered in the Mochras Farm Borehole, Gwynedd, but this is not firmly dated (Herbert-Smith, 1971). However, relatively extensive Neogene sands, gravels and clays deposited via solution-subsidence into karstic cavities from around Brassington, Friden and the Weaver Hills in Derbyshire and Staffordshire, central England were termed the Brassington Formation (Boulter et al., 1971). The Brassington Formation appears to have formed a continuous pre-subsidence sheet of sediment which was >220 km^2, >70 m thick in places and approximately 10 km^3 in volume (Walsh et al., 1980). This unit was assigned a Late Miocene to Early Pliocene age by Boulter and Chaloner (1970), Boulter (1971a,b) and Walsh et al. (1996) based on floral comparisons with Germany and The Netherlands. This contribution aims to reassess the age of the Brassington Formation based on a restudy of the original data of Boulter (1971b) and new material from Kenslow Top Pit near Friden, Derbyshire (Fig. 2.1).

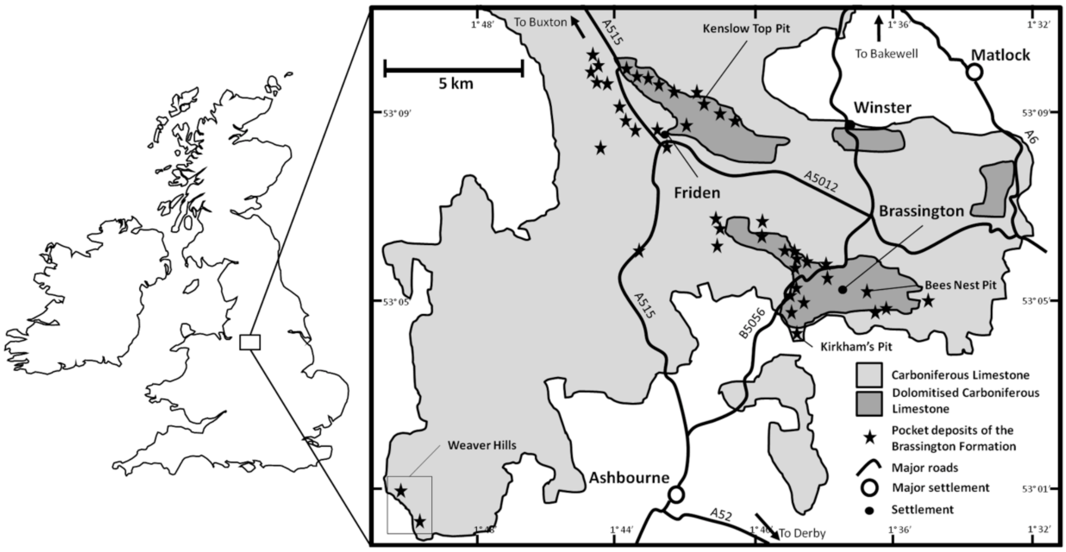


Figure 2.1. Sketch geological map of the southern part of the main Carboniferous Limestone outcrop of Derbyshire and Staffordshire illustrating the distribution of karstic hollows which contain the Brassington Formation and the location of Kenslow Top Pit (modified from Ford and King 1968, fig. 49).

2.2. The geological setting of the Brassington Formation

The Brassington Formation is a Neogene siliciclastic unit which is up to 70 m thick and is confined to over 60 infills of steep-sided collapsed karst solution cavities in Derbyshire and Staffordshire, UK. These collapsed infills are highly variable in areal extent and depth. This unit was referred to as "pocket deposits" by Howe (1897) and was formally defined by Boulter et al. (1971) who recognised three subdivisions: the Kirkham, Bees Nest and Kenslow members. These sands, gravels and clays represent a stratigraphically-coherent, fining-upwards succession (Ijtaba, 1973), which typically forms synclinal structures, especially in the larger cavities. The majority of these karstic fillings are present in a relatively narrow northwest-southeast belt within the limestone plateau from Carsington Pastures to Parsley Hay and beyond, which is approximately 19 km long and typically associated with the highly porous dolomitised Carboniferous Limestone. However the Brassington Formation occupies an area approximately 30 km wide (Fig. 2.1). Approximately 60 of the "pocket deposits" have been quarried between around 1900 to the early 1970s for silica sands and fireclay in order to manufacture refractory bricks used for lining furnaces (Yorke, 1954). This industry was stimulated by the relatively low transport costs to centres of the steel industry such as Sheffield, and production has ceased due to the decline in this sector.

The origin of the Brassington Formation has been extensively debated. The consensus is that the succession was initially deposited via fluviatile and lacustrine processes throughout much of the southern part of the Carboniferous Limestone outcrop. Small outcrops of these sediments subsequently slumped into karstic cavities thereby protecting them from glacial erosion during the Quaternary (Walsh et al., 1972). Clastic sands of the Kirkham Member are dominantly erosion products derived from the Triassic Sherwood Sandstone Group that were shed onto the plateau, which was at least partially covered by the Carboniferous (Serpukovian to Early Bashkirian) Bowland Shale Formation (formerly the Namurian Edale Shales) at the time, from the retreating sandstone escarpments. The Kirkham Member contains many bleached quartzite pebbles which were clearly derived from the Sherwood Sandstone Group. Sheets of pebbly sand were created by extensive small scale drainage onto the limestone and shale from the Triassic scarp slopes, and much of this material would have been incorporated onto rivers draining eastwards towards the North Sea. The Bees Nest and Kenslow members of the Brassington Formation represent lacustrine and shallow lacustrine/swampy palaeoenvironments respectively, and were deposited after significant erosive retreat of the Sherwood Sandstone Group from this area.

The Triassic escarpments have now retreated to the west, south and east of the Derbyshire Massif; the closest one is now about 8 km to the south. Because the Brassington Formation infillings are relatively uniform, the eroded Triassic sands must have formed a largely continuous sheet over at least the southern part of the Peak District. In several of the “pocket deposits”, the lowermost sediments, especially around the walls of the cavities, comprise a coarse chert gravel and/or blocks of black Bowland Shale Formation. The chert gravel represents an insoluble residue derived from the weathering of the limestone which originally covered the karst cavities. The shale blocks were derived from the former cover of Bowland Shale Formation and some of these show evidence of intensive weathering.

Today, the Brassington Formation lies between 300-360 m above sea-level. During deposition, this area must have been between 150 m and 250 m lower in elevation in order to allow eroded Triassic material to be washed onto it. The clastic material is interpreted as being derived from the north (Hughes, 1952) and/or the south (Ford and King, 1969). However, the palaeocurrent studies of Walsh et al. (1980) represent persuasive evidence that the source area was to the south. Hence the southern Pennines must have been significantly uplifted since Kenslow Member times (Walsh et al., 1980). This would mean that, if the flora were of Early Pliocene age, an average rate of uplift of 0.1-0.13 mm yr^{-1} must have occurred to bring the southern Pennines to their present elevation (Walsh et al., 1980; Westaway, 2009).

The age of the Brassington Formation has proved controversial. It was originally thought to be Middle Carboniferous (Scott, 1927) and Kent (1957) assigned this unit to the Permian-Triassic on heavy mineral evidence. The Kenslow Member has yielded a flora that has been confidently assigned to the Late Miocene to Early Pliocene (Boulter, 1971b). However, the age of the formation has subsequently been quoted as being Late Miocene (Bott and Bott, 2004; Walsh et al., 1996) and Early Pliocene (Ford, 1972; Westaway, 2009) not based on any specific stratigraphical evidence.

2.3. Previous research on the palaeobotany and palynology of the Brassington Formation

Boulter (1971a) recorded a diverse flora of 75 taxa of leaves, pollen, seeds, spores and wood from the Kenslow Member (Tab. 2.1). Although the majority of these are pollen and spores, *Actinidia*, *Cryptomeria anglica*, *Cyrilla thompsoni*, *Eurya*, *Hypnodendron*, *Smilax* and *Trapa* were only recorded as macrofossils (Boulter, 1969; 1971a). The Kenslow Member flora has been recovered from lignite and coloured clays from Bees Nest, Heathcote, Hindlow, Kenslow Top, Kirkham's, Minninglow and Mountain Ash pits (Walsh et al., 1980). The most abundant and best preserved of these floras are from Bees Nest and Kenslow Top pits (Boulter, 1971b). However, these two pits have yielded the same overall flora but with significantly different proportions of pollen and spores. Bees Nest Pit is dominated by *Pinus* (28%), *Tricolpopollenites microhenrici* (10%), *Sciadopitys* (9%) and *Tricolporollenites margaritatus* (8%) (Boulter, 1971b). By contrast, the Kenslow Top Pit flora predominantly comprises Ericaceae (10-37%) and triporate pollen grains (15-30%) (Boulter, 1971b). Varying conditions of deposition, climate variability and fire dynamics may have influenced these marked differences in floral proportions (Boulter, 1971b).

Order	Family	Taxa	Order	Family	Taxa
Fungi	Dothideomycetes	*Callimothallus* sp.	Angiosperma	Actinidiaceae	*Actinidia* sp.
		Microthalittites sp.		Aquifoliaceae	*Tricolporopollenites iliacus*
	Ascomycetes	*Sphaerites areolatus*			*T. margaritatus*
Bryophyta	Hypnodendraceae	*Hypnodendron sp.*		Araliaceae	*Hedera* sp.
	Sphagnaceae	*Stereisporites crucis*			*Tricolpopollenites edumundi*
		S. germanicus rheanus		Betulaceae	*Alnus* sp.
		S. granisteroides			*Carpinus* sp.
		S. magnoides			*Corylus* sp.
		S. microzonales			*Trivestibulopollenites betuloides*
		S. minimoides		Cyrillaceae	cf. *Cyrilla thompsoni*
		S. minor microstereis		Ericaceae	*Calluna* sp.
		S. pliocenious pliocenious			*Empetrum* sp.
		S. semigranulus			*Erica* sp.
		S. stereoides stereoides			*Rhododendron* sp.
		S. wehningensis		Fabaceae	*Tricolpopollenites ipilenses*
Pteridophyta	Lycopodiaceae	*Lycopodium* sp.			*T. liblarensis fallax*
	Gleicheniaceae	*Gleicheniidites senonicus*			*T. liblarensis liblarensis*
	Osmundaceae	*Osmunda* sp.		Fagaceae	*Tricolporopollenites microhenrici*
	Polypodiaceae	*Laevigatosporites haardti*		Hamamelidaceae	*Liquidambar* sp.
		Verrucatosporites favus		Icacinaceae	*Compositoipollenites rizophorus*
	Polypodiaceae (?)	*Leiotrilites wolffi brevis*		Juglandaceae	*Carya* sp.
		Triplanosporites microsinuosus			*Juglans* sp.
	Shizaeaceae (?)	*Leiotriletes wolffi wolffi*		Liliaceae	*Periporopollenites echinatus*
Gymnosperma	Cupressaceae	*Cryptomeria anglica*			*Smilax* sp.
		C. sp.		Myricaceae	*Myrica* sp.
		Inaperturopollenites hiatus		Nyssaceae	*Nyssa* sp.
		I. dubius		Onagraceae	*Corsinipollenites maii*
	Pinaceae	*Abies* sp.		Pentaphylacaceae	*Eurya* sp.
		Cedrus sp.		Poaceae	*Graminidites media*
		Keteleeria sp.		Salicaceae	*Salix* sp.
		Picea sp.			*Tricolpopollenites retiformis*
		Pinus sylvestris – type		Sapotaceae	*Tetracolporopollenites sapotoides*
		P. haploxylon – type		Symplocaceae	*Porocolpopollenites rotundus*
		P. sp.			*P. vestibulum*
		Tsuga canadensis – type		Trapaceae	cf. *Trapa* sp.
		T. diversifolia – type		Ulmaceae	*Ulmus* sp.
		T. sp.			
	Podocarpaceae (?)	*Podocarpoidites libellus*			
	Sciadopityaceae	*Sciadopitys* sp.			

Table 2.1. The flora of the Kenslow Member of the Brassington Formation taken from Boulter (1969; 1971a).

2.4. Material and methods

New sample material from the Kenslow Member at Kenslow Top Pit was recently collected by the author. The Kirkham Member of Kenslow Top Pit was worked for silica sand by DSF Refractories and Minerals Limited (formerly Derbyshire Silica Firebrick Limited), but has been disused for several decades and is now heavily overgrown (Fig. 2.2). The pit is located at latitude 53° 09’ 00’’ N and longitude 01° 43’ 40’’ W, approximately 0.5 km east of the minor road between Friden and Middleton-by-Youlgreave (Fig. 2.1).

Figure 2.2. Field photograph of the east end of Kenslow Top Pit near Friden. The arrow indicates the location where the Kenslow Member succession was sampled.

During the work on the Brassington Formation by Boulter et al. (1971), a lignite bed was recorded at the top of the Kenslow Member. This lignite is no longer present at Kenslow Top Pit, having apparently been removed during quarrying operations. The grey clays of the Kenslow Member, which directly underlie the lignite, are the youngest part of the Brassington Formation now exposed at Kenslow Top Pit. These clays were sampled for this study. Twelve bulk samples were taken at approximately 30 cm intervals from the base of the Quaternary Till through the grey and coloured clays of the Kenslow Member (Fig. 2.3, 2.4). The samples were processed using the sodium hexametaphosphate technique of Riding and Kyffin-Hughes (2004; 2006). Of the twelve samples collected, only one (MPA 60995) yielded moderately abundant pollen and spores (Fig. 2.3, 2.4). These are relatively well-preserved, but pale in colour and thus were stained using saffranine (Plate 1). The remaining 11 samples proved barren or virtually barren of palynomorphs. This is consistent with Boulter (1971b), who reported very erratic pollen/spore content within the Kenslow Member, from 25 to 500 palynomorphs per equal unit of dry sediment measured to the nearest milligram (Boulter, 1971b). This variability and the relative sparseness of pollen and spores in the Kenslow Member may be due to hydrothermal alteration of these clays. The remaining Brassington Formation in Kenslow Top Pit lies close to the steep limestone walls and there is sporadic mottling with manganese oxides and halloysite (Ford, 1972; 2001). The source of the manganese oxides is probably the weathered dolomitised limestone (Ford, 2001), whereas halloysite is typically formed by the hydrothermal alteration of clay minerals (Kerr, 1972). Hydrothermal processes would tend to destroy sedimentary organic material including palynomorphs (Traverse, 2007).

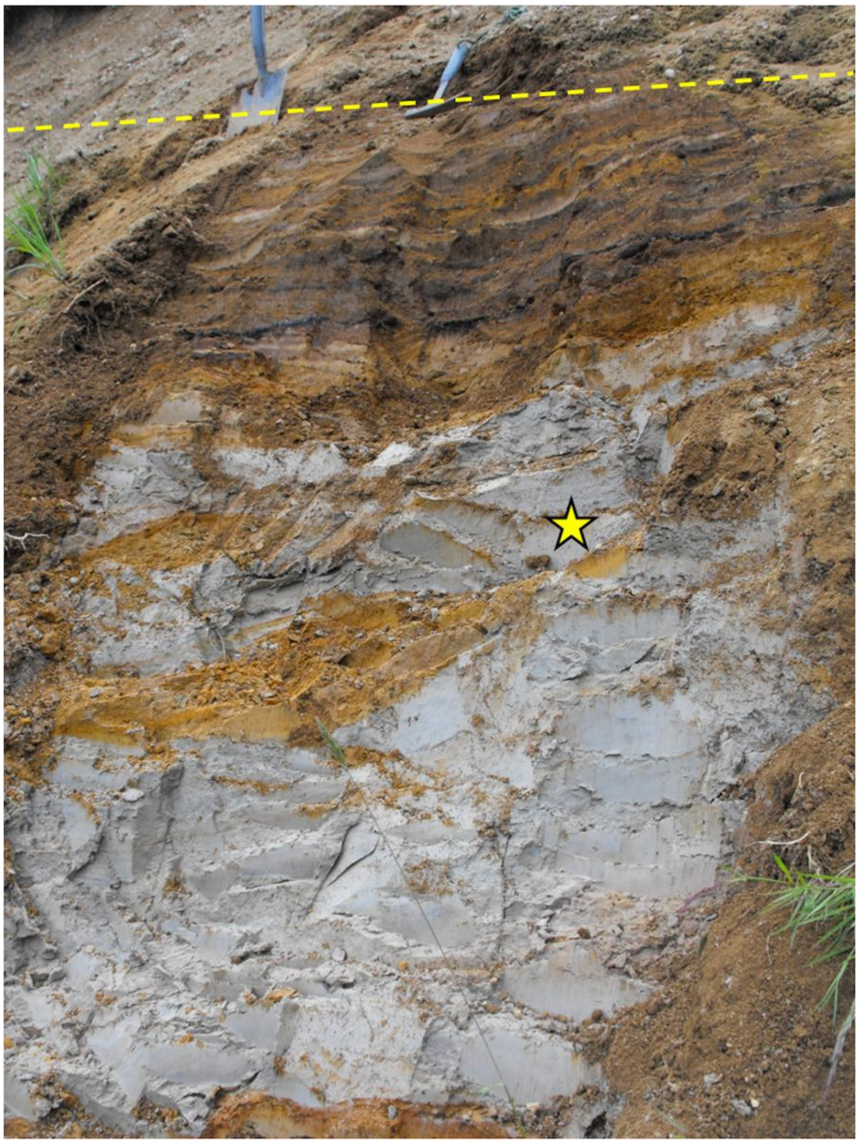


Figure 2.3. Field photograph of the uppermost part of the Kenslow Member at the southeast corner of Kenslow Top Pit near Friden. The dashed line represents the contact between the Kenslow Member and the overlying Quaternary till. The star indicates the location of BGS sample MPA 60995, the single palynologically productive sample in this study. Note the brown-grey mottled or lens-like nature of the majority of the Kenslow Member.

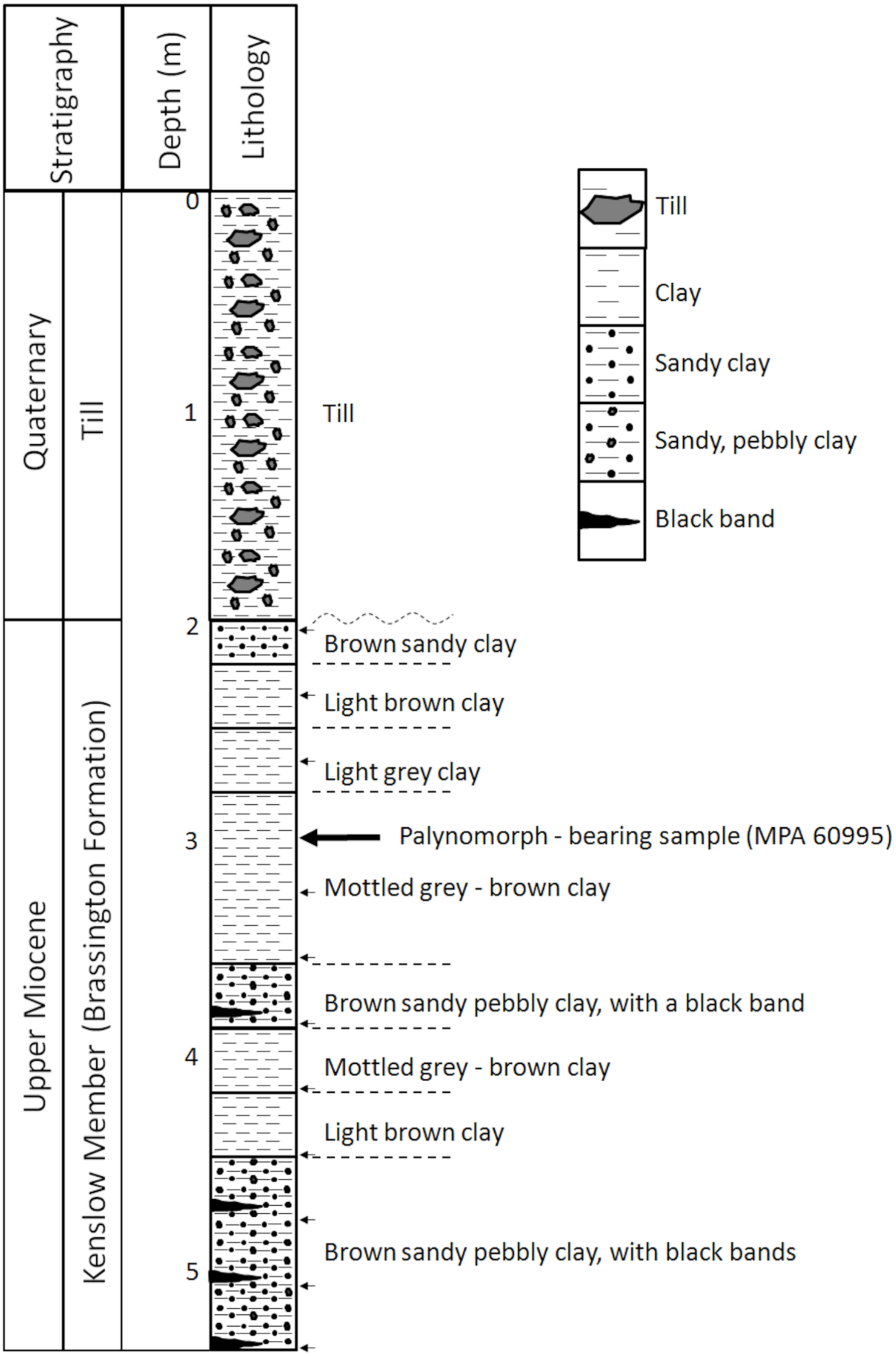


Figure 2.4. A graphic log of the uppermost five metres of the Kenslow Member at Kenslow Top Pit which were sampled at the site shown in Figure 2.2. The productive sample MPA 60995 at 3 m from the top of the succession is marked and the other 11 barren samples are indicated by the small arrows.

2.5. Palynostratigraphy

2.5.1. A revised palynostratigraphy of the data in Boulter (1971a,b)

Boulter (1971a,b) and Boulter et al. (1971) assigned the Brassington Formation to the Late Miocene to Early Pliocene interval based on the occurrence of both Miocene and Pliocene floral elements within the so-called Neogene Component of Von der Brelie (1959; 1967) and Zagwijn (1960). This was based on material from the uppermost, plant-bearing dark grey clays of the Kenslow Member, which are apparently no longer exposed (Boulter et al., 1971, fig. 3). The key age-diagnostic taxa were summarised by Boulter (1971a, tab. 2.2), who commented that forms within the 'Miocene Element' in Europe disappear from the record in this region due to southerly floral migrations in response to a cooling palaeoclimatic trend (Leopold, 1968). It is generally agreed that, in the Neogene of Europe, the principal floral changes are due to migrations as opposed to evolutionary factors such as extinctions. Some of the 'Pliocene elements' mentioned by Boulter (1971a, tab. 2.2) such as *Liquidambar*, *Nyssa*, *Sciadopitys* and *Tsuga* are common in the Miocene of central Europe, e.g. the Czech Republic (Konzalová, 1976), Germany (Thiele-Pfeiffer, 1980), the Polish lowland (Piwocki and Ziembińska-Tworzydło, 1997) and Slovakia (Planderová, 1972).

The pollen assemblages described by Boulter (1971a,b) from the uppermost Kenslow Member represent a mixture of closed/forest types (e.g. *Pinus* and *Quercus* [= *Tricolporopollenites* spp.]) and open/herbaceous types (e.g. Ericaceae and Poaceae). Boulter (1971a, figs. 5, 6) indicated that grass pollen (Poaceae) and 'cold' temperate forms are subordinate to forest types. This is corroborated by the present study, and is indicative of the Miocene rather than the Pliocene (Boulter, 1971a). The proportions of Poaceae and other 'cold' temperate forms such as herbs increased markedly in the Pliocene due to the deteriorating climate in Europe (Klotz et al., 2006; Mosbrugger et al., 2005; Sadowska, 1994; Traverse, 2007). This palaeoclimatic trend has recently been quantified and age-calibrated, resulting in a climatic cooling from around 27 °C to ca. 14 °C between 17 and 5 Ma ago and punctuated by short-term variations (Donders et al., 2009).

Based on pollen biostratigraphical evidence, the Brassington Formation of Kenslow and Bees Nest pits is considered herein to be of Tortonian (Late Miocene) age. The key pollen grains are *Symplocos* spp. (i.e. *Porocolpopollenites rotundus* and *Symplocoipollenites vestibulum*), *Tricolpopollenites liblarensis* and *Tricolporopollenites microhenrici*. Despite there being no extensive terrestrial floral extinctions at the Miocene/Pliocene transition, these are typically subtropical taxa that are abundant in the Miocene pollen floras of continental Europe. *Symplocos* spp. and *Tricolporopollenites microhenrici* have not been recorded from the Pliocene of Bulgaria, The Netherlands, Poland, Slovakia, Turkey and the UK (Donders et al., 2009; Head, 1998; Ivanov, 2004; Ivanov et al., 2010; Kuhlmann et al., 2006; Planderová, 1990; Stuchlik, 1994; Traverse, 2007; Wazynska, 1998). Furthermore, *Tricolpopollenites liblarensis* has been recorded from the Miocene, but not the Pliocene, of Poland (Stuchlik, 1994). A Mid Miocene age is precluded by the relatively low pollen diversity, the lack of high proportions of *Carya* (see Larsson et al., 2011) and the absence of palm pollen (Donders et al., 2009; Piwocki and Ziembińska-Tworzydło, 1997). Palm pollen is rare and typically absent in the Late Miocene and Pliocene (Larsson et al., 2011; Sadowska, 1994).

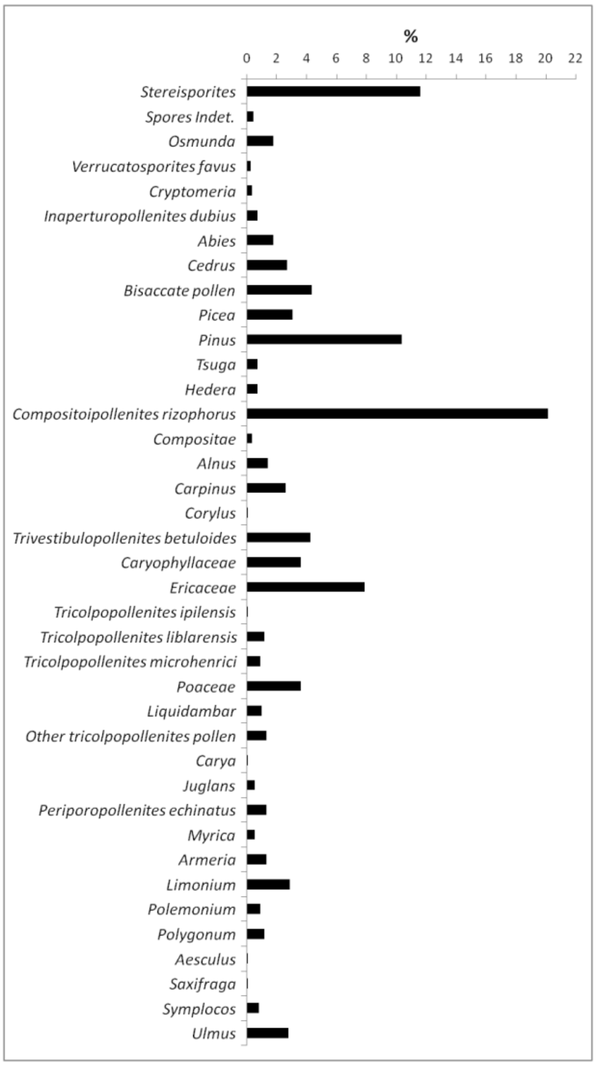


Figure 2.5. Pollen diagram for BGS sample MPA 60995, the single palynologically productive sample of the Kenslow Member in this study.

Order	Family	Taxon name of Boulter (1971b)	Number of grains	%
Bryophyta	Sphagnaceae	*Stereisporites*	125	11.58
Pteridophyta	Indeterminate	Spores	5	0.46
	Osmundaceae	*Osmunda*	19	1.76
	Polypodiaceae	*Verrucatosporites favus*	3	0.28
Gymnospermae	Cupressaceae	*Cryptomeria*	4	0.37
		Inaperturopollenites dubius	8	0.74
	Pinaceae	*Abies*	19	1.76
		Cedrus	29	2.69
		Bisaccate pollen	47	4.36
		Picea	33	3.06
		Pinus	112	10.38
		Tsuga	8	0.74
Angiospermae	Araliaceae	*Hedera*	8	0.74
	Asteraceae (Compositae)	Compositae	4	0.37
	Betulaceae	*Alnus*	15	1.39
		Carpinus	28	2.59
		Corylus	1	0.09
		Trivestibulopollenites betuloides	46	4.26
	Caryophyllaceae	Caryophyllaceae	39	3.61
	Ericaceae	Ericaceae	85	7.88
	Fabaceae?	*Tricolpopollenites ipilensis*	1	0.09
		Tricolpopollenites liblarensis	13	1.20
	Fagaceae?	*Tricolporopollenites microhenrici*	10	0.93
	Icacinaceae	*Compositoipollenites rizophorus*	217	20.11
	Hamamelidaceae	*Liquidambar*	11	1.02
	Indeterminate	Other *Tricolpopollenites* pollen	14	1.30
	Juglandaceae	*Carya*	1	0.09
		Juglans	6	0.56
	Liliaceae	*Periporopollenites echinatus*	14	1.30
	Myricaceae	*Myrica*	6	0.56
	Plumbaginaceae	*Armeria*	14	1.30
		Limonium	31	2.87
	Poaceae	Poaceae	39	3.61
	Polemoniaceae	*Polemonium*	10	0.93
	Polygonaceae	*Polygonum*	13	1.20
	Sapindaceae	*Aesculus*	1	0.09
	Saxifragaceae	*Saxifraga*	1	0.09
	Symplocaceae	*Symplocos*	9	0.83
	Ulmaceae	*Ulmus*	30	2.78
Total			1079	100.00

Table 2.2. The palynomorph content of BGS sample MPA 60995 from the Kenslow Member of the Brassington Formation of Kenslow Top Pit.

2.5.2. The palynostratigraphy of the Kenslow Member of Kenslow Top Pit

From the palynomorph-yielding clay of the Kenslow Member at Kenslow Top Pit, a total of 1079 pollen grains were counted. The dominant elements of the flora are *Compositoipollenites rizophorus* (20.1%), *Stereisporites* spp. (11.6%), *Pinus* spp. (10.4%), Ericaceae (7.9%) and *Trivestibulopollenites betuloides* (4.3%) (Fig. 2.5, tab. 2.2). The presence of *Symplocos* (Plate 1, figure 6), *Tricolpopollenites liblarensis* (Plate 1, figure 3) and *Tricolporopollenites microhenrici* (Plate 1, figure 4) confirm a Late Miocene, rather than Pliocene age, for the Kenslow Member. An older date for the Kenslow Member is precluded based on the sparsity of *Carya* and the absence of palm pollen. The palynoflora recovered here is broadly comparable to that reported from the Kenslow Member by Boulter (1971b). However, taxa unique to this study were recognised, for example *Armeria*, Caryophyllaceae, *Eucommia* (Plate 1, figure 9), *Limonium* (Plate 1, figure 11), *Polemonium*, *Polygonum* (Plate 1, figure 5) and *Saxifraga*. Conversely, there are forms which were reported by Boulter (1971b) that were not found herein (Tab. 2.1, 2.2). These subtle palynofloral differences may be related to the depositional setting of the Kenslow Member. The coloured clays of the Kenslow Member contain lens-like structures (Fig. 2.3) that may represent occasional slumping of material into the karstic hollow, and thus contain slightly different pollen assemblages. This however would imply that, although the deposition of the Brassington Formation was largely continuous, there may have been some breaks in sedimentation followed by subsidence. The Kirkham Member could have subsided as a single depositional unit, but the Kenslow and Bees Nest members may represent the final filling of the karstic cavities and thus may include lenses of material slumped into the hollow or into a lacustrine setting (Fig. 2.3; Kent, 1957; Ford and King, 1969). A lacustrine regime would be consistent with the now absent lignite bed at the top of the Kenslow Member at this locality which represented a wetland or marshy environment in the hollow before it was completely infilled and then partially eroded by glacial processes during the Quaternary.

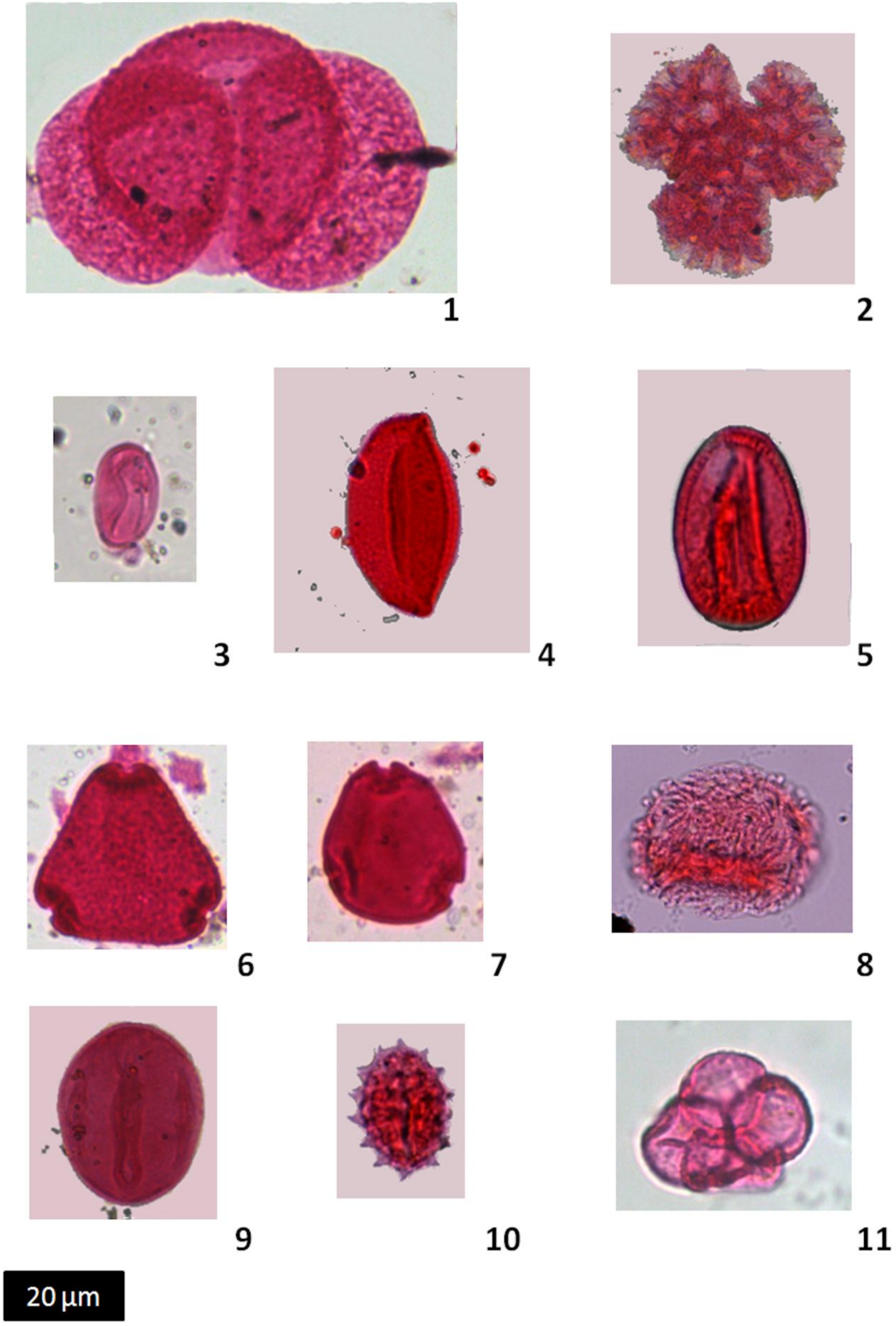


Plate 1. Selected pollen grains from the Kenslow Member at Kenslow Top Pit. Figures 1, 2, 5, 6, 10 and 11 are from BGS sample MPA 60995 and the specimens are curated in the 'MPK' collection of the British Geological Survey, Keyworth, Nottingham, UK. Figures 3, 4, 7, 8 and 9 (prefixed with V) are from the material of Boulter (1971b) and curated in the collections of the Natural History Museum, London. The scale bar refers to all specimens. 1. *Pinus* (V55662), 2. *Limonium* (MPK 14213), 3. *Tricolpopollenites liblarensis* (V55661), 4. *Tricolporopollenites microhenrici* (V55635), 5. *Polygonum* (MPK 14214), 6. *Symplocos* (V55659), 7. *Symplocos* (V55659), 8. *Polemonium* (MPA60995D), 9. *Eucommia* (V55635), 10. *Compositoipollenites rizophorus* (MPK 14216), 11. Ericaceae (MPK 14217).

2.6. The Late Miocene palaeoecology and palaeoclimate of Derbyshire

The Kenslow Member palynoflora was interpreted by Boulter (1971b) as representing two communities, a dominant lowland forest assemblage and a distal Ericaceous heathland from the hills to the north. We agree with the presence of a mixed lowland forest, but not the distal Ericaceous heathland. In Europe, Ericaceae during the Miocene ranged from 1 to 17% of the overall floras, and heathers are often interpreted as forming part of the understory vegetation (E.M. Friis personal communication, 2011; Harzhauser et al., 2008; von der Brelie and Wolf, 1981;). However the presence of *Armeria*, *Limonium*, *Polemonium* and *Saxifraga*, together with significant Poaceae, represent more open and/or disturbed conditions, possibly with some local salt water influence, at the time of clay deposition relative to the overlying peat deposit. In particular, the occurrence of *Armeria* indicates a possible maritime influence (Tutin et al., 1972), possibly suggesting that this part of Derbyshire was relatively close to sea level during the Miocene. However, *Armeria* is known to grow inland on rocky or lead rich soils and therefore does not have to indicate maritime influence (Mabey, 1996). The Kenslow Member forest was likely to have been of warm-temperate character, containing taxa comparable with other European Late Miocene warm-temperate forests such as *Abies*, *Cedrus*, *Keteleeria*, *Liquidambar*, *Symplocos* and *Tricolporopollenites microhenrici* (? = *Quercus*) (Blanc et al., 1974; Boulter, 1971b; Nagy, 1967; Utescher et al., 2011a; Worobiec et al., 2009).

Using the coexistence approach of Mosbrugger and Utescher (1997) and Utescher and Mosbrugger (2010), a mean annual temperature (MAT) of 15.7 to 16.5°C has been calculated for the total Kenslow Member flora (Fig. 2.6a; Tab. 2.1, 2.2). Simply using the palynoflora recovered from sample MPA 60995 (Tab. 2.2) to calculate the MAT gives a range of 15.6 to 18.4°C (Fig. 2.6b). Despite the differences in the range of possible MATs from the full flora and the one productive sample in this study, the median value of both ranges is approximately 16°C. This is around twice the current MAT for this part of Derbyshire (Cramer and Leemans, 2001). A coexistence approach of only the macrofossils also yields a MAT of 16.2±2.6°C. This consistency in reconstructed MAT between the full flora, sample MPA 60995 and the macrofossils is a good indicator that the result is reliable. Especially as each of the different coexistence approaches has different taxa defining the climate envelope: The full flora is controlled by *Keteleeria*, *Lycopodium* and *Sciadopitys*; sample MPA 60995 is controlled by *Cedrus*, *Inaperturopollenites* and *Symplocos*; and the macrofossil coexistence approach is controlled by *Cyrilla* and *Smilax*. Of note is the presence of three outliers in the coexistence approach; *Empetrum* sp., *Pinus sylvestris* – type (Fig. 2.6a) and Saxifraga (Fig. 2.6b). These outliers require colder MAT values than the rest of the flora and are likely to reflect errors in the coexistence approach. Errors such as the assignment of a fossil taxon to the wrong NLR and the database not containing complete climate information on NLR taxa (Mosbrugger and Utescher, 1997; Utescher and Mosbrugger, 2010).

A MAT for the Tortonian of 18 to 21°C in the Netherlands was recently suggested by Donders et al. (2009); this is slightly warmer than has been reconstructed for the Kenslow Member flora and may be due to the Netherlands being further south than Derbyshire. The temperatures derived by Donders et al. (2009) are regarded as reliable; however there may be a calibration or seasonality skew of the archeal membrane lipid-based proxy (Sinninghe Damsté et al., 2008) despite the calibration to a global dataset of MAT. Further palaeoclimatic information can be derived from the presence of *Eucommia*, which may indicate a mean spring temperature of between 13 and 21°C because this is the controlling factor for germination (Wang et al., 2003).

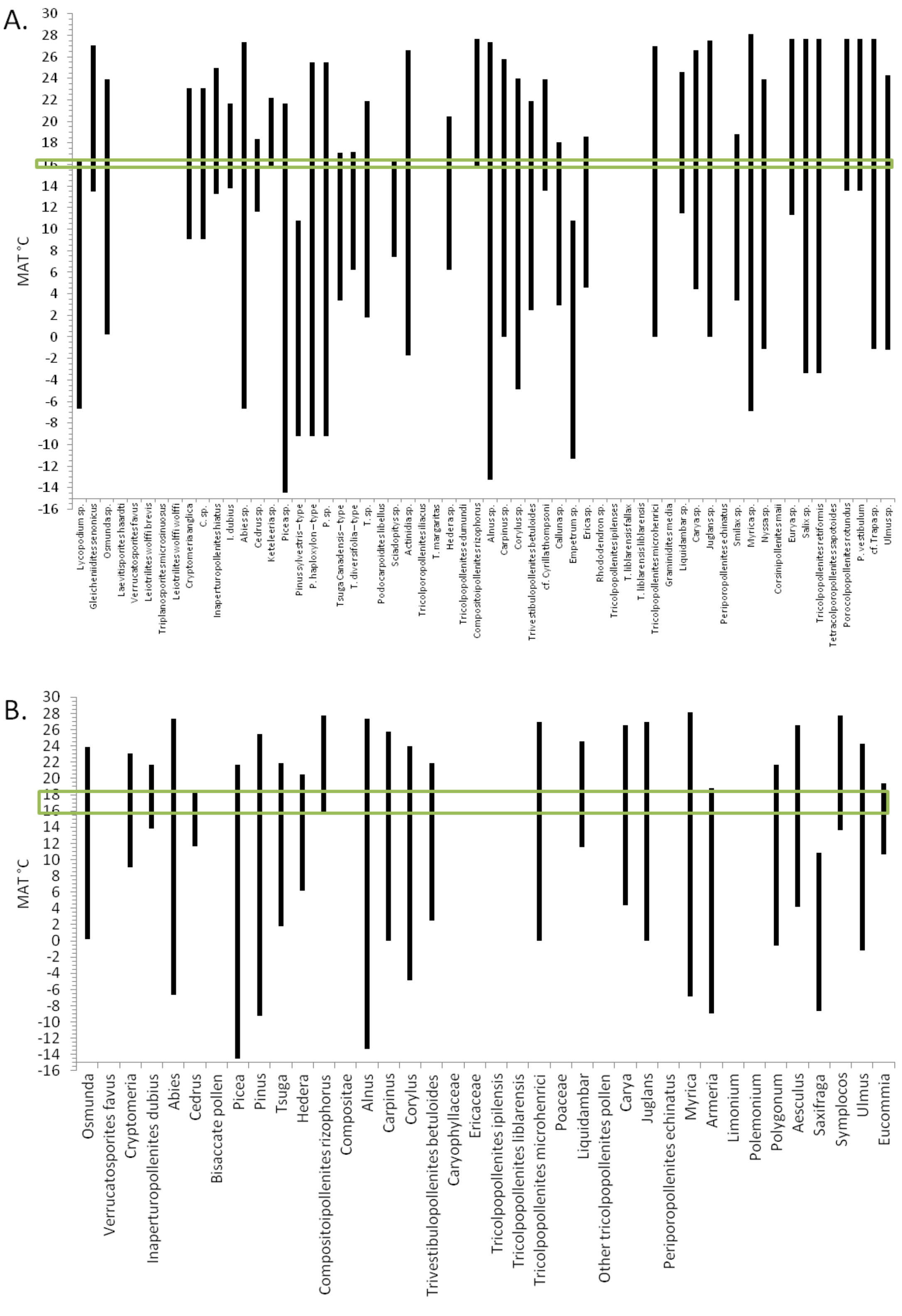


Figure 2.6. The coexistence approach results for the Kenslow flora, Brassington Formation. A. The original flora from Boulter (1969; 1971a). B. The palynoflora recovered from sample MPA 60995. Green box indicates the envelope of coexistence. Taxa without MAT estimates are not available in the original dataset (Utescher and Mosbrugger, 2010).

2.7. Conclusions

This revised pollen biostratigraphy of the Kenslow Member clearly demonstrates that the Brassington Formation of Derbyshire and Staffordshire is of Tortonian (Late Miocene) age. Because the underlying Kirkham and Bees Nest members are unequivocally part of the same genetic depositional succession, with no hiatuses, the three members of the Brassington Formation are interpreted as being both conformable and of the same origin (Ford, 1972; Ijtaba, 1973). Therefore the entire Brassington Formation is considered to be of Tortonian age. This refines the Late Miocene-Early Pliocene interpretation of Boulter and Chaloner (1970) and Boulter (1971a,b) to a stage-specific level. An Early Pliocene age is precluded due to the presence of the pollen taxa *Symplocos*, *Tricolpopollenites liblarensis* and *Tricolpopollenites microhenrici*, which are all absent from the Pliocene of northwest and central Europe. The Late Miocene age of the Brassington Formation indicates that the rates of uplift of the southern Pennines structural block during the Pliocene/Early Pleistocene interval were significantly lower than has been recently suggested (Westaway, 2009). Based on this revised age, and assuming the Kenslow Member was deposited near sea level (Walsh et al., 1980; Westaway, 2009), a continuous uplift rate for the southern Pennines would be 0.03-0.06 mm yr^{-1}; this is considerably lower than previous estimates of 0.1-0.13 mm yr^{-1} (Westaway, 2009). Using the coexistence approach for the Kenslow Member palynofloras, a median value for the MAT is around 16°C. Derbyshire during the Tortonian was inhabited by a warm – temperate mixed lowland forest (Fig 2.7). There is evidence for more open areas in the form of herbaceous taxa and even possible salt water influence from the presence of *Armeria*.

Figure 2.7. The forest preserved in the Kenslow Member may have been similar to the warm – temperate forest of Doi Inthanon mountain, Doi Inthanon National Park, Thailand. The warm - temperate forest of Doi Inthanon is found at 2500 meters above sea level and is mainly composed of *Quercus* – *Castanopsis* – *Pinus* with a fern – shrub understory and abundant *Sphagnum*.

Chapter 3
Global vegetation dynamics and latitudinal temperature gradients during the mid to Late Miocene (15.97 - 5.33 Ma)

Vegetation is the visible crystallised climate – Vladimir Köppen, 1936

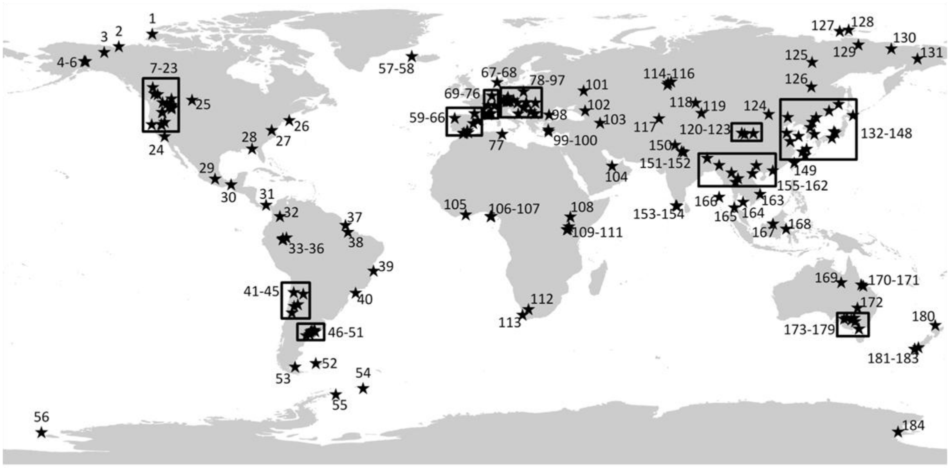
3.1. Introduction

In the previous chapter I presented the vegetation of a single point on the globe, during a specific time. That point was Derbyshire, UK and the time was 9 – 7.25 Ma. During the time it took for the sands clays and lignite of the Brassington Formation to be deposited in this part of central England, a warm – temperate mixed forest grew under an ambient MAT of 16°C. This already provides valuable insight into how much warmer and wetter this part of the world was during the late Tortonian, as the MAT of Derbyshire today is around 8°C and the potential natural vegetation would be temperate deciduous broadleaf woodland (Fig. 1.6). However, it is but a single dot on a map and one occurrence in the archives of the geological records of the Miocene.

In Chapter 1 I introduced the common technique, to study modern global patterns, of using satellite imagery. This is of course impossible for geological time, but through the synthesis of global data it should be possible to get a “pseudo” satellite view of vegetation. This chapter will present such a synthesis, providing a view of the global evolution of vegetation and climate from the Langhian to the Messinian.

Within this chapter I present a 634 site palaeobotanical dataset for the Middle and Late Miocene. This is the most comprehensive dataset of its kind suitable for use in palaeoclimate and palaeoecology studies. Within the paper the dataset is used to explore the climate that is reconstructed from the fossil vegetation. The climate inferred from the distribution of vegetation for the Langhian, Seravallian, Tortonian and Messinian is then compared to the various CO_2 proxies. This is an attempt to better understand Miocene climate and CO_2 evolution. By seeing if major climate changes, recorded as major biome changes, match the dynamics of reconstructed atmospheric CO_2 levels. The vegetation has been reconstructed using the 28 biome scheme of the BIOME4 vegetation model (Fig. 1.6; Table 3.1), which makes it suitable for data – model comparison studies. The presented data can also be used to generate global vegetation maps in combination with vegetation models to explore the impacts of Miocene vegetation on climate (Salzmann et al., 2008). This will be the subject of the following two chapters, whereas this chapter focuses on a review of available palaeobotanical data. Within this chapter the latitudinal temperature gradients are also explored to gain an insight into how much warmer, than pre – industrial, the Miocene was. For the pre – industrial era the latitudinal temperature gradients were relatively steep: warm temperatures at the equator cooling rapidly to the poles. For warmer intervals in the geological record it has been proposed that the latitudinal temperature gradient was much shallower (Ballantyne et al., 2010).

A) Langhian (15.97 – 13.65 Ma)



B) Serravallian (13.65 – 11.61 Ma)

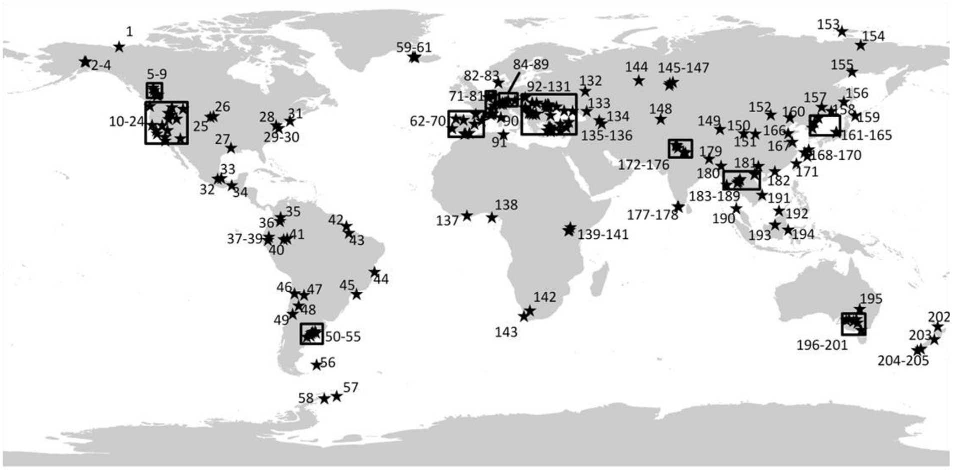
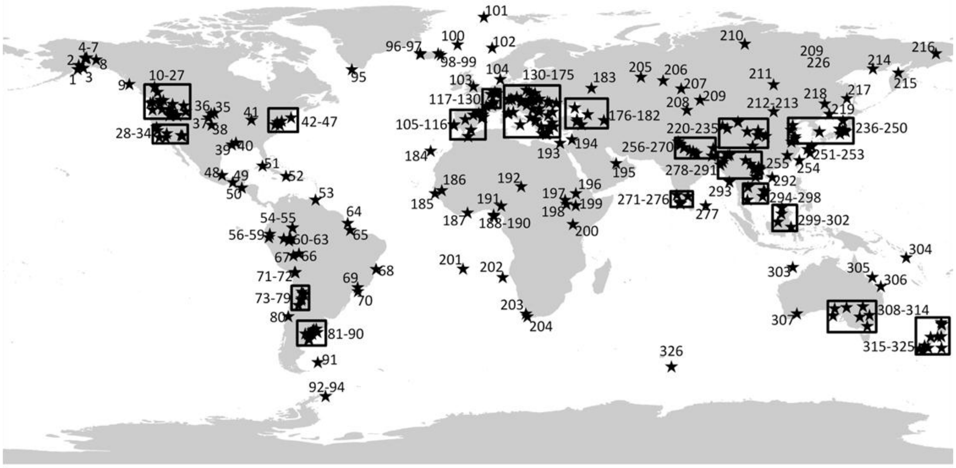


Figure 3.1. Distribution of Langhian (N = 184) (A) and Seravallian (N = 205) (B) palaeobotanical locations. The references for the locations are listed in Appendices A and B.

A) Tortonian (11.61 – 7.25 Ma)



B) Messinian (7.25 – 5.33 Ma)

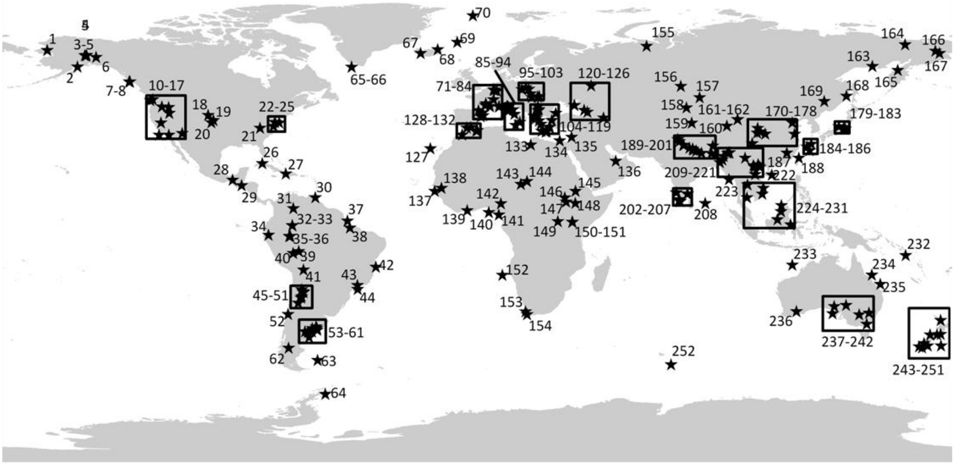


Figure 3.2. Distribution of Tortonian (N = 326) (A) and Messinian (N = 252) (B) palaeobotanical locations. The references for the locations are listed in Appendices A and B.

3.2. Methods

3.2.1. Constructing the vegetation database

Using TEVIS (Tertiary Environments Vegetation Information System) (Salzmann et al., 2008), which is a Microsoft Access and ArcGIS 9 based database, 634 Middle to Late Miocene vegetation sites (Fig. 3.1; 3.2) have been collected from the literature and recorded in an internally consistent manner. Using the author's interpretation of the fossil assemblage, the reconstructed palaeovegetation has been translated into biomes using the classification scheme of the BIOME4 mechanistic vegetation model (Kaplan, 2001). TEVIS not only records the vegetation of the palaeobotanical site but also the latitude and longitude, sedimentology, method used to date the sample and a quality indicator – to ascertain the resolution of the chronology. Where available from literature, numerical climatic parameters such as MAT and

MAP are also recorded in TEVIS. Extracting climatic parameters from fossil assemblages can be achieved by a number of techniques and the majority of the estimates in the TEVIS database come from either the co-existence approach (Bruch et al., 2006) or CLAMP (Spicer, 2007; Spicer et al., 2009; Wolfe, 1979; 1993), both of these were introduced in Chapter 1.

It has been possible to confidently assign all literature-based vegetation reconstructions to a corresponding BIOME4 classification (Fig. 1.6). However, it should be noted that although the BIOME4 classification represents biomes of the modern world these are not identical, in species composition, to those of the Miocene and in some regions the Miocene biome has no modern analogue. The correspondence between a Miocene biome and a modern analogue becomes more uncertain with increasing age. By the Langhian some biomes, particularly those of the high northern latitudes, begin to show a species assemblage not seen in the modern world. An excellent example of this is the high latitude (>69°N) forests from the Middle Miocene of North America. These forests had a composition of *Fagus*, *Glyptostrobus*, *Liquidambar*, *Metasequoia*, *Picea*, *Pinus*, *Quercus*, *Taxodium* and *Ulmus* (White and Ager, 1994; White et al., 1997; Williams et al., 2008). This is a very different assemblage to the modern flora of boreal and arctic North America (Barbour and Billings, 2000). Despite the taxonomic differences between this Middle Miocene flora and the modern floras of North America, the structure and estimated productivity of this forest is comparable to modern biomes (Williams et al., 2008).

3.2.2. Bioclimatic zones

To gain a better insight into the latitudinal temperature gradients of the Middle to Late Miocene the latitudinal vegetation distribution can be compared to the pre - industrial potential vegetation distribution. The pre - industrial potential natural vegetation shows progressively colder biomes from the equator, as latitude increases. In simple terms this reflects the latitudinal temperature gradient, which is highest at the equator and lowest at the poles. This requires a simplified scheme to provide an understandable view of the latitudinal temperature gradients for the Langhian, Seravallian, Tortonian and Messinian stages. To facilitate this each fossil site, within TEVIS, is assigned to one of seven megabiomes and one of six bioclimatic zones (Table 3.1), as well as assigning each fossil site to one of the 28 biomes of the BIOME4 classification (Salzmann et al., 2009). The bioclimatic zone classifications are based on the seven megabiome classification scheme presented in Salzmann et al., (2009). Megabiomes are broader categories grouping numerous biomes. The six bioclimatic zones are; tropical, subtropical/warm-temperate, temperate, boreal, tundra and ice. These classifications reflect a simplified qualitative view of the temperature range of the 28 biomes used in the BIOME4 model. However certain biomes can be included in multiple bioclimatic zones, for example the temperate deciduous broadleaf savanna biome. This biome is referred to as a temperate vegetation type (Gnibidenko et al., 1999) and a warm – temperate vegetation type (Thomasson, 2005). To avoid complications from biomes that are more climatically controlled by seasonality and precipitation than they are by temperature, only forest, woodland or tundra biomes were used in the construction of the bioclimatic zone gradients (Table 3.1).

Biome code	BIOME4 Vegetation type (Kaplan, 2001)	Megabiome type (Salzmann et al., 2009)	Bioclimatic Zone
1*	Tropical evergreen broadleaf forest	Tropical forest	Tropical
2*	Tropical semi-evergreen broadleaf forest	Tropical forest	Tropical
3*	Tropical deciduous broadleaf forest and woodland	Tropical forest	Tropical
4*	Warm - temperate evergreen broadleaf and mixed forest	Warm - temperate forest	Subtropical/ Warm - temperate
5*	Temperate deciduous broadleaf forest	Temperate forest	Temperate
6*	Temperate evergreen needleleaf forest	Temperate forest	Temperate
7*	Cool - temperate mixed forest	Temperate forest	Temperate
8*	Cool evergreen needleleaf forest	Temperate forest	Temperate
9*	Cool-temperate evergreen needleleaf and mixed forest	Temperate forest	Temperate
10*	Cold evergreen needleleaf forest	Boreal forest	Boreal
11*	Cold deciduous forest	Boreal forest	Boreal
12	Tropical savanna	Savanna and dry woodland	Tropical
13	Tropical xerophytic shrubland	Savanna and dry woodland	Tropical
14	Temperate xerophytic shrubland	Savanna and dry woodland	Temperate
15*	Temperate sclerophyll woodland and shrubland	Savanna and dry woodland	Temperate
16	Temperate deciduous broadleaf savanna	Savanna and dry woodland	Temperate
17	Temperate evergreen needleleaf open woodland	Savanna and dry woodland	Temperate
18	Cold parkland	Savanna and dry woodland	Boreal
19	Tropical grassland	Grassland	Tropical
20	Temperate grassland	Grassland	Temperate
22*	Graminoid and forb tundra	Tundra	Tundra
23*	Low and high-shrub tundra	Tundra	Tundra
24*	Erect dwarf-shrub tundra	Tundra	Tundra
25*	Prostrate dwarf-shrub tundra	Tundra	Tundra
26*	Cushion-forb, lichen, and moss tundra	Tundra	Tundra
21	Desert	Desert	N/A
28*	Ice	Land Ice	Ice

Table 3.1. A summary of the BIOME4 vegetation scheme (Kaplan, 2001), its translation into the seven megabiome scheme (Salzmann et al., 2009) and the six bioclimatic zone scheme. An * denotes that the biome was suitable to be used in the bioclimatic zone gradients.

Two transects were chosen to reconstruct the latitudinal bioclimatic zonal gradients. The west Pacific transect (WPT) and the west Atlantic transect (WAT) (Fig. 3.3) were selected due to the good data coverage, not only spatially but also temporally. These transects also avoid most of the major mountain regions (though the Himalayas may have influenced part of the WPT), which minimises the complicating factor of altitude.

Using the latitudinal transects in Figure 3.3 the maximum pole - ward extent of each bioclimatic zone has been plotted, for each of the four studied time slabs. These have been compared to the maximum pole ward extent of pre - industrial potential natural vegetation generated using the BIOME4 model (Kaplan, 2001), driven by observed climate (Fig. 1.6). The methodology does not provide numerical climate data to reconstruct the latitudinal temperature gradient, but does compare the maximum pole ward extent of bioclimatic zones. The method shows the relative change in the qualitative bioclimatic zones over time and provides an insight into how different the latitudinal temperature gradient would have been during the studied geological stages.

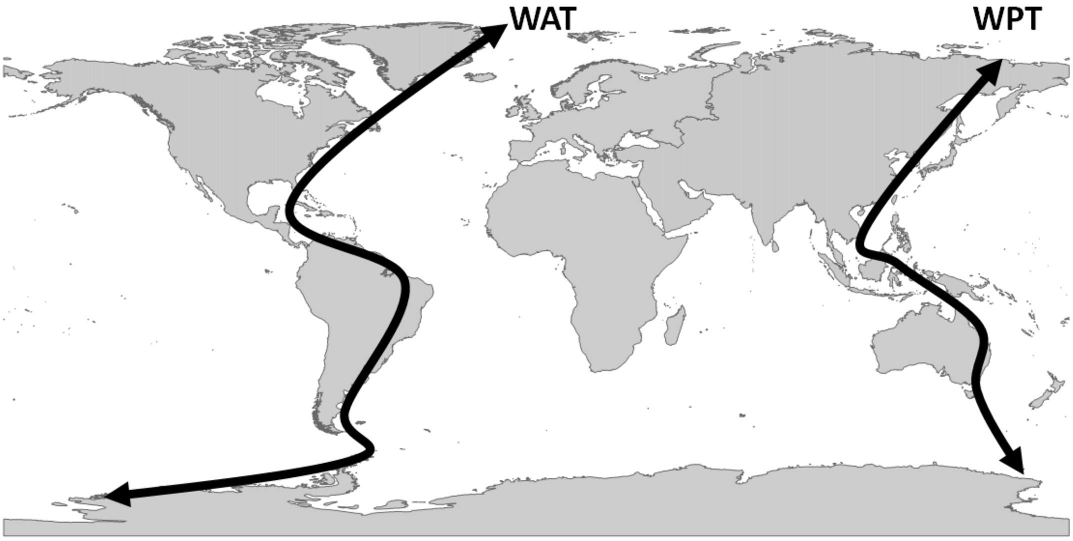
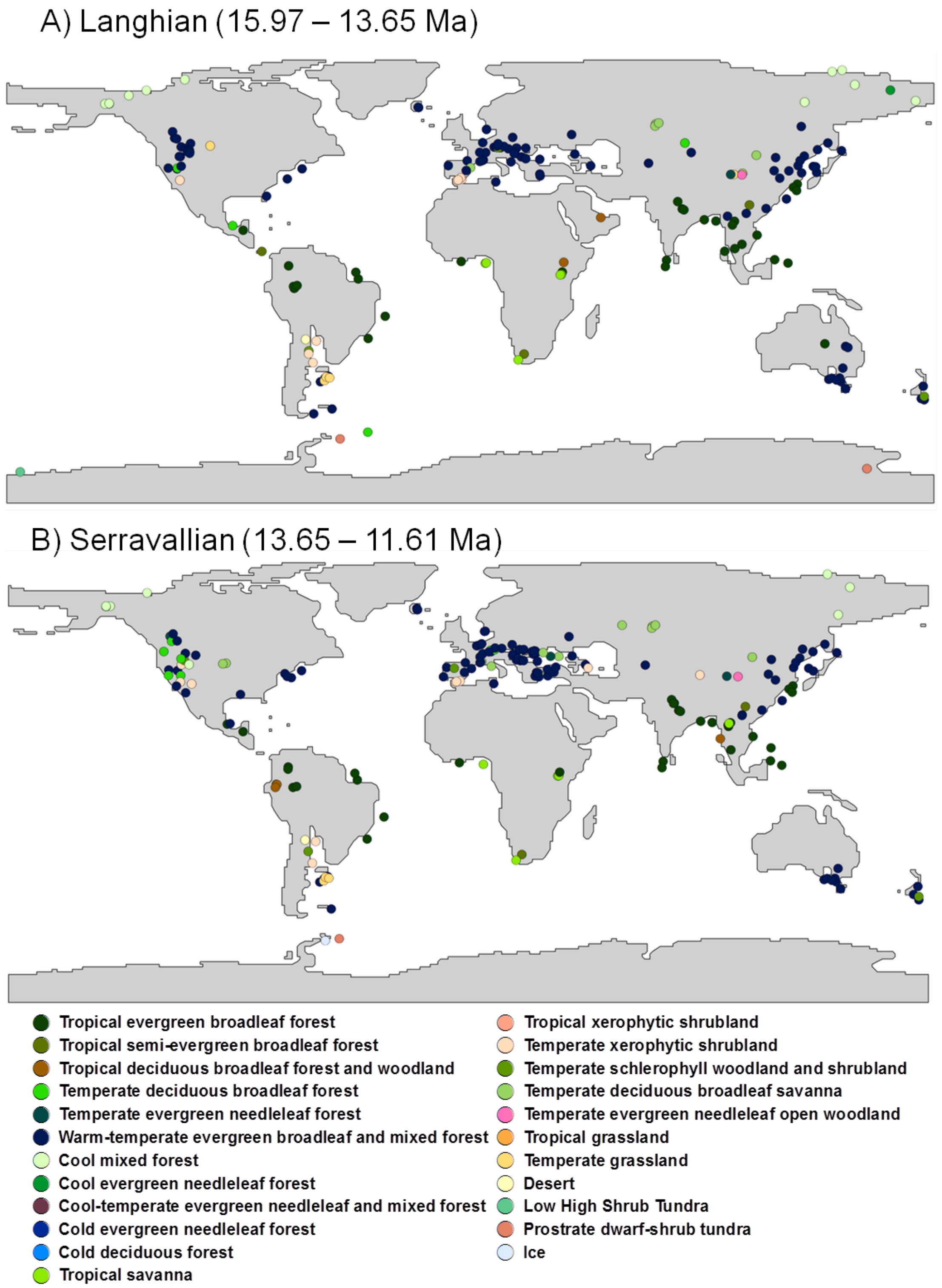


Figure 3.3. The location of the latitudinal transects used for reconstructing the latitudinal distribution of bioclimatic zones.


A) Langhian (15.97 – 13.65 Ma)

B) Serravallian (13.65 – 11.61 Ma)

Figure 3.4. The vegetation distribution of the Langhian (A) and Seravallian (B) from palaeobotanical data, translated into the 28 biome scheme of the BIOME4 model.

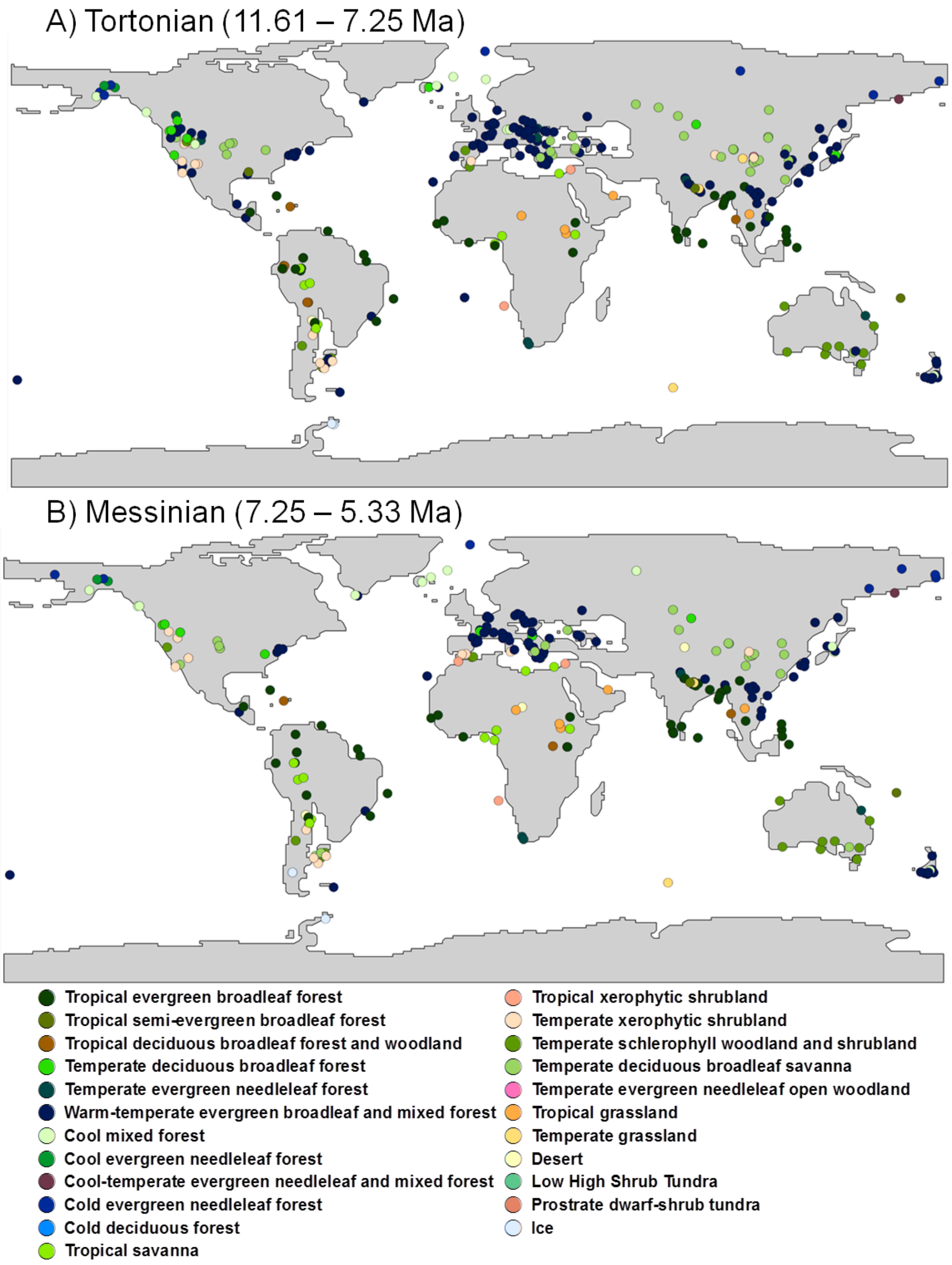


Figure 3.5. The vegetation distribution of the Tortonian (A) and Messinian (B) from palaeobotanical data, translated into the 28 biome scheme of the BIOME4 model.

3.3. Global vegetation change from Langhian to Messinian

3.3.1. Global biome distributions through time

The plotted biomes, from the 634 fossil vegetation sites in TEVIS, provide an insight into Middle to Late Miocene vegetation and climate. The Langhian stage is represented by 184 fossil sites (Fig. 3.4A), the Seravallian by 205 sites (Fig. 3.4B), the Tortonian by 326 sites (Fig. 3.5A) and the Messinian by 252 sites (Fig. 3.5B). Some of these sites cover multiple time stages whilst others may be better dated and correspond to an interval smaller than the assigned geological stage. The ages assigned to the geological stages follows Gradstein et al. (2004). There is excellent data coverage, for all stages, in temperate and tropical Eurasia. North and South America also have good data coverage. Whilst the high northern latitudes, Africa and central Australia have poor data coverage. All the data points are presented in the supplementary information with their modern day latitude – longitude, age range, biome and megabiome code and references (Appendices A and B).

The vegetation change shown by the 634 palaeobotanical sites indicates a global cooling trend from the Langhian to the Messinian. During the Middle Miocene (Langhian and Seravallian) cool - temperate mixed forests were above 60°N with no evidence for boreal forests. By the Late Miocene (Tortonian and Messinian) boreal forests are abundant above 60°N, though in places temperate biomes are still present. The cooling trend is also indicated by the subtropical/warm temperate megabiome, which is most widely distributed during the Langhian. Through the remaining Miocene it gradually becomes more restricted, being displaced by cooler and/or drier biomes. Linked with this cooling and drying trend is the expansion of deserts. During the Langhian there is evidence for an Atacama Desert in South America, by the Messinian there is evidence for a Sahara (Africa) and Taklimakan (Asia) desert.

In the following section the global vegetation pattern, distribution and changes from the Middle Miocene to the Messinian will be discussed by regions (Fig. 3.6). Specific fossil localities will be referred to using the site numbers (Fig. 3.1; 3.2) in parentheses with a prefix denoting the geological stage it has been assigned to (L = Langhian; S = Seravallian; T = Tortonian; M = Messinian). Climatic data are also presented below in the form of Mean Annual Temperature (MAT) in °C and Mean Annual Precipitation (MAP) in mm per year. The climatic data are also presented in Tables 3.2, 3.3, 3.4, 3.5.

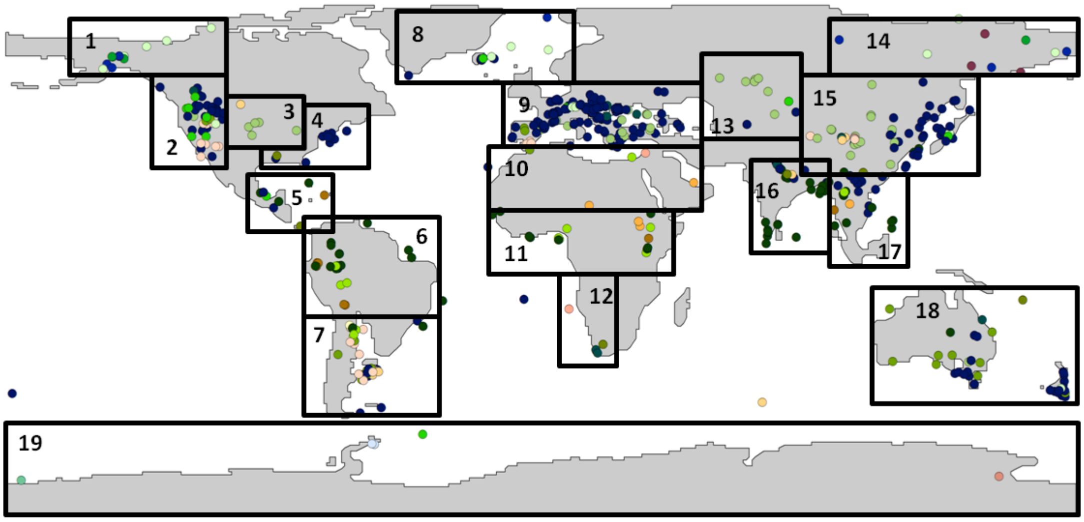


Figure 3.6. The distribution of the 20 regions used to discuss the global vegetation changes through time.

3.3.1.1. Northern North America

Overall this region changes from being dominated by cool - temperate forests in the Middle Miocene, to an area dominated by boreal forests in the Messinian. This cooling trend is associated with an increase in biome types but a reduction in taxa diversity and a loss of more thermophilic elements, except in southern coastal Alaska (Reinink-Smith and Leopold, 2005).

In northern North America (above 60°N) reported Middle to Late Miocene fossil floras are restricted to Alaska and north-west Canada. During the Langhian a cool - temperate mixed forest is found on Banks Island (74°N), the Mackenzie Delta (69.5°N) and at numerous sites in Alaska (Sites L1 – L6) (Fig. 3.4A). This cool - temperate mixed forest was taxonomically diverse with *Fagus, Glyptostrobus, Liquidambar, Metasequoia, Picea, Pinus, Quercus, Taxodium* and *Ulmus* and has a reconstructed MAT of 8 - 9°C (Table 3.2) (White and Ager, 1994; White et al., 1997; Williams et al., 2008). The cool - temperate mixed forest biome still dominated this region during the Seravallian (Sites S1 – S4) (Fig. 3.4B), although CLAMP derived climate estimates suggest a climatic cooling lowered regional MAT to as low as 4°C by 12 Ma (Table 3.3) (White et al., 1997).

By the Tortonian northern North America showed a more diverse array of biomes (Fig. 3.5A). The cool - temperate mixed forest which dominated the region during the Middle Miocene was still present between 60°N at Homer (Site T1) and 65°N at Coal Creek (Site T7). The Coal Creek flora changed biome type at around 9 Ma to a cool evergreen needleleaf forest. This biome is also preserved at Tatlinaka Creek (Site T4) which has a pollen assemblage dominated by *Betula* and *Pinus* spp., with an estimated MAT of 5°C (Table 3.4) (Leopold and Liu, 1994;

Wahrhaftig et al., 1969). During the Tortonian a cold evergreen needleleaf forest was also present in the northern North America region (Site T2, T3 & T6), this can be considered to have been a taxonomically richer form of the present day boreal forests, with a MAT of 4±1°C (Wolfe, 1994a; Wolfe and Leopold, 1967). During the Messinian the biome distribution of north-west North America appears to reflect a continued cooling (Fig. 3.5B). The cool - temperate mixed forest was still present but only up to 59°N (Site M2). North of 60°N the vegetation was a mix of cool evergreen needleleaf forests (Sites M3, M4 & M6) and cold evergreen needleleaf forests (Sites M1 & M5) (Fig. 3.5B). The cold evergreen needleleaf forest preserved at Lava Camp, Alaska is dominated by *Larix* and *Pinus monticola*, the regional MAT for this biome is reconstructed to be between -10 to +6°C (Table 3.5) (Matthews Jr. and Ovenden, 1990; White et al., 1997).

3.3.1.2. Western North America

During the Langhian this region was dominated by a warm – temperate evergreen broadleaf and mixed forest. Through the Seravallian and Tortonian a drier climate caused the warm-temperate mixed biome to gradually become more restricted and was replaced by more open biomes. By the Messinian the warm-temperate biome was replaced by a north to south pattern of progressively drier biomes.

During the Langhian western North America was dominated by a warm – temperate evergreen broadleaf and mixed forest biome between 40°N and 54°N (Fig. 3.4A). At Purple Mountain (Site L23), a late Langhian to early Seravallian locality, the warm – temperate evergreen broadleaf and mixed forest biome is estimated to have had a MAT of 11.5°C and a MAP of 825±65mm (Axelrod, 1995). There is evidence for drier biomes at Pyramid (Site L22) and Tenachapi (Site L24), which have been reconstructed as a temperate deciduous broadleaf forest and temperate xerophytic shrubland, respectively. These biomes located south of 40°N suggest a drier climate regime existed in the south-west of North America. During the Seravallian the vegetation of western North America was much less uniform when compared to the Langhian. Whilst areas of warm – temperate evergreen broadleaf and mixed forest still existed these had become separated by areas of drier and/or cooler biome types (Fig. 3.4B). At Esmeralda (Site S20) a diverse palaeobotanical fossil assemblage records an oak – juniper woodland (temperate deciduous broadleaf forest) estimated to have grown under a MAP of 406±51mm (Axelrod, 1940; Berry, 1927). At Cougar Point (Site S15) a pollen flora dominated by *Artemisia* and Poaceae shows the existence of a xerophytic shrubland at ca. 12 Ma (Davis and Ellis, 2010).

By the Tortonian palaeobotanical evidence suggests that the extensive warm – temperate evergreen broadleaf and mixed forest of the Langhian, that began to fragment in the Seravallian, had become even more restricted. During the Tortonian the warm – temperate evergreen broadleaf and mixed forest was present between 43°N and 48°N (Sites T13 – T17, T19 & T26) and along the coast between 31°N and 33°N (Sites T30 – T32) (Fig. 3.5A). A drill hole in Willamette Valley, Oregon (Site T17) yielded a rich palynomorph assemblage derived from the warm – temperate evergreen broadleaf and mixed forest biome, the assemblage contains *Carya, Castanea, Cedrus*, *Fagus, Liquidambar, Nyssa, Platanus, Pterocarya, Sequoia* and *Ulmus* (Roberts and Whitehead, 1984). Climate estimates from the warm – temperate evergreen broadleaf and mixed forest biome suggests it existed under an MAT of 11 - 19°C and a MAP of 617.5 – 1250mm (Table 3.4). The lower MAP estimate of 617.5mm seems rather too low to support the warm – temperate evergreen broadleaf and mixed forest biome but this reflects an unusual setting of one palaeobotanical site (Site T30) which may have been a forest supported by summer fog (Axelrod, 2000). Separating the two areas of warm – temperate evergreen broadleaf and mixed forests during the Tortonian there was a mixture of temperate deciduous broadleaf forest, temperate deciduous broadleaf savanna and temperate sclerophyll woodland and shrubland. Further south there was temperate xerophytic shrubland (Sites 22, 24, 29, 31 & 33). These biomes are estimated to have had a MAT comparable to the warm – temperate evergreen broadleaf and mixed forest but with a lower MAP (Table 3.4). North of 48°N there was a temperate deciduous broadleaf forest (Sites T11 – T13) and temperate evergreen needleleaf forest (Site T10) further north. At Skonun Point (Site 9) a pollen assemblage reminiscent of the high latitude Langhian cool - temperate mixed forest biome with abundant *Alnus, Pinus*, *Quercus* and Taxodiaceae (Martin and Rouse, 1966; White et al., 1994) represents the southernmost evidence for the biome seen in Alaska (Sites T1 & T7) during this stage.

By the Messinian the warm – temperate evergreen broadleaf and mixed forest was gone from western North America. The drier biomes, that had been gradually replacing the warm – temperate evergreen broadleaf and mixed forests, were present continuously from 31°N to 48°N. On Queen Charlotte Island the cool - temperate mixed forests (Sites M7 & M8), present during the Tortonian, still inhabited the region – suggesting little change in MAT between the Tortonian and Messinian. Further south from Queen Charlotte Island at 48°N evidence exists for a temperate deciduous broadleaf forest (Sites M9, M10 & M12) with similarities to the modern eastern American deciduous forests (Sparks et al., 1972). South of this a mixture of temperate xerophytic shrubland (M11, M13 & M15) and temperate sclerophyll woodland and shrubland (Site M14) inhabited what would have been a much drier region than existed during the Langhian.

3.3.1.3. Central North America

Palaeobotanical evidence for the Langhian is limited for this region. Kleinfelder Farm, Canada (Site L25) shows the presence of temperate grassland at 49°N, 107°W. Gabel et al (1998) suggested that the region has been vegetated with savanna and grasslands since at least the Middle Miocene. There is evidence for a temperate deciduous broadleaf savanna (Sites S35 & S36) in this region during the Seravallian, Tortonian (Sites T35 – T38) and Messinian (Sites M18 – M20). At Minium Quarry, USA a diverse fossil assemblage records a temperate deciduous broadleaf savanna estimated to have had a MAT of 19°C and a MAP of 875±125mm (Thomasson et al., 1990).

3.3.1.4. Eastern North America

Three sites (L26 - L28) show that during the Langhian the vegetation of eastern North America consisted of warm – temperate evergreen broadleaf and mixed forest from at least 29°N to, at least, 39°N. At Martha's Vineyard (Site L26) a pollen bearing locality dated to the Middle Miocene has been estimated to have been deposited under a MAT of 13.3±5°C (Axelrod, 2000; Frederiksen, 1984). The warm – temperate evergreen broadleaf and mixed forest continued to be the dominant biome during the Seravallian (S27 – S31). During the Tortonian the warm – temperate evergreen broadleaf and mixed forest continued to be dominant (Fig. 3.5A) but there is also evidence for tropical semi-evergreen forest in Louisiana during this time (Site T40), that was rich in ferns and palm trees (Wrenn et al., 2003). Further inland, at 86°W the Pipe Creek sinkhole (Site T41) contains diverse macrofloral fossils with common *Platanus* leaves and a pollen assemblage dominated by Juglandaceae and Pinaceae; this has been interpreted to represent a temperate deciduous broadleaf savanna (Farlow et al., 2001; Shunk, 2009). During the Tortonian the warm – temperate evergreen broadleaf and mixed forest that dominated the eastern USA is estimated to have had a MAT of 15±9°N and a MAP of 1270mm. Palaeobotanical evidence can only confirm the warm – temperate evergreen broadleaf and mixed forest between 36°N and 38°N during the Messinian (Fig. 3.5B). At Gray Fossil Site (Site M21) a palynological assemblage records the presence of a temperate deciduous broadleaf forest dominated by *Carya, Pinus* and *Quercus* (DeSantis and Wallace, 2008).

3.3.1.5. Central America and the Caribbean

Palaeobotanical evidence from Central America and the Caribbean is limited. During the Langhian stage, two sites (Sites L30 – L31) located between 17°N and 7°N provide evidence for a tropical climate in Central America. A third site (Site L29) records a temperate deciduous broadleaf forest which is interpreted to have been derived from altitude to explain the presence of a temperate biome in the tropics (Lenhardt et al., 2006). Further south at the Panama Canal (Site L31) a leaf flora records the presence of a tropical semi-evergreen broadleaf forest with a MAT of 15.5±4.9°C and MAP of 658.2±483.8mm (Retallack and Kirby, 2007). During the Seravallian the well dated site of Panolta (Site S32) shows the presence of a tropical evergreen broadleaf forest at 18°N (Castañeda-Posadas et al., 2009). Again there is evidence of quite diverse palaeoaltitude in this region with a pollen spectrum at Jalapa (Site S33) reflecting a warm *Liquidambar - Quercus* forest rather than a tropical rainforest (Graham, 1975). During the Tortonian and Messinian there was also a warm – temperate evergreen broadleaf and mixed forest (with palms) preserved as a palynological assemblage at Location B, Guatamala (Graham, 1998). On the islands of Haiti and Cuba tropical deciduous broadleaf woodland and a tropical evergreen broadleaf forest are present, respectively (Site T51 & T52). These contrast with the prominence of warm – temperate evergreen broadleaf and mixed forest preserved on mainland Central America at similar latitudes.

3.3.1.6. Northern South America

In the northern half of South America, all palaeobotanical sites indicate a tropical evergreen broadleaf forest during the Langhian (Fig. 3.4A). In the Seravallian the tropical evergreen broadleaf forest continued to exist with an estimated MAP of 1750±250mm at La Venta (Kay and Madden, 1997). However, the western most three sites (Sites S37 – S39) record a tropical deciduous broadleaf forest and woodland suggesting a lower rainfall than at La Venta. During the Tortonian more open biomes became abundant(Fig. 3.5A) with tropical savanna between 5°S and 12°S (Sites T61, T66 & T67) and tropical deciduous broadleaf forest and woodland further south (Sites T71 & T72). This southern forest is estimated to have had a MAT of between 16.1 – 23.5°C and a MAP of 550±180mm (Gregory-Wodzicki, 2002; Gregory-Wodzicki et al., 1998). During the Messinian a mixture of tropical evergreen broadleaf forest and tropical savanna existed in this region (Fig. 3.5B). At Pislepampa, Bolivia (Site M41) the tropical evergreen broadleaf forest is estimated to have grown under a MAT of 20±5°C and a MAP of 1250±250mm (Graham et al., 2001).

3.3.1.7. Southern South America

The western side of southern South America between 26°S and 35°S contained arid type biomes during the Langhian (Fig. 3.4B). There may have been an Atacama desert present (Site L41) with temperate xerophytic shrubland and temperate sclerophyll woodland and shrubland further south. On the east side south of 35°S there was a mixture of warm – temperate evergreen broadleaf and mixed forest and temperate grassland (Sites L46 – L51). At 55°S a warm – temperate evergreen broadleaf and mixed forest inhabited Tierra del Fuego (Site L53) and the Falkland Islands (Site L52) during the Langhian (Fig. 3.4A). The palaeobotanical bearing deposits on the Falklands have not been well dated (Macphail and Cantrill, 2006). The better dated deposits on Tierra del Fuego are of a comparable biome type suggesting they may be coeval, however the Falkland Island site has still been included in the younger datasets until its age has been confirmed. The Forest Beds of the Falkland Islands show a flora dominated by *Dacrydium*, *Lagarostrobos*, *Nothofagus* and *Podocarpus,* this forest community that had a MAT of 12±1°C and a MAP of around 1200mm (Macphail and Cantrill, 2006). There is very little difference in the biome types of southern South America between the Langhian and the Seravallian (Fig. 3.4); this is mostly due to the uncertainty in the resolution of dating of sites in this region.

By the Tortonian there were more humid biomes to the south of the Atacama Desert (Fig. 3.5A). Tropical evergreen broadleaf forest inhabited mountain slopes and areas with adequate moisture (Sites T74 & T75), whilst tropical savanna dominated the lowlands (Sites T76 - T78). Between 31°S and 44°S, a mixture of temperate sclerophyll woodland and shrubland, temperate xerophytic shrubland and isolated coastal warm – temperate evergreen broadleaf and mixed forests were present (Fig. 3.5A). These warm – temperate evergreen broadleaf and mixed forests were replaced by temperate deciduous broadleaf savanna during the Messinian. Other than the loss of the warm – temperate evergreen broadleaf and mixed forests there is very little difference between the Tortonian and the Messinian and this is due to the age uncertainties of the localities used in the reconstruction. There is evidence for glaciers being present at 47°S (Site M62) during the Messinian (Mercer and Sutter, 1982).

3.3.1.8. North Atlantic islands

For the Langhian and Seravallian the only vegetation evidence for this region comes from Iceland (Fig. 3.4A,B). During the Middle Miocene Iceland was inhabited by a warm – temperate evergreen broadleaf and mixed forest with taxa such as Betulaceae, *Glyptostrobus,* *Fagus, Fraxinus, Magnolia, Sequoia* and *Ulmus* (Grimsson et al., 2007). During the Tortonian Iceland continued to have warm – temperate evergreen broadleaf and mixed forests until 10 – 9 Ma when temperate deciduous broadleaved forests and cool - temperate mixed forests become the main biome type of the island. The early Tortonian warm – temperate evergreen broadleaf and mixed forest grew under a MAT of 7.7±0.1°C and a MAP of 1075±0.5mm (Denk et al., 2005). Other evidence for the North Atlantic comes from Ocean Drilling Project (ODP) and Deep Sea Drilling Project (DSDP) sites. Off the southern tip of Greenland a pollen assemblage has been recovered showing the existence of warm – temperate evergreen broadleaf and mixed forests on Greenland during the Tortonian (Site T95). North of Iceland, between 67°N and 69°N pollen assemblages provide evidence of a cool - temperate mixed forest on either Greenland, northern Eurasia or both (Sites T100 & T102). Further north at 78°N a cold evergreen needleleaf forest was present (Site T101). By the Messinian the warm – temperate evergreen broadleaf and mixed forests were gone from the region, the last fossil evidence being from offshore southern Greenland at 6.5 Ma (Site M66). Between 58°N and 68°N pollen recovered from marine cores shows that the predominant biome of this region was cool - temperate mixed forest with cold evergreen needleleaf forest at 78°N (Fig. 3.5B).

3.3.1.9. Europe

From the Langhian to the Messinian the vegetation of Europe shows a gradual response to a cooling and drying climate. The dominance of warm – temperate evergreen broadleaf and mixed forests present throughout the Langhian begins to be broken up by areas of cooler and drier biomes. This pattern is particularly evident in the east of Europe where temperate deciduous broadleaf savanna becomes a major biome during the Late Miocene breaking up the extensive warm – temperate evergreen broadleaf and mixed forest (Akgün and Akyol, 1999).

On the Iberian Peninsula during the Langhian warm – temperate evergreen broadleaf and mixed forest dominated the landscape (Fig. 3.4A). At Rubielos de Mora, Spain (Site L62) a pollen and macro-fossil assemblage shows that the warm – temperate evergreen broadleaf and mixed forest was chiefly composed of *Acer*, *Betula, Carya, Corylus, Fraxinus, Glyptostrobus, Juglans*, *Quercus, Salix* and *Sequoia* (Ramis and Marron, 1994). On the southern coast of the Iberian Peninsula there was an arid region of temperate xerophytic shrubland (Sites L63 – L66) and on the eastern coast there was an area of temperate deciduous broadleaf savanna (Site L61). To the north and east of the Pyrenees palaeobotanical evidence shows the presence of a warm – temperate evergreen broadleaf and mixed forest throughout Europe between the latitudes of 36°N and 53°N and the longitudes of 1°W and 47°E (Fig. 3.4A). This warm – temperate evergreen broadleaf and mixed forest is estimated to have grown under a MAT of 13.6 - 21°C and a MAP of 823 – 2500mm, in Turkey the MAT is estimated to have been slightly higher with a range of 16. 5 – 21.3°C (Table 3.2) (Akgün and Akyol, 1999; Akgün et al., 2007; Kayseri and Akgün, 2010). The only exception to this widespread warm – temperate evergreen broadleaf and mixed forest was a small area of temperate sclerophyll woodland and shrubland in southern Germany (Sites L82 – L83), which is estimated to have had a MAT comparable to the warm – temperate evergreen broadleaf and mixed forest but a lower MAP (Table. 2) (Böhme et al., 2007).

During the Seravallian the warm – temperate evergreen broadleaf and mixed forest biome continued to dominate Europe but some areas had begun to develop drier biomes (Fig. 3.4B). On the Iberian Peninsula a vegetation pattern similar to that of the Langhian existed (Fig. 3.4A), with the exception of evidence for a temperate sclerophyll woodland in central Spain (Site S64). In southern France there is evidence for temperate deciduous broadleaf savanna (Sites S80 & S91) as well as warm – temperate evergreen broadleaf and mixed forest. Further disruption to the warm – temperate evergreen broadleaf and mixed forest occurs in southern Germany where temperate deciduous broadleaf forest occurred (Fig. 3.4B) and east of 28°E where more open areas of temperate deciduous broadleaf savanna (Sites S118, S124 & S127) occupied drier regions. The warm – temperate evergreen broadleaf and mixed forest during the Seravallian is estimated to have grown under a MAT and MAP comparable to that of the Langhian (Table 3.2). The temperate deciduous broadleaf savanna found east of 28°E is estimated to have had a MAT of 9.5±4.9°C and a MAP of 951±216mm (Syabryaj et al., 2007), showing that not only was this biome drier than the dominant warm – temperate evergreen broadleaf and mixed forests but also colder.

The expansion of colder and drier biomes continued into the Tortonian, although large areas of warm – temperate evergreen broadleaf and mixed forest still dominated much of Europe (Fig. 3.5A). The Iberian Peninsula during the Tortonian had a vegetation pattern similar to that of the Seravallian (Fig. 3.5A). Climate estimates from the Tagus Basin, Portugal suggests the MAT of the warm – temperate evergreen broadleaf and mixed forests was around 11°C. The warm – temperate evergreen broadleaf and mixed forests were still dominant across Europe until 23°E, where more open biomes began to intermingle with the warm – temperate evergreen broadleaf and mixed forest (Fig. 3.5A). The warm – temperate evergreen broadleaf and mixed forests were typically composed of *Abies, Betula*, *Cedrus, Craigia, Engelhardtia*, *Keteleeria, Liquidambar, Myrica Pinus, Quercus* and *Taxodium* as well as other taxa and occasionally palms (Blanc et al., 1974; Kvacek et al., 2002; Nagy, 1967; Chapter 2).

Reconstructed climate of this warm – temperate evergreen broadleaf and mixed forest for the Tortonian provides a MAT range of 11.6 – 18.4°C and a MAP of around 1153mm (Table 3.4) (Bruch et al., 2006). West of 23°E a small area of cool - temperate mixed forests of *Fagus, Liquidambar* and *Quercus* inhabited a small area of southern Germany, possibly indicating an area of palaeo-altitude (Gregor et al., 1989). East of 23°E a mixture of warm – temperate evergreen broadleaf and mixed forests, temperate evergreen needleleaf forests and temperate deciduous broadleaf savanna was found (Fig. 3.5A). In Turkey, the warm – temperate evergreen broadleaf and mixed forest inhabited a region warmer than that in the rest of Europe with a reconstructed MAT of 15.6 – 21.3°C and a MAP of 823 – 1574mm (Table 3.4) (Akgün et al., 2007). The temperate deciduous broadleaf savanna of Turkey had a comparable reconstructed climate (Table 3.4).

During the Messinian the vegetation patterns that had developed in the Tortonian continued (Fig. 3.5B). The warm – temperate evergreen broadleaf and mixed forest continued to dominate Europe up to 23°E, with a reconstructed MAT of 9 – 19.8°C and a MAP of 700 – 1759mm (Table 3.5) (Bruch et al., 2006). Evidence from the Iberian Peninsula is limited, though it still shows the presence of temperate xerophytic shrubland along the southern coast and warm – temperate evergreen broadleaf and mixed forests in the Pyrenees (Fig. 3.5B). Some palaeobotanical sites show evidence for areas of temperate deciduous broadleaf forest (Sites M76 &M106), temperate evergreen needleleaf forest (Sites M101 & M102) and temperate xerophytic shrubland (Site M94). These had MATs comparable to the warm – temperate evergreen broadleaf and mixed forests of around 15°C but with lower MAP, below 1000mm (Table 3.5). East of 23°E there was a mixture of warm – temperate evergreen broadleaf and mixed forests and temperate deciduous broadleaf savanna, similar to the Tortonian (Fig. 3.5A).

3.3.1.10. North Africa and the Middle East

Evidence for the Langhian and Seravallian is very scarce for this region. The only evidence comes from Enfidha, Tunisia (Site L77; S91) and Jabal Barakah, UAE (Site L104). At Enfidha, a warm – temperate evergreen broadleaf and mixed forest dominated by *Carya* and Myricaceae inhabited this region (Planderová, 1971). At Jabal Barakah, a high proportion of grass pollen, as well as, *Alchornea, Celtis,* Myrtiaceae and Palm indicate a tropical deciduous broadleaf woodland with mangroves along the coast (Jacobs et al., 2010; Whybrow and McClure, 1980). By the Tortonian numerous sites show the existence of tropical savanna, tropical grassland, tropical xerophytic shrubland and temperate sclerophyll woodland and shrubland throughout North Africa and the Middle-East (Fig. 3.5A). This pattern continues into the Messinian with the addition of evidence for desert conditions starting at around 7 Ma (Site M144). Although the origin of these deposits has come under contest (Kroepelin, 2006; Schuster et al., 2006a,b; Swezey, 2006) and wider sedimentary evidence shows that the Sahara region was predominantly fluvial in deposition before the major onset of northern hemisphere glaciations (Swezey, 2009).

Region and biome type	Location	MAT	MAP
North-west North America			
Cool temperate mixed forest	3, 4, 5	7 - 9	
Western North America			
Warm-temperate mixed forest	20, 23	11.5	760 - 890
Temperate xerophytic shrubland	24	0 - 37	381 - 635
Eastern North America			
Warm-temperate mixed forest	26	8.3 - 18.3	
Central America			
Tropical semi-evergreen broadleaf forest	31	10.6 - 20.4	174.5 - 1142
South America			
Warm-temperate mixed forest	52	11 - 13	1200
Europe			
Warm-temperate mixed forest	67, 68, 69, 88 ,91 ,92, 94, 96, 97, 98	13.6 - 21	823 - 2500
Temperate sclerophyll woodland and shrubland	82, 83, 84	15.8 - 20.8	828 - 1362
Turkey			
Warm-temperate mixed forest	99, 100	16.5 - 21.3	1182.5 - 1321.5
Russia - Omsk			
Temperate deciduous broadleaf savanna	114, 115, 116	8 - 10	700
South-east Asia			
Warm-temperate mixed forest	132, 133	9 - 15	1000
Australia			
Warm-temperate mixed forest	178, 179	19	1500 - 2200

Table 3.2. Climate data derived from palaeobotanical evidence for the Langhian. Mean annual temperature (°C) and mean annual precipitation (mm/year) are presented for regions of the world (Fig. 3.6) subdivided by biome type. Mean annual temperature and mean annual precipitation estimates are derived from CLAMP (Wolfe, 1979; Spicer, 2007), Coexistence Approach (Mosbrugger and Utescher, 1997) and other techniques described in the source literature. Site numbers refer to Fig. 3.1A. References for the sites and the climatic data from them can be found in Appendices A, B.

Region and biome type	Location	MAT	MAP
North-west North America			
Cool temperate mixed forest	2, 4	9	
Western North America			
Warm-temperate mixed forest	11, 18	10 - 14	760 - 1250
Temperate xerophytic shrubland	21	0 - 37	381 - 635
Eastern North America			
Warm-temperate mixed forest	31	8.3 - 18.3	
South America			
Tropical evergreen broadleaf forest	36		1500 - 2000
Europe			
Warm-temperate mixed forest	74, 76, 82, 83, 89, 94, 96, 97, 98, 99, 100, 101, 102, 103, 104, 105, 106, 107, 108, 109, 110 114, 119	13.5 - 21	823 - 2500
Temperate evergreen needleleaf forest	126	15.6	1304 - 1356
Temperate deciduous broadleaf savanna	118	4.6 - 14.4	735 - 1167
Turkey			
Warm-temperate mixed forest	120, 122, 125, 128, 129, 130, 131	16.7 - 21.3	629 - 1520
Africa			
Tropical evergreen broadleaf forest	139	21.9	
Russia – Omsk			
Temperate deciduous broadleaf savanna	145, 147	8 - 10	700
South-east Asia			
Warm-temperate mixed forest	160	9 - 15	1000
Australia			
Warm-temperate mixed forest	201	19	1500 - 2200

Table 3.3. Climate data derived from palaeobotanical evidence for the Seravallian. Mean annual temperature (°C) and mean annual precipitation (mm/year) are presented for regions of the world (Fig. 3.6) subdivided by biome type. Mean annual temperature and mean annual precipitation estimates are derived from CLAMP (Wolfe, 1979; Spicer, 2007), Coexistence Approach (Mosbrugger and Utescher, 1997) and other techniques described in the source literature. Site numbers refer to Fig. 3.1B. References for the sites and the climatic data from them can be found in Appendices A, B.

3.3.1.11. Equatorial Africa

Data for this region is restricted to a narrow band between 1°S and 12°N and records the changes between tropical closed and tropical open vegetation. During the Langhian, the region of Africa to the west of the Niger Delta was dominated by tropical evergreen broadleaf forest (Site L105), whilst pollen assemblages from the Niger Delta record the existence of regional tropical savanna (Fig. 3.4A). In East Africa tropical deciduous broadleaf woodland is recorded at 12°N (Site L108) and tropical evergreen broadleaf forest at 0.2°S (Site L109). South of the tropical evergreen broadleaf forest a younger site; Fort Ternan and Sondu, Kenya (Sites L110 & L111) shows evidence for tropical savanna. The Seravallian is only represented by four sites for this region which shows a vegetation pattern comparable to the Langhian (Sites S137 – S140). At Kabasuro, Kenya the MAT of the tropical evergreen broadleaf forest is estimated to be around 21.9°C (Jacobs and Deino, 1996; Jacobs and Kabuye, 1989).

During the Tortonian, in western Equatorial Africa tropical evergreen broadleaf forest dominated from 16°W to 8°E, up to 12°N. At 6°N, 8°E pollen from Oku Lake shows the presence of tropical savanna dominated by Cyperaceae and Poaceae (Médus et al., 1988). Drill cores from the Niger Delta show a predominance of tropical evergreen broadleaf forests growing along its source rivers until 7.6 Ma when there was a shift to tropical savanna suggesting a possible drying of the region (Sites T188 – T190). In east equatorial Africa a mixture of tropical evergreen broadleaf forest (Sites T196 & T200), tropical savanna (Site T199) and tropical grassland (Sites T197 & T198) inhabited the region. By the Messinian, tropical evergreen broadleaf forest continued to inhabit the western part of equatorial Africa from 16°W to 4°W, the Niger Delta was inhabited by tropical savanna during the Messinian (Fig. 3.5B). In east equatorial Africa a pattern similar to the Tortonian existed except south of 1°N. Here tropical deciduous broadleaf woodland (Sites M149 & M150) with a MAT of 21.7±2.5°C and a MAP of 1045±200mm (Bonnefille, 2010; Jacobs and Deino, 1996) was present close to tropical evergreen broadleaf forest (Site M151).

3.3.1.12. Southern Africa

As with much of Africa data is scarce for southern Africa and only allows the difference between the Middle and Late Miocene to be determined. During the Middle Miocene (Langhian and Seravallian) the vegetation of South Africa was tropical (Fig. 3.4A,B). Evidence exists for tropical savanna (Sites L113; S143) and tropical semi-evergreen broadleaf forest (Sites L112; S142). By the Late Miocene (Tortonian and Messinian) the vegetation of South Africa suggests a cooler climate with temperate evergreen needleleaf forest along the western coast. Offshore Namibia, DSDP Site 530A contains a pollen assemblage showing the presence of tropical xerophytic shrubland in modern day Namibia during the Late Miocene (van Zinderen Bakker Sr., 1980). Other evidence suggests that the Namib Desert may have been present since the Early Miocene (Senut et al., 2009).

Region and biome type	Location	MAT	MAP
North-west North America			
Cool temperate mixed forest	1	0 - 20	
Cool evergreen needleleaf forest	5, 8	5	
Cold evergreen needleleaf forest	2	3 - 5	
Western North America			
Warm-temperate mixed forest	19, 30	11 - 19	616.5 - 1250
Temperate deciduous broadleaf forest	20	14	508 - 762
Temperate sclerophyll woodland and shrubland	18	10 - 15	800 - 1000
Cool temperate mixed forest	25	7 - 15	1143 - 1270
Eastern North America			
Warm-temperate mixed forest	46, 47	6 - 24	1270
South America			
Tropical deciduous broadleaf forest and woodland	71,72	16.1 - 23.5	370 - 730
Iceland			
Warm-temperate mixed forest	99	7.6 - 7.8	1075 - 1076
Iberian Peninsula			
Warm-temperate mixed forest	105	11	
Europe			
Warm-temperate mixed forest	103, 104, 119, 120, 140, 148, 151, 153, 157, 159, 161, 165, 170	11.6 - 18.4	579 - 1929
Temperate deciduous broadleaf savanna	163	12 - 18	559 - 760
Turkey			
Warm-temperate mixed forest	180	15.6 - 21.3	823 - 1574
Temperate deciduous broadleaf savanna	179	16.5 - 20.8	887 - 1520
South-east Asia			
Tropical evergreen broadleaf forest	283, 302	13.3 - 27.15	803.55 - 1254.75
Warm-temperate mixed forest	284	16.7 - 19.1	1215 - 1639
Australia			
Warm-temperate mixed forest	312		1500
Temperate sclerophyll woodland and shrubland	303, 307		600 - 1500

Table 3.4. Climate data derived from palaeobotanical evidence for the Tortonian. Mean annual temperature (°C) and mean annual precipitation (mm/year) are presented for regions of the world (Fig. 3.6) subdivided by biome type. Mean annual temperature and mean annual precipitation estimates are derived from CLAMP (Wolfe, 1979; Spicer, 2007), Coexistence Approach (Mosbrugger and Utescher, 1997) and other techniques described in the source literature. Site numbers refer to Fig. 3.2A. References for the sites and the climatic data from them can be found in Appendices A, B.

Region and biome type	Location	MAT	MAP
North-west North America			
Cool temperate mixed forest	2	0 - 20	
Cool evergreen needleleaf forest	3	5	
Cold evergreen needleleaf forest	1, 6	-10 - 5	
Western North America			
Temperate deciduous broadleaf forest	12	14	508 - 762
Temperate sclerophyll woodland and shrubland	14	13.3	1016
Temperate xerophytic shrubland	11	10 - 15	200 - 600
Central North America			
Temperate deciduous broadleaf savanna	19		750 - 1000
South America			
Tropical evergreen broadleaf forest	41	15 - 25	1000 - 1500
Europe			
Warm-temperate mixed forest	83, 90, 99, 100, 104, 105, 108, 114	9 - 19.8	700 - 1759
Temperate deciduous broadleaf forest	106	12 - 18	370 - 1500
Temperate evergreen needleleaf forest	101	12 - 16	840 - 1010
Africa			
Tropical deciduous broadleaf forest and woodland	149, 150	19.2 - 24.2	845 - 1245
South-east Asia			
Tropical evergreen broadleaf forest	215	13.3 - 20.9	803.55 - 1254.75
Australia			
Temperate sclerophyll woodland and shrubland	233, 236		600 - 1500

Table 3.5. Climate data derived from palaeobotanical evidence for the Messinian. Mean annual temperature (°C) and mean annual precipitation (mm/year) are presented for regions of the world (Fig. 3.6) subdivided by biome type. Mean annual temperature and mean annual precipitation estimates are derived from CLAMP (Wolfe, 1979; Spicer, 2007), Coexistence Approach (Mosbrugger and Utescher, 1997) and other techniques described in the source literature. Site numbers refer to Fig. 3.2B. References for the sites and the climatic data from them can be found in Appendices A, B.

3.3.1.13. West Asia

During the Langhian a latitudinal south to north drying and cooling trend existed for this region. Between 41°N and 46°N a warm – temperate evergreen broadleaf and mixed forest inhabited the region, with a composition of mainly *Betula, Carpinus, Carya, Fagus, Juglans, Liquidambar, Magnolia, Quercus, Pinus* and *Zelkova* (Liu and Leopold, 1994; Sun and Zhang, 2008). North of the warm – temperate evergreen broadleaf and mixed forest at 48°N a temperate deciduous broadleaf forest was present and north of this between 56°N and 57°N temperate deciduous broadleaf savanna, with an estimated MAT of 9±1°C and a MAP of around 700mm (Gnibidenko et al., 1999) existed (Fig. 3.4A). The pattern is still present in the Seravallian, though the warm – temperate evergreen broadleaf and mixed forest was restricted to 41°N (Fig. 3.4B). By the Tortonian the warm – temperate evergreen broadleaf and mixed forests were replaced by temperate deciduous broadleaf savanna from 45°N to

57°N. From Travolzhansky, Russia (Site T206), a pollen flora shows that the temperate deciduous broadleaf savanna was composed of *Alnus, Betula, Carpinus, Carya,* Compositae, Gramineae, *Picea*, *Quercus, Tsuga* and *Ulmus* (Volkova et al., 1986). By the Messinian this region had desert at 38°N (Site M159). North of the desert, between 45°N and 53°N, there existed a region of temperate deciduous broadleaf forest and temperate deciduous broadleaf savanna (Fig. 3.5B). Further north at 68°N a cool-temperate mixed forest was present (Fig. 3.5B) containing; *Ilex*, Juglandaceae, Myrtaceae, *Nyssa* and Taxodiaceae (Belkin, 1964).

3.3.1.14. Northeast Asia

During the Langhian this region was vegetated with cool - temperate biomes (Fig. 3.4A). The main biome was a cool - temperate mixed forest (Sites L125, L128, L129 & L131), these forests were dominated by conifers but contained angiosperms such as *Alnus, Betula, Juglans, Quercus* and *Tilia* (Baranova et al., 1970; Lavrushin and Alekseev, 2005). Also present during the Langhian were cool evergreen needleleaf forests dominated by *Larix* and other gymnosperms, but containing some angiosperms (Site L130). During the Seravallian the cool – temperate mixed forest continued to be the dominant biome between 61°N and 77°N with no evidence for other biomes being present (Fig. 3.4B). By the Tortonian the main biome in the northeast Asian region was cold evergreen needleleaf forest between 61°N and 70°N (Fig. 3.5A). South of the cold evergreen needleleaf forest a cool – temperate evergreen needleleaf and mixed forest inhabited the coast (Site T215). This forest was mainly composed of Fagaceae, *Larix*, *Picea* and Taxodiaceae (Nikitin, 2007). During the Messinian the cold evergreen needleleaf forest continued to dominate the northeast Asian region (Sites M163, M164, M166 & M167) with smaller amounts of cool – temperate evergreen needleleaf and mixed forest along the coast (Fig. 3.5B).

3.3.1.15. Eastern Asia

During the Langhian this region was principally vegetated by the warm – temperate evergreen broadleaf and mixed forest from 21°N to 56°N (Fig. 3.4A). This biome contained a diverse assemblage of both gymnosperms and angiosperms including *Carya, Castanea, Corylus, Engelhardtia, Keteleeria, Liquidambar, Metasequoia, Pinus, Quercus, Sequoia, Taxodium* and *Zelkova* (Kong, 2000; Liu and Leopold, 1994). Climatic estimates for this biome, north of 36°N, indicate a MAT of 12±3°C and a MAP of around 1000mm (Table. 2) (Liu and Leopold, 1994; Sun et al., 2002; Tao, 1997). Along the coast between 31°N and 33°N a tropical evergreen broadleaf forest exisited (Sites L146 – L148). West of 111°E a drier region vegetated by a mixture of temperate deciduous broadleaf forest, temperate evergreen needleleaf open woodland and temperate evergreen needleleaf forest existed during the Langhian (Fig. 3.4A). During the Seravallian the warm – temperate evergreen broadleaf and mixed forest continued to dominate the region, between 22°N and 50°N (Fig. 3.4B). Tropical evergreen broadleaf forest was still present between 31°N and 33°N (Sites S168 – S170), as was the drier region west of 111°E (Fig. 3.4B). Drying in this region had continued from the Langhian and at 90°E a pollen assemblage from Quaidam, China (Site S149) shows that a temperate xerophytic shrubland inhabited this region from around 14 Ma.

By the Tortonian the warm – temperate evergreen broadleaf and mixed forest was still present from 20°N to 48°N but had become more restricted in its distribution longitudinally (Fig. 3.5A). Climatic estimates for the warm – temperate evergreen broadleaf and mixed forest, at 23°N, show it grew under a MAT of 17.9±1.2°C with a MAP of 1427±212mm (Xia et al., 2009). The drier biomes, present in the Middle Miocene as far east as 111°E, now spread as far east as 118°E (Fig. 3.5A). The major dry biome was a temperate deciduous broadleaf savanna, which was present from 28°N to 55°N throughout inland eastern Asia. Within this extensive temperate deciduous broadleaf savanna there were isolated areas of more humid warm – temperate evergreen broadleaf and mixed forest and drier regions of temperate xerophytic shrubland (Fig. 3.5A). At Sikouzi, China (Sites T227 – T230) a high resolution pollen sequence shows that in this region the vegetation changes from temperate evergreen needleleaf open woodland at 11.35 Ma to temperate xerophytic shrubland, this then changes again at 8.3 Ma to a more humid temperate deciduous broadleaf savanna and finally changes back to temperate xerophytic shrubland at 8.05 Ma (Jiang and Ding, 2008).

By the Messinian the dominant biome in eastern Asia was the temperate deciduous broadleaf savanna (Fig. 3.5B). The warm – temperate evergreen broadleaf and mixed forest was restricted to the coast to as far north as 39°N (Site M179) and possibly as far north as 50°N (Sites M168 – M169), though these sites would only represent the earliest Messinian (Ca. 7 Ma). Further west, away from the coastal warm – temperate evergreen broadleaf and mixed forests, within the more extensive temperate deciduous broadleaf savanna isolated areas of temperate xerophytic shrubland existed (Site M171).

3.3.1.16. The Indian subcontinent

For the Langhian all palaeobotanical evidence shows that the Indian subcontinent was vegetated by a tropical evergreen broadleaf forest (Fig. 3.4A). This dominance of tropical evergreen broadleaf forest, on the Indian subcontinent, continued into the Seravallian (Fig. 3.4B). The Langhian and Seravallian tropical evergreen broadleaf forests were composed mainly of *Bursera*, *Dialium Dipterocarpus*, *Dracontomelum, Sterculia* and abundant ferns (Prasad, 1993; Sarkar and Singh, 1994). By the Tortonian the tropical evergreen broadleaf forests continued to be dominant on the southern tip of the Indian subcontinent, however in the north, more biomes were present (Fig. 3.5A). On the Himalayan Front a mixture of tropical evergreen broadleaf forest (Sites T258, T262, T264, T266 & T267), tropical semi – evergreen broadleaf forest (Site T263), warm – temperate evergreen broadleaf and mixed forest (Sites T256, T260, T261 & T268), temperate evergreen needleleaf forest (Site T257) and temperate grassland existed at around 8 Ma (Site T265). This mixture of biomes in such close proximity probably reflects the regional topography at the time, with tropical forests on the lowlands and the warm – temperate and temperate biomes at altitude. This diversity of biomes continued into the Messinian along the Himalayan Front, but with the tropical forests 2° further south than during the Tortonian (Fig. 3.5B). Tropical evergreen broadleaf forests continued to dominate the Indian subcontinent Peninsula (Site M202 – M208).

3.3.1.17. South-east Asia

During the Langhian the vegetation of south-east Asia was tropical evergreen broadleaf forest (Fig. 3.4A). The tropical evergreen broadleaf forest continued to dominate south-east Asia during the Seravallian, but isolated areas of tropical savanna (Site S186) and tropical deciduous broadleaf forest and woodland (Site S189) shows that some drying of the region had occurred. By the Tortonian the once extensive tropical evergreen broadleaf forest had become more disjointed with regions of tropical deciduous broadleaf forest and woodland, tropical grassland and warm – temperate evergreen broadleaf and mixed forest occupying much of the region between 12°N and 20°N (Fig. 3.5A). This pattern is also seen in the Messinian though this may be related to uncertainties in dating of some of the sites. When the coexistence approach is applied to the tropical evergreen broadleaf forests of Sarawak (Site T302), a MAT of 27.15 ± 0.55°C is reconstructed.

3.3.1.18. Australia and New Zealand

For the Langhian data is only available for east Australia. In the North a tropical evergreen broadleaf forest (Site L169) existed to as far south as 28°S, below 28°S a warm – temperate evergreen broadleaf and mixed forest inhabited the region (Fig. 3.4A). This warm – temperate evergreen broadleaf and mixed forest grew under a MAT of around 19°C and a MAP of between 1500 and 2200mm (Holdgate et al., 2007; Kershaw, 1997).During the Langhian New Zealand was also dominated by the warm – temperate evergreen broadleaf and mixed forest with isolated regions of drier temperate sclerophyll woodland and shrubland (Fig. 3.4A). During the Seravallian data only exists to confirm the presence of a warm – temperate evergreen broadleaf and mixed forest in south – east Australia (Fig. 3.4B), growing under a climate similar to that of the Langhian (Table 3.2). New Zealand also shows a biome distribution comparable to that of the Langhian (Fig. 3.4B). By the Tortonian a dramatic drying of Australia had begun. The main biome on the continent was now the temperate sclerophyll woodland and shrubland (Fig. 3.5A), estimated from Lake Tay (Site T307) to have grown under a MAP of between 600 and 1500mm (Macphail, 1997). There were still isolated patches of warm – temperate evergreen broadleaf and mixed forests in the south-east of the continent (Site T312) with a MAP of at least 1500mm and areas of temperate deciduous broadleaf savanna (Site T311). Along the northeast coast a temperate evergreen needleleaf forest existed (Fig. 3.5A). New Zealand continued to be dominated by a warm – temperate evergreen broadleaf and mixed forest, but evidence exists to suggest cool – temperate mixed forests may have inhabited higher altitudes (Fig. 3.5A). During the Messinian the drying and the expansion of the temperate sclerophyll woodland and shrubland continued (Fig. 3.5B). No palaeobotanical data show the existence of major areas of warm – temperate evergreen broadleaf and mixed forest during the Messinian, though this biome was still dominant on New Zealand (Fig. 3.5B).

3.3.1.19. Antarctica and the surrounding islands

During the Langhian low- and high– shrub tundra and prostrate dwarf – shrub tundra were present on the fringes of Antarctica (Fig. 3.4A). ODP Site 696 (Site L54) contains evidence that South Georgia and the South Sandwich Islands (62°S) were vegetated by a temperate deciduous broadleaf forest rich in ferns, Podocarpaceae and *Nothofagus* (Mohr, 2001). By the end of the Seravallian vegetation was probably extinct on Antarctica (Anderson et al., 2011; Lewis et al., 2008). Except for isolated communities of limited tundra on the Antarctic Peninsula, which may have survived until 12.8 Ma (Site S57) (Anderson et al., 2011). By around 12 Ma glaciers may have been at their present extent, shown by glacial deposits on the Antarctic Peninsula (Dingle and Lavelle, 1998; Marenssi et al., 2010). Although vegetation was probably gone from Antarctica after the Langhian the islands in the Southern Ocean provide some insight into the climate during the Late Miocene. On Heard Island at 51°S (Site

T326; M252) a temperate grassland existed with a composition comparable to that seen on islands at 40°S in the present day.

3.3.2. Latitudinal temperature gradients derived from megabiome distribution

By grouping biomes into megabiomes and bioclimatic zones (Table 3.1) an easily accessible view of the latitudinal temperature gradient throughout the Middle to Late Miocene has been achieved. Although no estimate of absolute temperatures or temperature change can be currently applied, the pattern shows that throughout the Middle to Late Miocene the world was warmer than at present day. The pattern of bioclimatic zones (Fig. 3.7; 3.8) shows that the latitudinal temperature gradient was much shallower in the Langhian and became progressively steeper throughout the remaining Miocene. However the gradient did not change uniformly in both the northern and southern hemispheres. From the vegetation data it appears that the southern hemisphere latitudinal temperature gradient became more modern-like by the Seravallian (Fig. 3.7; 3.8). Conversely the northern hemisphere latitudinal temperature gradient appears to have become more modern at a slower pace; cold evergreen needleleaf forests were still at higher latitudes during the Messinian than they are today (Fig. 3.7; 3.8).

During the Langhian the latitudinal distribution of bioclimatic zones indicates a latitudinal temperature gradient very different from the modern world (Fig. 3.7A; 3.8A). Along both the west Pacific transect (WPT) (Fig. 3.7) and the west Atlantic transect (WAT) (Fig. 3.8) all the bioclimatic zones, in both hemispheres, are at higher than modern latitude. This is also the case in the Seravallian, although not by much in the southern hemisphere (Fig. 3.7B, 3.8B). By the Tortonian, the southern hemisphere latitudinal distribution of bioclimatic zones appears comparable to modern (Fig. 3.7C, 3.8C). The northern hemisphere however still shows vegetation at higher latitudes than in the modern potential natural vegetation especially along the WAT (Fig. 3.8C). During the Messinian the WPT shows a latitudinal vegetation gradient very comparable to that of the present day potential natural vegetation (Fig. 3.7D), however along the WAT, in the northern hemisphere, the Messinian latitudinal vegetation distribution was still higher than that of the present day (Fig. 3.8D).

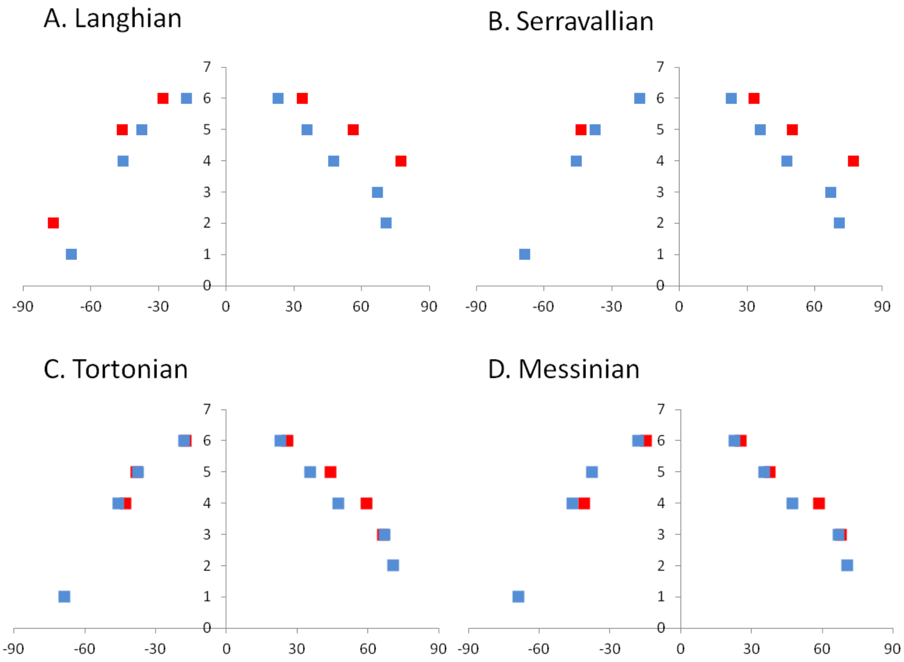


Figure 3.7. West Pacific transect (WPT) of maximum poleward distribution of bioclimatic zones for the Langhian (A), Seravallian (B), Tortonian (C) and Messinian (D). The X-axis shows degrees latitude from the South Pole (-90°) to the North Pole (90°). The Y-axis represents the bioclimatic zone: 1) Ice, 2) Tundra, 3) Boreal, 4) Temperate, 5) Warm-temperate, 6) Tropical. Blue squares are pre - industrial potential natural vegetation, red squares represent poleward - most fossil evidence for that vegetation zone.

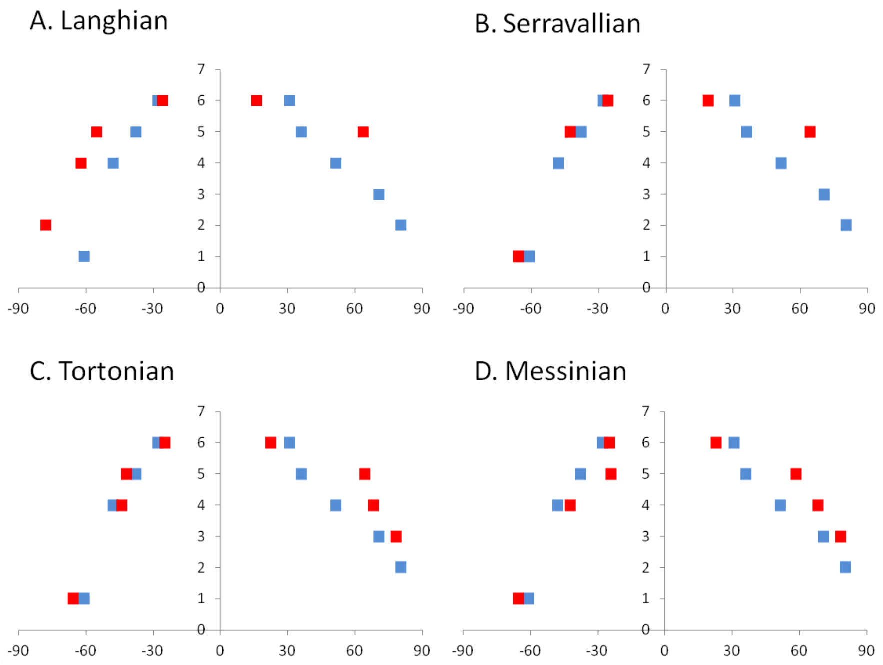


Figure 3.8. West Atlantic transect (WAT) of maximum poleward distribution of bioclimatic zones for the Langhian (A), Seravallian (B), Tortonian (C) and Messinian (D). The X-axis shows degrees latitude from the South Pole (-90°) to the North Pole (90°). The Y-axis represents the bioclimatic zone: 1) Ice, 2) Tundra, 3) Boreal, 4) Temperate, 5) Warm-temperate, 6) Tropical. Blue squares are pre - industrial potential natural vegetation, red squares represent poleward - most fossil evidence for that vegetation zone.

3.4. Discussion

3.4.1. Middle to Late Miocene vegetation evolution and CO_2

From 634 palaeobotanical sites, translated into the 28 biome scheme of the BIOME4 model, it can be seen that there is a global cooling and drying trend from the Langhian to the Messinian. This is in accordance with the results of different proxies reported in numerous other studies (e.g. Zachos et al., 2008).

During the Langhian (15.97 – 13.65 Ma), the period of time referred to as the Mid – Miocene Climatic Optimum (MMCO) was ending. The MMCO was a significant warm interval recorded in the deep sea records (Flower and Kennett, 1994; Zachos et al., 2008) and in the Antarctic (Anderson et al., 2011; Lewis et al., 2008; Williams et al., 2008). The MMCO and the Langhian also correspond to a peak in atmospheric CO_2 concentration, stomatal indices indicate atmospheric concentrations of between 460 and 564 ppmv (Beerling et al., 2009b; Kürschner et al., 2008) whilst estimates from boron isotopes suggest 300 ppmv (Pearson and Palmer, 2000) and alkenone based estimates place it at a more modest 220 ppmv (Pagani et al., 2005). Although the 300 ppmv recorded in the boron isotopic record does not appear to be “high”, it does represent a peak in that particular CO_2 reconstruction. The alkenone record does not present the MMCO as a period of elevated CO_2 within the rest of the Miocene (Pagani et al., 1999). These elevated levels of CO_2, in all the records except the alkenone based reconstruction, and the warming recognised in the benthic oxygen isotope curve during the Langhian are reflected in the biome pattern; cool – temperate forests at the high northern latitudes, extensive warm – temperate evergreen broadleaf and mixed forests in the middle latitudes, a broader tropical zone and tundra on Antarctica (Fig. 3.4A).

During the Seravallian (13.65 – 11.61 Ma) the biome pattern is still similar to that of the Langhian however changes had occurred. The benthic oxygen isotope curve shows from about 14 Ma to around 10 Ma either the bottom water temperature was dropping, significant land ice was developing or a combination of the two (Flower and Kennett, 1994; Zachos et al., 2008). The CO_2 proxies also record falling atmospheric concentrations to; 300 – 330 ppmv from the stomatal indices (Beerling et al., 2009b; Kürschner et al., 2008); 268 – 290 ppmv from boron isotopes (Pearson and Palmer, 2000) and alkenone estimates of 194 – 252 ppmv concentration (Pagani et al., 2005). The biome distribution still shows cool – temperate mixed forest at the high northern latitudes, though not as high as it was during the Langhian. Whilst in the middle latitudes the warm-temperate evergreen broadleaf and mixed forest had begun to be replaced by drier and cooler biomes (Fig. 3.4B). In the tropics too, drier biomes had begun to spread and on Antarctica, current records suggest extensive tundra was no longer present (Fig. 3.4B).

The biome pattern of the Tortonian (11.61 – 7.25 Ma) is markedly different from that of the Seravallian. In terms of the benthic oxygen isotopic record the Late Miocene shows relative stability, after the warming of the MMCO and the cooling seen in the late Langhian and Seravallian, with isotopic levels reflecting an increased (ice free world) bottom water temperature range of 0 to +2°C (Zachos et al., 2008). The CO_2 reconstructions give mixed estimates of the atmospheric concentration of this greenhouse gas during the Tortonian. The stomatal indices show an increase of CO_2 from the Seravallian to 350 – 370 ppmv (Kürschner et al., 1996; Stultz et al., 2011), whilst the boron isotopes record a fall in CO_2 from the Seravallian to between 212 – 236 ppmv (Pearson and Palmer, 2000) and the alkenone based reconstructions show that CO_2 concentrations fluctuated between 190 – 330 ppmv with a general increasing trend towards the end of the Tortonian (Pagani et al., 2005; 2010). The biome pattern of the Tortonian reflects a cooler and drier world than that of the Seravallian. Cold evergreen needleleaf forests are found at the high northern latitudes for the first time during the Middle to Late Miocene (Fig. 3.5A). In the middle latitudes the warm – temperate evergreen broadleaf and mixed forest continued to be restricted and replaced by drier and cooler biomes (Fig. 3.5A). In the tropics the major change from the Seravallian was the appearance of tropical savanna in South America. The changes in biome distribution from the Seravallian to the Tortonian would appear to agree with the boron isotope reconstructed CO_2 trend more than the stomatal indices. However, the distribution of Tortonian palaeobotanical data compares best against GCM simulated vegetation that is driven by climate under higher atmospheric levels of CO_2 than both these reconstructions suggest (Micheels et al., 2007; 2009a).

During the Messinian (7.25 – 5.33 Ma) the biome distribution was similar to that of the Tortonian. The benthic oxygen isotope records also resemble the Tortonian records, with increased amplitude between the peaks and troughs of the record (Zachos et al., 2008). CO_2 reconstructions are also comparable to the Tortonian with stomatal indices showing atmospheric concentrations of 270 – 360 ppmv (Kürschner et al., 1996), boron isotopes indicating levels of between 268 – 305 ppmv (Pearson and Palmer, 2000) and alkenone based reconstructions showing atmospheric concentrations of 230 – 360 ppmv (Pagani et al., 2005; 2010). Although biome distribution was similar to the Tortonian, during the Messinian, some important regional changes had occurred. Warm – temperate evergreen broadleaf and mixed forest was no longer present in western North America or Australia (Fig. 3.5B), indicating progressing aridification. Further evidence for a global drying comes from the expansion of desert in North Africa and central Asia (Fig. 3.5B). Again during the Messinian both the stomatal indices and boron isotope reconstructions differ. The stomatal indices show a decrease from the Tortonian whilst the boron isotopes increase. The global distribution of biomes appears to support the stomatal indices more than the boron isotope based reconstructions due to regional extinctions of warm – temperate evergreen broadleaf and mixed forests, an expansion of deserts and temperate biomes not reaching as far north (Fig. 3.5B)

So far the alkenone records have not been mentioned with regard to the observed changes in global biome distribution. This is because the atmospheric CO_2 levels reconstructed from alkenones show very little trend from the Langhian to the end of the Messinian. According to the alkenone based reconstructions the atmospheric concentration of CO_2 fluctuated from as low as 190 ppmv to as high as 360 ppmv (Pagani et al., 2005; 2010). This would suggest that either the alkenone based CO_2 reconstruction requires further study, or that the changes in global biome distribution were not related to changes in the atmospheric CO_2 levels. This would contradict the two other main CO_2 reconstructions, which show that the cooling and drying trend seen in the palaeobotanical record from the Langhian through to the Messinian is accompanied by falling atmospheric concentrations of CO_2 and by the pattern in the bottom water oxygen isotopes (Zachos et al., 2008). As the changes of biomes, during the Middle to Late Miocene, are happening at a global scale it requires a forcing agent that can operate at all latitudes; the most likely candidate would be a greenhouse gas, such as CO_2.

3.4.2. Middle to Late Miocene latitudinal gradients

In the Langhian stage the latitudinal bioclimatic gradient shows a significantly flatter equator to pole temperature gradient in both hemispheres, than pre - industrial (Fig. 3.7A; 3.8A). This, coupled with the distribution of biomes (Fig. 3.4A) must reflect a significantly warmer planet associated with elevated atmospheric CO_2 levels, seen in the stomatal indices and boron isotope reconstructions, associated with the end of the MMCO. The high northern latitudes had a MAT around 14°C higher than the pre – industrial (White and Ager, 1994), whilst the MAT of the temperate zone may have been around 9°C warmer than the pre – industrial (Table 3.2). Estimates of climate parameters from the tropics, for the Langhian, are limited at the moment but from the global distribution of tropical evergreen broadleaf forests the tropics likely occupied a greater latitudinal extent and may not have had a significantly different MAT from pre – industrial. By the Seravallian the latitudinal vegetation gradient had changed significantly in the southern hemisphere due to a global cooling and the full glaciation of Antarctica indicated by the absence of vegetation evidence and the presence of glacial deposits (Fig. 3.4B). The northern hemisphere gradient still reflects a significantly warmer world, whilst the latitudinal vegetation distribution of the southern hemisphere was more similar to the pre – industrial. This cooling continued into the Late Miocene and with it the latitudinal distribution of biomes continued to become more pre – industrial like (Fig. 3.7; 3.8).

For the Tortonian the available palaeobotanical data suggests the latitudinal distribution of vegetation in the southern hemisphere was almost identical to the pre – industrial. However MAT estimates from Upper Jakokkota, Bolivia suggest that this site was around 9°C warmer in the Tortonian than during the pre – industrial (Gregory-Wodzicki, 2002). This significant difference in MAT may, in part, be explained by the uplift of the Andes, which is estimated to have proceeded at a rate of 0.2 – 0.3 mm/year (Gregory-Wodzicki, 2000). The vegetation gradient of the northern hemisphere continued, in the Tortonian, to be greater than during the pre – industrial. MAT estimates for the Tortonian suggests the high northern latitudes may have been up to 10°C warmer than pre – industrial and Europe may have been 5 - 8°C warmer than pre – industrial (Table 3.4). Recent work in the Netherlands has reconstructed a MAT for Europe of 18 - 21°C for the Tortonian (Donders et al., 2009). Estimates of cold month mean temperature, using the co – existence approach, suggests the high latitudes of Asia were 9 - 40°C warmer in the Tortonian than the pre – industrial and the warm month mean temperature was 7 - 20°C warmer than pre – industrial (Utescher et al., 2011b). The latitudinal vegetation distribution of the Messinian was very comparable to the pre – industrial. The southern hemisphere as in the Tortonian, was essentially pre – industrial in latitudinal distribution of biomes, whilst the northern hemisphere continued to be warmer than the pre – industrial as shown by the latitudinal distribution of biomes. In the high northern latitudes MAT may have been 5 - 6°C higher than pre – industrial, whilst Europe may have been between 1 - 11°C warmer than pre – industrial (Table 3.4).

3.5. Conclusions

The palaeobotanical changes from the Langhian to the Messinian reflect a global cooling and drying of the planet, linked to falling atmospheric CO_2 concentrations. The biome distribution of the studied 10 Ma period reflects a warmer and wetter world, when compared to the pre – industrial era.

The Langhian shows the warmest biome distribution with cool – temperate mixed forests at the high northern latitudes, extensive warm – temperate mixed forests in the middle latitudes and tundra on Antarctica. Significant cooling had occurred by the Seravallian and current records suggest extensive vegetation was no longer present on Antarctica. The warm – temperate evergreen broadleaf and mixed forests were partly replaced by cooler and drier temperate biomes. This cooling of global climate continued into the Tortonian with the first sign of cold evergreen needleleaf forests in the high northern latitudes. Within the mid – latitudes the warm – temperate evergreen broadleaf and mixed forest continued to be replaced by cooler and drier biomes. Whilst tropical savanna expanded in northern South America at the expense of tropical evergreen broadleaf forest. By the Messinian the global distribution of biomes reflects a significant cooling from the Langhian. Cold evergreen needleleaf forests occupied the high latitudes and an expanse of drier and cooler biomes had replaced much of the warm – temperate mixed forests in the middle latitudes.

The distribution of biomes and their change in distribution through time reflects the changes in the benthic oxygen isotope record, showing that it is a global signal. The changing biome distribution and the changing climate inferred from this reflects the changes in the CO_2 concentrations, reconstructed from the stomatal indices and boron isotopes more than the alkenone based reconstruction. The latitudinal bioclimatic gradients show that the Langhian gradient was significantly flatter than the pre – industrial. By the Seravallian the southern hemisphere bioclimatic gradient was more modern whilst the northern hemisphere bioclimatic gradient was still flatter. The northern hemisphere gradient continued to steepen through the Late Miocene, but was still shallower than the pre – industrial during the Messinian. The latitudinal bioclimatic gradients presented within this chapter provide an initial view of the information the terrestrial realm maybe able to contribute to the understanding of the evolution of the latitudinal temperature gradient through time.

This comprehensive biome dataset is now suitable for further palaeoclimate studies including the incorporation into and assessment of GCM simulations of the Miocene climate. This will be explored in the following chapter were the Tortonian data will be used to evaluate a suite of GCM simulations.

Chapter 4
A data – model hybrid map of vegetation for the Tortonian age

The whole is more than the sum of its parts. – Aristotle

4.1. Introduction

In the preceding two chapters I have presented the Miocene vegetation and palaeoclimate of Derbyshire using palynology and of the world by synthesising global palaeobotanical data. This has provided a dataset of 634 vegetation localities for the Langhian to Messinian stages. However, these vegetation sites are not uniformly distributed across the globe, leaving significant gaps in our understanding of Miocene vegetation and climate (Fig. 3.4; 3.5). Previously, data based global vegetation reconstructions have relied on extrapolating biome boundaries from the limited distribution of palaeobotanical sites (e.g. Wolfe, 1985). More recently the ability to generate vegetation using the climate generated by a GCM has led to global biome maps using a combination of data and models (e.g. Salzmann et al., 2008).

Within the data presented in the previous chapter, the Tortonian has the greatest number of vegetation localities making it an obvious choice to be used in generating a data – model hybrid biome map. A hybrid global vegetation map uses the output from a vegetation model to fill in the gaps where no Tortonian palaeobotanical data has been reported. By first evaluating a suite of model outputs with the data, the model experiment with the best fit to the palaeobotanical record can be used. Previous global maps of Tortonian vegetation have been generated using unpublished data sets (François *et al.*, 2006) or vegetation reconstructed from a small (<50) number of palaeobotanical sites (Micheels, 2003; Micheels *et al.*, 2007). These reconstructions have also been based on a modern geography, instead of the appropriate Tortonian palaeogeography, and have classified Tortonian vegetation into a small (maximum 14) number of biome types. The reconstruction presented here builds and improves on these by using the 326-site palaeobotanical dataset (Chapter 3), combined with a state of the art GCM driven vegetation model experiment, to form a global vegetation reconstruction based on a 27 biome classification scheme (Prentice *et al.*, 1992; Kaplan, 2001).

4.2. Methods

4.2.1. Description of the HadAM3 GCM and BIOME4 models

A suite of Late Miocene atmosphere-only General Circulation Model (AGCM) runs have been carried out using the Hadley Centre Atmospheric Model Version 3 (HadAM3; Lunt et al., 2008; Pope et al., 2000) and the climatologies used to run the mechanistic vegetation model BIOME4 (Kaplan 2001). A brief outline of the model and boundary conditions used in the simulations can be found below. A fuller description of the modelling methodology can be found in Lunt et al. (2008).

HadAM3 has a horizontal resolution of 2.5° latitude × 3.75° longitude, this equates to a spatial resolution of 278 × 417 km at the equator. The model has 19 vertical layers, a time step of 30 minutes and includes the Edwards and Slingo (1996) radiation scheme, the Gregory et al. (1997) convection scheme, a sea ice model that is largely the same as in HadAM2 (Cattle and Crossley, 1995) and MOSES (Cox et al., 1999) a land surface scheme capable of simulating freezing and melting of soil moisture (Pope et al., 2000). HadAM3 has been successfully applied to numerous palaeoclimate intervals of the pre-Quaternary (e.g. Haywood and Valdes, 2006; Haywood et al., 2009).

The Late Miocene palaeogeography, orography and ice sheet extent were derived from Markwick (2007). Crucially this gives a significant decrease in altitude of the Tibetan Plateau relative to the present day, as well as the western cordillera of North and South America. The land surface scheme was set to globally homogeneous values (in this case shrubland). Shrubland was chosen to initialise the model as its physical characteristics are least biasing in terms of climate prediction. Atmospheric CO_2 levels were set at 395 ppmv which is at the higher end of available estimates yet it should be noted that given prescribed sea surface temperatures in this model the exact CO_2 value chosen does not have a large effect on the climate predicted by the model.

In the absence of diagenetically unaltered proxy sea surface temperature estimates (SSTs) (Williams et al., 2005), the Late Miocene SST distribution was derived from a pre-industrial surface temperature distribution, $T^*_{\text{pre-industrial}}$, in the following way (Lunt et al., 2008):

$$\mathrm{SST}_{LateMiocene} = \mathrm{T}^*_{pre-industrial} + \mathrm{A} + (\mathrm{B}(\Phi) + \mathrm{C}(\Phi)\cos(2\pi(\frac{\mathrm{m}-2}{12})))\mathrm{f}(\Phi)$$

Where m is the number of the month (January=1), Φ is the latitude, A is a measure of the global mean warming relative to the pre - industrial, B is a measure of the reduction in the meridional temperature gradient relative to the pre - industrial, and C is a measure of the reduction in seasonality relative to the pre – industrial (Lunt et al., 2008). The precise numbers for these parameters are provided in Lunt et al. (2008; Table 1). $T^*_{\text{pre-industrial}}$ is derived from the means from years 1870–1900 of the Hadley Centre sea surface temperature (SST) and sea ice climatologies (HadISST, Rayner et al., 2003). This formulation allows the sensitivity of the global warming, the amount of polar warmth, the seasonality of the polar warmth, and the form of the latitudinal gradient of warming, to be tested using just 4 key parameters; A, B, C, and f(Φ).We address the inherent uncertainty associated with the prescribed boundary conditions by carrying out a suite of seven Late Miocene simulations, with different values of A, B, C and f (Lunt et al., 2008, table 1). The resulting distributions, from this calculation, are illustrated in and summarised in Lunt et al. (2008; Fig.2, table 2). The prescribed SSTs all have a lower equator to pole temperature gradient than the pre-industrial, in agreement with proxy data (e.g. Pearson et al., 2007), with a maximum change in Northern Hemisphere winter. This is also consistent with the idea that the current strength of the thermohaline circulation developed through the Miocene (e.g. Jakobsson et al., 2007). These seven distributions are identical to those contemplated by Gladstone et al. (2007) in relation to the hydrological budget in the Mediterranean of the Late Miocene. For all simulations, where the value of $SST_{\text{LateMiocene}}$ is below the freezing point of ocean water, T_{freeze}, sea ice is allowed to form. In these instances, the SST is set to T_{freeze}, and the surface temperature is no longer prescribed but is computed by the sea ice component of HadAM3. Certain coastal SSTs had to be extrapolated due to the difference between the modern and Late Miocene land–sea masks, but this is a minor effect.

BIOME4 (Kaplan, 2001) is a mechanistic equilibrium vegetation model which predicts global biome distribution from monthly averages of temperature, precipitation, cloudiness and absolute minimum temperature. Biomes are predicted based on the bioclimatic tolerances of 12 Plant Functional Types (PFT) ranging from cushion forbs to tropical evergreen trees (Prentice et al., 1992). At the core of the model is a coupled carbon-water flux scheme which maximises Net Primary Productivity (NPP) for any given PFT through the determination of Leaf Area Index (LAI). This is calculated on a daily simulation of the soil water balance, canopy conductance, photosynthesis and respiration. The woody PFT that achieves the highest annual NPP at its maximised LAI for a given grid square is considered dominant. This however is not the case for grass-tree areas such as savannas; here a weighted NPP is calculated and inferred fire risks are both used to determine the forest-grassland boundary. The model then orders all the PFTs that could exist under ambient conditions in a grid cell based on NPP, LAI and mean annual soil moisture. It then uses semi-empirical rules to decide on which of the 27 biomes should be plotted in the cell (Kaplan 2001). For the Late Miocene simulations BIOME4 was run in anomaly mode. This is a standard technique that removes known systematic errors in the climate prediction of HadAM3 and has been employed in numerous modern and palaeoclimate/palaeobotanical studies (e.g. Haxeltine and Prentice, 1996; Salzmann et al., 2008; Texier et al., 1997).

	Cohen's Kappa Statistic		Data comparison (r^2)		Sea Surface Temperature (°C) by latitude						
Model	27 biome	7 Megabiome	MAT	MAP	-60	-40	-20	0	20	40	60
Pre-industrial	-	-	-	-	-2.36	14.47	25.49	27.7	23.93	18.07	8.16
Mioc1	0.114	0.241	0.734	0.057	1.9	18.46	28.38	28.7	29.07	26.28	18.33
Mioc2	0.112	0.237	0.731	0.049	-1.94	15.9	27.01	28.7	29.07	26.28	18.33
Mioc3	0.185	0.284	0.720	0.069	-0.16	16.46	26.38	26.7	27.07	24.28	16.33
Mioc4	0.096	0.181	0.663	0.027	1.9	18.46	28.38	28.7	30.43	28.86	21.79
Mioc5	0.137	0.295	0.761	0.043	1.9	18.46	28.38	28.7	26.99	24.16	17.25

Table 4.1. Cohen’s Kappa statistic for the data – model comparison using both the 27 biome scheme and 7 megabiome scheme. The comparison between model predicted MAT/MAP and the values reconstructed proxy data (Table 4.2). Also shown are the sea surface temperatures along a latitudinal profile at 30°W, prescribed to the AGCM from Lunt *et al.* (2008).

4.2.2. Coupling of the data and model

To provide a global vegetation reconstruction it is necessary to fill the regions with limited palaeobotanical data (Fig. 3.5) with vegetation. In this study the technique of Salzmann et al. (2008), using a state-of-the-art model simulation and merging this with the palaeobotanical data is employed. Before the process of merging the data and model into a hybrid reconstruction of global Tortonian vegetation it was first necessary to determine which Late Miocene HadAM3 experiment was best suited for this purpose. The original HadAM3 experiments presented in Lunt et al. (2008; Mioc1-Mioc7) were all used to produce BIOME4 vegetation predictions. Mioc1-Mioc7 represent seven HadAM3 experiments with different SST gradient profiles, generated with the equation described in subsection 4.2.1. The resulting BIOME4 estimates were compared to the Tortonian data collected in Chapter 3, using ArcGIS9 software. Before comparison could begin the palaeobotanical data were first palaeo-rotated to its Tortonian latitude and longitude (using the palaeo-rotation codes of Paul Markwick ensuring consistency between our data and the Tortonian palaeogeography used in HadAM3). To aid comparison and selection, Cohen's Kappa statistic (Cohen, 1960) was used to highlight the statistically most comparable BIOME4 model simulation (Table 4.1). Cohen's Kappa statistic measures the agreement between two sets of categorizations while taking into account chance agreements between categories, where 0 means the agreement is no better than chance and 1 shows a perfect fit (Cohen, 1960; Jenness and Wynne, 2005). BIOME4 simulations Mioc1 – Mioc7 were compared using both the full and mega biome classification schemes of the BIOME4 model. The use of the broader mega biome scheme, following Harrison and Prentice (2003) and Salzmann et al. (2009) (Table 3.1), was necessary to avoid the Kappa statistic becoming meaningless due to some categories containing a low number of sample points for the full biome scheme. Of the experiments, Mioc5 compared most favourably to the palaeobotanical data (i.e. achieved the highest Kappa score using the mega biome scheme) and this experiment was therefore chosen for use in the construction of the data-model hybrid. Mioc5 also compared most favourably to the MAT reconstructions from the palaeobotanical data (Table 4.1). Mioc5 represents a reduced equator to pole gradient in the Northern Hemisphere, with SSTs around 9°C warmer at 60°N (compared to the pre-industrial). The equator to pole gradient in the Southern Hemisphere is slightly reduced when compared to the pre-industrial gradient but with SSTs 3 - 4°C higher. Equatorial SSTs are 1°C warmer than in the pre-industrial (Table 4.1).

The strategy used to join the databased vegetation with model predicted vegetation is summarised in Fig. 4.1 and based on the techniques used in Salzmann et al. (2008). The merger was undertaken on a grid by grid basis; examining each model predicted grid cell and, if necessary, correcting it using available palaeobotanical data. This is most visible in Fig. 5, which shows the consistency of the data – model comparison and the degree of correction. Areas with low or no palaeobotanical data are left unchanged as model predicted vegetation.

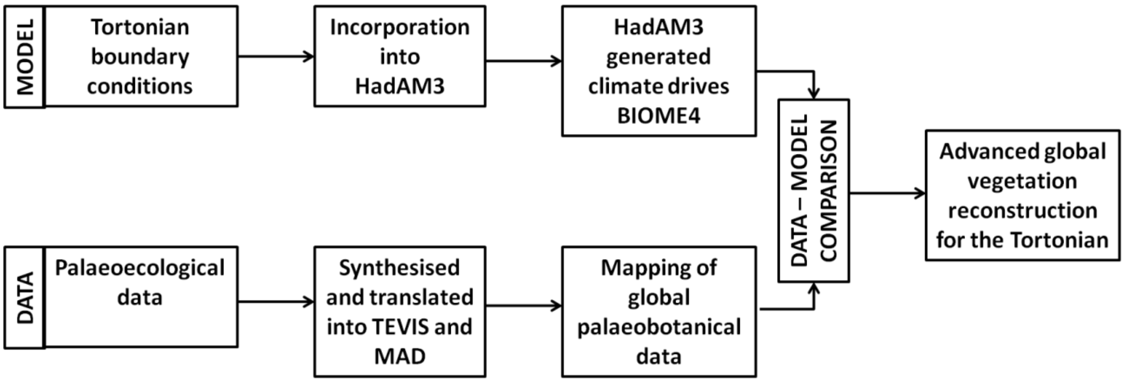


Figure 4.1. Flow diagram explaining the data-model comparison approach. The “model” branch of the process is from Lunt et al., 2008. The “data” branch of the flow diagram was presented in Chapter 3. Adapted from Salzmann *et al.* (2008).

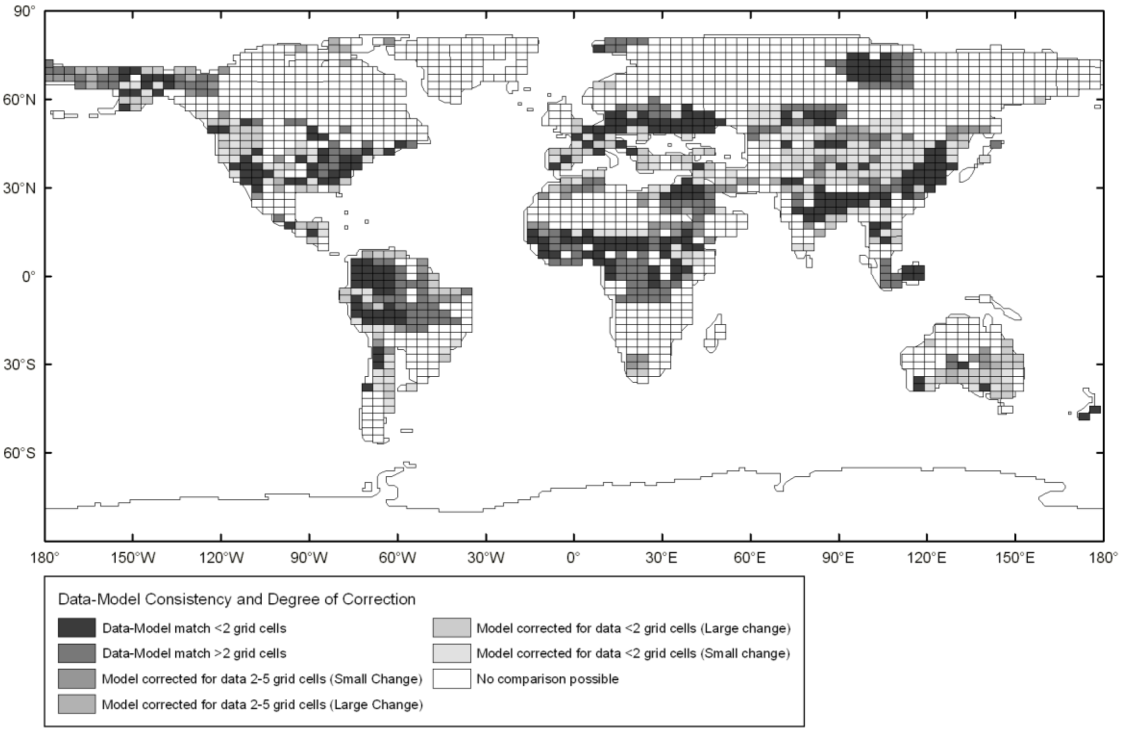


Figure 4.2. A map of the Tortonian world illustrating the degree of consistency between the HadAM3/BIOME4-predicted vegetation and the palaeoecological data. The map also shows the degree to which the model predicted vegetation was corrected by the palaeoecological data. “Small change” represents a relatively minor change in biome type (e.g. tropical evergreen broadleaf forest to tropical semi-evergreen broadleaf forest) and a “Large change” represents a significant change in biome type (e.g. tropical xerophytic shrubland to warm-temperate evergreen broadleaf and mixed forest)

4.3. Global data-model hybrid Tortonian vegetation reconstruction

The plotted biomes, based on the 326 TEVIS data points from Chapter 3, provide an insight into Late Miocene vegetation and climate. There is good data coverage in western USA, Europe, India, southeast Asia and western South America, allowing a confident vegetation reconstruction for these regions. Data coverage also allows a confident reconstruction of Alaska, central Africa, parts of Asia and southern Australia. However, data coverage is not uniform and thus areas lacking adequate coverage rely on modelled vegetation for the reconstruction. These areas include most of the high latitude Northern Hemisphere including much of Canada and northeast USA, Greenland, Scandinavia and Russia. Other areas of poor coverage also include eastern South America, southern Africa and northern Australia.

The Tortonian vegetation reconstruction from both the palaeobotanical data and the BIOME4 model prediction show a warmer and wetter world (Fig.6A). The following section describes and highlights regional vegetation patterns from the Tortonian world. As with the previous chapter numbers in parentheses refer to palaeobotanical site location numbers (Fig. 3.2). All references for specific sites, and the biome code assigned to each has been made available as supplementary information (Appendices A, B). Climatic data are also presented below in the form of MAT in °C and MAP in mm per year. The climatic data is also presented in Table 4.2.

4.3.1. Polar and boreal regions

During the Tortonian the polar and boreal regions (>60°N, >60°S) were dominated by cold evergreen coniferous forests and temperate grasslands. In Eurasia and Greenland there is also an extension of temperate deciduous broadleaved forests from the temperate region. Antarctica is not vegetated in this reconstruction, which is in agreement with the apparent extinction of tundra from Antarctica during the late Middle Miocene (Anderson et al., 2011; Lewis et al., 2008). The ANDRILL AND-2A core, drilled in McMurdo Sound, yielded a palynological assemblage showing the presence of tundra vegetation between 15.7-15.5 Ma. Following this warm period the content of palynomorphs decreases sharply until they are absent before the start of the Tortonian (Anderson et al., 2011; Warny et al., 2009). On Seymour Island and James Ross Island, Antarctic Peninsula the Hobbs Glacier formation has been dated as Late Miocene (Dingle and Lavelle, 1998; Marenssi et al., 2010).This succession of glacial diamictites is considered to have been deposited close to a glacier terminus suggesting the West Antarctic Ice Sheet was almost at its present extent on the Antarctic Peninsula, though with evidence for interglacial events and considerable ice dynamics (Smellie et al., 2006; Marenssi et al., 2010; Nelson et al., 2009). Previously tundra vegetation had been reported from the Pliocene of the Transantarctic Mountains (Ashworth and Cantrill, 2004). The dating of these deposits was based on the assemblage of reworked marine diatoms (Harwood, 1986), more recent work has suggested an age >5.1 Ma and likely much older (Ackert and Kurz, 2004; Ashworth et al., 2007). The growing body of evidence from Antarctica suggests that by the Tortonian the continent was largely glaciated.

The polar and boreal realms are not well constrained in the Tortonian reconstruction. A scarcity of Tortonian palaeobotanical data in Canada, Scandinavia and northern Russia (Fig. 4.3), combined with an extension of the continent into the modern Arctic Ocean north of Scandinavia and the Novosibirsk Islands extending to Svalbard in the palaeogeography means much of the high latitude biomes are model-defined. Likewise Antarctica is defined as having near-modern ice sheet cover in the model boundary conditions, meaning that the BIOME4 model would not predict vegetation on the Antarctic continent. There are some locations that provide evidence of vegetation at the high latitudes during the Tortonian. In Alaska, around the Cook Inlet and Nenana Coal Field (Sites T1-T6) there was a cool mixed forest to 61°N and a mix of cool needleleaf and cold evergreen needleleaf forest further north. Three of the five sites give a mean annual temperature of 4.5±1.5°C, 4±1°C and 10±10°C (Reinink-Smith and Leopold, 2005; White et al., 1997; Wolfe, 1994b); this is 4-10°C warmer than present. The palaeobotanical data and model agreed well on the position of the cold evergreen needleleaf forests but differed on the position of the cool mixed forest. In the BIOME4 model simulation the area with cool mixed forest palaeobotanical data is reconstructed to have temperate deciduous broadleaved forest and warm-temperate evergreen and mixed forest biomes. This discrepancy between the BIOME4 predictions and the palaeobotanical data is related to the SST profile used in the model boundary conditions.

In the North Atlantic (Sites T101-T102), ocean cores provide evidence of terrestrial biomes during the Tortonian. DSDP 338 provides evidence of a temperate forest dominated by coniferous trees at 67°N offshore Norway (Koreneva et al., 1976). ODP Leg 151 contains a pollen assemblage showing the presence of a swampy taiga at 77°N on the Hovgård Ridge (Boulter and Manum, 1997). In Russia there is evidence of the evergreen taiga forest at 70°N (Site T210) and a temperate evergreen forest at 59°N (Site T215). The model successfully predicts the presence of the cold evergreen needleleaf forest at 77°N, but does not predict the presence of the temperate evergreen needleaf forest seen at DSDP 338. Whether this relates to problems in the model prescribed SSTs or is due to the sample coming from an oceanic core rather than a terrestrial deposit will need to be explored in future work.

As data are scarce for the boreal and polar realms, these regions rely heavily on the BIOME4 model for the Tortonian reconstruction. Across North America, BIOME4 predicts a direct transition from boreal taiga to temperate grasslands at 60°N in central Canada and 68°N in western Canada (Fig. 4.3). In northernmost North America, BIOME4 predicts a mixture of temperate grassland, boreal taiga and temperate xerophytic shrubland. In northeast Russia, the model predicts extensive temperate grasslands from 66°N to 78°N with temperate deciduous broadleaved forest reaching 78°N between the longitudes of 25°E and 36°E. This then changes to cool needleleaf forest at 78°N, whereas, for most of the polar boreal region temperate grassland is predicted to change directly into boreal taiga forest, much as it does in North America (Fig. 4.3). There are also minor areas of cool mixed forest, cool needleleaf forests and temperate xerophytic shrubland within the extensive temperate grassland region, these same minor biomes are also found on the west coast. At 60°N the BIOME4 model predicts the presence of warm-temperate forest on the east coast of Eurasia (Fig. 4.3). In eastern Russia and the Kamchatka Peninsula the boreal taiga is predicted by BIOME4 to have had a much lower southern extent at 55°N and changes directly to temperate grassland. BIOME4 shows the presence of boreal forest mixed with some areas of temperate grassland and in the northernmost area, a small region of deciduous boreal taiga. Along the southern coast of the Kamchatka Peninsula, the model predicts a mix of cool mixed and cool needleleaf forest (Fig. 4.3).

Currently there are no published palaeobotanical sites for the Tortonian of Greenland. The BIOME4 model predicts a large expanse of temperate grassland in the northwest and central areas with temperate forests in the south and east. In the far northeast and northwest, small areas of temperate xerophytic shrubland are predicted to have existed (Fig. 4.3). In the boundary conditions of the GCM experiment, based on the palaeogeography (Markwick, 2007), the east Greenland highlands are covered by an ice-sheet and thus were not vegetated. Despite the lack of data on Greenland, good data coverage on Iceland (Sites T96-T99) shows a warm-temperate to temperate climate during the Tortonian. ODP Site 646, located off the southern point of Greenland shows a similar flora to those from Iceland. This provides some evidence to support temperate forest on Greenland at this latitude during the Tortonian. There are no model-predicted biomes for Antarctica because the palaeogeography used in the model boundary conditions has a modern Antarctic ice sheet.

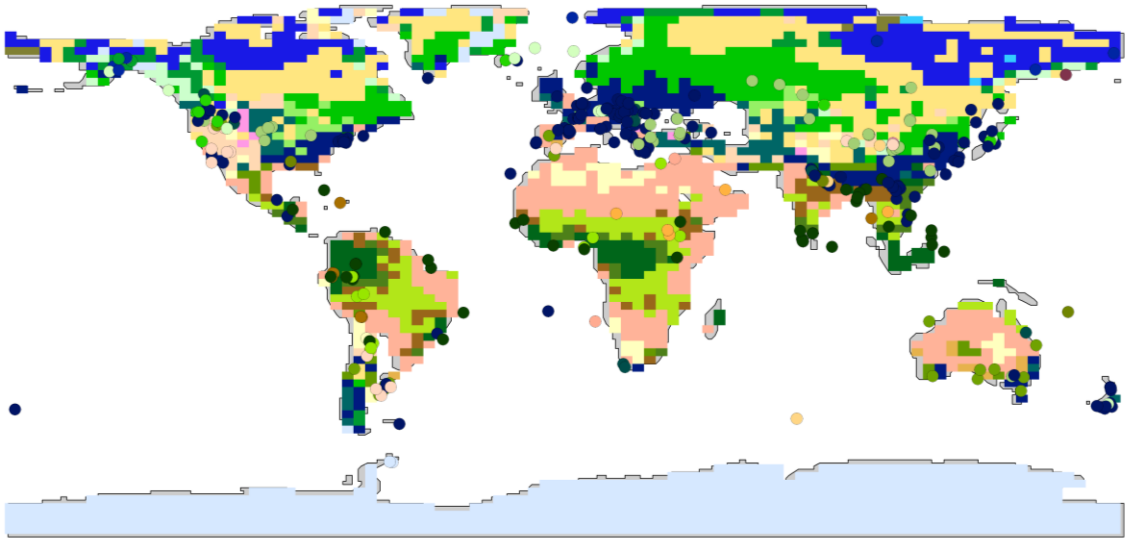


Figure 4.3. The palaeobotanical data sites (circles), from Chapter 3, overlaying the Mioc5 model predicted biome distribution. Biome colours are the same as Figures 1.6, 3.4 and 3.5.

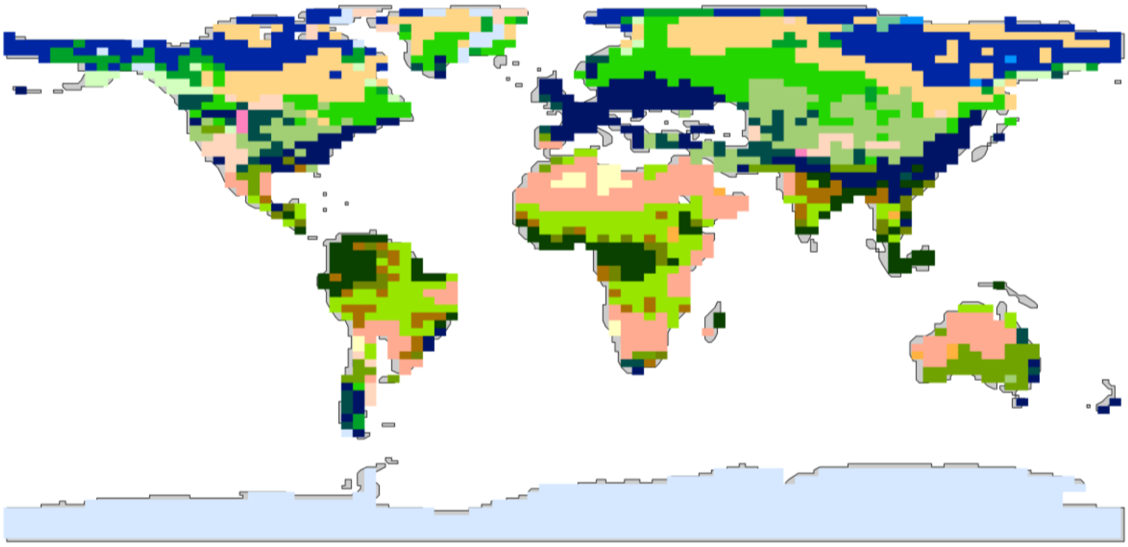


Figure 4.4. The vegetation and palaeogeography of the Tortonian. The merger of data and model creating the hybrid Tortonian vegetation reconstruction. Biome colours are the same as Figures 1.6, 3.4 and 3.5.

4.3.2. Temperate zones

The BIOME4 model predicts a considerable extension of the temperate zone into what is present boreal and polar regions. Data coverage in the temperate zone (23.5-60°N/°S) is good. Notable areas of absence are the Appalachians in the eastern USA, north Mexico, Australia and southernmost South America. Broadly the reconstruction shows a spread of warm-temperate evergreen broadleaved and mixed forest into Europe, Southeast Asia, eastern USA and areas of western USA and an expansion of temperate deciduous broadleaved savanna in Eurasia and central USA.

On the west of the Rocky Mountains, a mixture of forest, woodland and savanna occurred until 38°N, below this the area was dominated by temperate xerophytic shrubland with some coastal forests. At 55°N on what is now the Queen Charlotte Islands, Canada, there was a cool-temperate mixed forest (Site T9). To the south of this there was temperate needleleaf forest (Site T10) near the coast and temperate deciduous broadleaved forest further inland (Site T11). South of this at between 43°N and 48°N, many locations show the presence of a warm-temperate evergreen and mixed forest (Sites T13-T16, T17, T19, T26 and T27). The forest at Musselshell Creek (Baghai and Jorstad, 1995) had a MAT of 12.5±1.5°C and a MAP of 1250 mm (Site T19), this is 7°C warmer than at present and nearly 500 mm/yr wetter. South of this was temperate broadleaved savanna near the coast at Kimble Homestead (Site T18), which is estimated to have a MAT of 12.5±2.5°C, comparable to the warm-temperate evergreen and mixed forest but, with a MAP of 900±100 mm (Retallack et al., 2002). Further inland there was a mix of temperate broadleaved deciduous forest (Site T20) and temperate sclerophyll woodland and shrubland (Sites T21, T23). The former having a MAT of 14°C and a MAP of 635±180 mm (Dorf, 1938) and the latter estimated to have a MAT of 13.4±7.8°C and a MAP of 762 mm (Beuchler et al., 2007; Smith, 1941). For this area the climate data provided by the palaeobotanical locations suggests an increase in MAT of 7-8°C and an increase in MAP of 50-200 mm/yr compared to modern information. The model disagrees with the palaeobotanical data within this region on the amount of MAP, causing the model to predict much drier biomes. The Rocky Mountains are shown to have had some areas of cool mixed forest (Site T25) and areas of temperate needleleaf open woodland (Fig. 4.3, 4.4). South of 38°N, an open vegetation of temperate xerophytic shrubland is predicted by the BIOME4 model and supported by numerous palaeobotanical records (Sites T31, T29, T33 and T34). This open vegetation extended south to the tropical zone, apart from a coastal forest with a warm-temperate evergreen and mixed character (Sites T30, T32) at 31-33°N (Fig. 4.3, 4.4). The warm-temperate evergreen and mixed forest is estimated to have had a MAT of 15±4°C and a MAP of 679±62.5 mm (Axelrod, 2000); although the level of precipitation is rather low to support this type of forest, Axelrod (2000) compared it to cloud forests of Pacific Islands, suggesting it may have required extensive summer fogs. The modelled biomes and the palaeobotanical data agree well with the distribution and extent of the temperate xerophytic shrubland and the presence of coastal warm-temperate forest.

East of the open temperate xerophytic shrubland, the BIOME4 model and the palaeobotanical data agree on the presence of a mixture of temperate needleleaf forest and temperate deciduous broadleaved savanna (Sites T35-T38). Along the Gulf Coast there was a mixture of warm-temperate evergreen and mixed forest (Site T39) and tropical semi-deciduous broadleaved forest (Site T40). In Florida, mammalian fossils and pollen at the Moss Acres Racetrack site show the presence of a temperate to warm-temperate, deciduous broadleaved savanna (Lambert, 1994; 1997). On the east coast of the USA there was a warm-temperate evergreen mixed forest until 46°N (Sites T42-T43 and T46-T47). Further inland where the palaeobotanical data are absent, the BIOME4 model predicts a mixture of temperate deciduous broadleaved forests, temperate deciduous broadleaved savanna and temperate grasslands (Fig. 4.3, 4.4). The warm-temperate evergreen and mixed forest on the east coast, the warm-temperate evergreen and mixed forest biome at Martha's Vineyard and preserved in the Legler Lignite is predicted to have a MAT of between 13.3±5°C and 15±9°C with a MAP of 1270 mm (Axelrod, 2000; Frederiksen, 1984; Greller and Rachele, 1983).

In Europe the palaeobotanical data indicate a vast swathe of warm-temperate evergreen and mixed forest with subtropical elements, from 8°W to 51°E and from 38°N to 60°N (Sites T114-T130, T134-T154, T156-T159, T164-T167 and T169-T173). Within the warm-temperate evergreen and mixed forest biome, which is considered most comparable to the warm-temperate forests of southeast China, climate estimates for the Tortonian from the fossil remains are predicted to have had a MAT of 14.85±0.95°C – 16.8±1.2°C and a MAP of between 988.5±9.5 mm and 1242.5±55.5 mm (Bruch et al., 2006; Erdei et al., 2009; Figueiral et al., 1999; Ivanov et al., 2002; Kvacek et al., 2002; Syabryaj et al., 2007). The MAT is around 6.3°C warmer than at present (the range of difference is -2.4°C – +8.5°C) and the difference in MAP is between 159 mm to 740 mm when compared to modern data. Areas of difference to the widespread warm-temperate evergreen and mixed forest biome are the Iberian Peninsula and the land to the south of the Paratethys Sea in Turkey. In Turkey, the warm-temperate evergreen and mixed forest opened up into a region of temperate deciduous broadleaved savanna (Site T174, T178-T179) and BIOME4 predicted temperate needleleaf forest. Further east the vegetation returned to warm-temperate evergreen and mixed forest (Sites T180-T181). Continuing east from here there was a region of temperate deciduous broadleaved savanna (Brunet and Heintz, 1983), and BIOME4 predicted temperate needleleaf forest extending to 62°E (Fig. 4.3, 4.4). The model and palaeobotanical data agrees well for eastern Europe around the Panonnian Lake. However, the model makes western Europe anomalously dry when compared to the palaeobotanical data.

The Iberian Peninsula also had drier open vegetation than the rest of Europe. On the south coast there was a region of tropical xerophytic shrubland (Site T109), and along the west coast there was a small amount of temperate sclerophyll woodland and shrubland (Site T107). The modern Sahara was greatly reduced, if not absent altogether (Fig. 4.3, 4.4). Temperate sclerophyll woodland and shrubland (Sites T110-T111) and tropical savanna (Arambourg, 1959) inhabited coastal regions of northwest Africa (Tunisia, Morocco and Algeria). Further inland there is no vegetation data and the BIOME4 model predicts tropical xerophytic shrubland and small areas of desert (Fig. 4.3, 4.4). The mix of predominantly tropical xerophytic shrubland and desert continued east across the modern Sahara region until 21°E, from here until the east coast of the Arabian Peninsula there was extensive tropical xerophytic shrubland and an absence of desert. The area around the modern Nile delta had tropical savanna along the coast (Site T193). The BIOME4 model agrees with the palaeobotanical data in that the Iberian Peninsula has more open vegetation than the rest of Europe. However, there is some disagreement as to which biome types are present. The BIOME4 model also fails to predict the coastal vegetation of North Africa; this may be a problem with the model or a question of scale. The palaeobotanical data may reflect vegetation restricted to the coast whereas the model has predicted the overall biome for the grid cell; this will require further study to investigate the palaeobotany further inland.

Along the east coast of the Paratethys Sea, the BIOME4 model predicts a mixture of temperate xerophytic shrubland and temperate needleleaf forests (Fig. 4.3). The temperate needleleaf forests are predicted by BIOME4 to continue, in isolated patches, until 81°E. These forest patches are within an extensive temperate deciduous broadleaved savanna (Sites T205-T206, T208) which existed from 35°N to 58°N in Asia. At the northern extent of the savanna area it is bordered by temperate deciduous woodland which inhabited some of the boreal realm during the Tortonian (Fig. 4.3, 4.4). At its southern limit, the BIOME4 model predicts that the temperate savanna blended into temperate needleleaf forest and temperate needleleaf parkland. The palaeobotanical data shows that the model simulation for this region produces a biome pattern with anomalously high levels of forest.

South of the Himalayas on the Indian subcontinent a band of warm-temperate evergreen and mixed forest ran longitudinally between 28°N and 33°N (Sites T259, T269). Below this there was a mixture of tropical evergreen broadleaved forest, tropical deciduous forest and tropical savanna (Sites T262-T266, T268), and the tropical evergreen broadleaved forest, tropical deciduous forest and tropical savanna biome types continued into the tropical zone (Fig. 4.3, 4.4). In China and southeast Asia, the warm-temperate forests continued in the longitudinal band between 23.5°N and 33°N (Sites T281, T284). Fossils from the Xiolongtan coal mine in

China are estimated to have lived with a MAT of 17.9±1.2°C with a MAP of 1427±212 mm (Xia et al., 2009), both the MAT and MAP are nearly at modern levels for this region. As this band of warm-temperate evergreen and mixed forest reached the east coast of Asia it followed it north, reaching 48°N (Sites T218-T219, T234, T237, T249, T239). In Japan, many fossil sites indicate the warm-temperate evergreen and mixed forest biome also existed there (Sites T240, T244, T246, T247). Throughout India and southeast Asia the model compares very well to the palaeobotanical data and only required slight alterations to create the hybrid reconstruction.

On the Himalayan Plateau and further north a patchwork of temperate xerophytic shrubland (Site T230), temperate deciduous broadleaved savanna (Sites T211-T213, T221-T223, T231-T233, T236), temperate deciduous broadleaved forest (Site T209) was present during the Tortonian. At the northern limit of the temperate zone, BIOME4 predicted cool needleleaf forest existed at this time (Fig. 4.3, 4.4). The mixture of temperate xerophytic shrubland, temperate deciduous broadleaved savanna and temperate deciduous broadleaved forest biome types continued north until it bordered an extensive temperate grassland predicted by BIOME4. In north central Asia the transition from temperate biomes to the cold evergreen needleleaf forest biome occurred as far south as 55°N (Fig. 4.3, 4.4); currently there is no available data to confirm the transition. This region in the BIOME4 simulation is heavily influenced by the orography which is the reason for minor differences with the palaeobotanical data. For the majority of this region the model predicted temperate grassland or temperate deciduous broadleaved forest, whereas the palaeobotanical data reflected a temperate deciduous broadleaved savanna.

In South America, the temperate zone contains many sites along the western side and sparse data along the east. On the east coast BIOME4 predicts a continuation of tropical vegetation into the temperate zone, this is mainly tropical xerophytic shrubland with some areas of semi-deciduous to deciduous tropical forest (Fig. 4.3, 4.4). At Taubate, Brazil (Site T69) pollen provides evidence of a subtropical to warm-temperate forest along the coast (Garcia et al., 2008). On the west side of the South American temperate zone, tropical xerophytic shrubland changed to tropical savanna (Sites T76, T78) and a proto-Atacama desert (Site T73) at 24-26°S. South of this, an area of temperate xerophytic shrubland occupied a narrow band (Site T79) before changing into temperate sclerophyll woodland and shrubland (Site T80). South of this area there is scarce data, apart from an area of temperate xerophytic shrubland (Sites 64-66) between 39°S and 46°S. For the rest of southern South America, BIOME4 predicts a mixture of warm-temperate to cool-temperate forests (Fig. 4.3, 4.4). The palaeobotanical data and BIOME4 model compare well for temperate South America. Model-predicted biomes that required altering for the hybrid reconstruction were either too dry or too wet. This seemingly contradictory statement is probably related to the uncertainty estimating the orography; both within the model boundary conditions and in terms of the altitude the palaeobotanical data is derived from.

The temperate zone of southern Africa is small and poorly-covered by data. The temperate zone is predicted, by BIOME4, to start with a continuation of the tropical xerophytic shrubland until 28°S to 31°S where tropical semi-deciduous and deciduous forests are predicted to begin. The nearest data points to this model predicted transition are at 34°S, from western South Africa and they show the presence of a temperate needleleaf forest (Sites T203-T204). For the South African Cape, BIOME4 predicts a warm-temperate evergreen and mixed forest (Fig. 4.3, 4.4). The model-predicted biomes around the South African Cape were too dry to match the limited palaeobotanical data for the area. This shows there is some problem in the amount of precipitation generated by the model for this region.

In Australia, the temperate zone was dominated by temperate sclerophyll woodland and shrubland during the Tortonian (Sites T306-T307, T310, T313-T314). Location T307 at Lake Tay predicts this biome to have had a MAP of 1375±125 mm (Macphail, 1997), which is an increase of around 1100 mm/yr when compared to modern data. A small area of temperate grassland was present in southeast Australia (Site T311) and BIOME4 predicts coastal warm-temperate evergreen and mixed forest and temperate needleleaf forest along the east coast (Fig. 4.3, 4.4). In central Australia, the model also predicts an area of tropical grassland. On New Zealand, many data points agree with the BIOME 4 prediction of warm-temperate evergreen and mixed forest (Sites T316, T318, T321). Overall the palaeobotanical data and model-generated biomes for temperate Australia compare well in places, but broadly the model predicts biomes that are too dry

Region	Site	Mean Annual Temperature °C		
		Present	Model	Palaeo - data
Southern Alaska				
Cool mixed forest	1	1.7	3.4	10.0±10.0
Cool evergreen needleleaf forest	5, 8	-6.9	0.6	5
Cold evergreen needleleaf forest	2	-3.2	0.4±0.4	4±1
Western U.S.A.				
Warm-temperate evergreen mixed forest	19, 30	5	8.6	15±4
Temperate deciduous broadleaved forest	20	5.5	10.8	14
Temperate schlerophyll woodland and shrubland	18	6.3	15.2	12.5±2.5
Temperate xerophytic shrubland	21, 23	6	11.4	13.4±7.8
Cool temperate mixed forest	25	6.4	12.2	11±4
Eastern U.S.A.				
Warm-temperate evergreen mixed forest	46, 47	10.5±0.4	19.4±0.4	14.2±0.8
Europe				
Warm-temperate evergreen mixed forest	103, 104, 105, 119, 120, 140, 148, 151, 153, 157, 159, 161, 165, 170	7.8±1.4	18.5±2.5	14.8±3.2
Temperate deciduous broadleaved savanna	163	10.9	19.9	15±3
Turkey				
Warm-temperate evergreen mixed forest	180	9	17.7	18.4±2.9
Temperate deciduous broadleaved savanna	179	7	16.7	18.6±2.2
South-east China				
Tropical evergreen broadleaved forest	283	13.6	14.5	17.1±3.8
Warm-temperate evergreen mixed forest	284	16.6	16.6	17.9±1.2
Indonesia				
Tropical evergreen broadleaved forests	302	26.86	27.8	27.15±0.55
Australia				
Warm-temperate evergreen mixed forests	312			
Temperate schlerophyll woodland and shrubland	303, 307	-	-	-

Table 4.2. Climate data derived from palaeobotanical evidence. Mean annual temperature (°C) and mean annual precipitation (mm/year) is presented for various regions of the world subdivided by biome type. The palaeo data is from Table 3.4 and is compared to the average Mioc5 climate for each region and the average modern climate.

Region	Site	Mean Annual Precipitation mm/yr		
		Present	Model	Palaeo - data
Southern Alaska				
Cool mixed forest	1	-	-	-
Cool evergreen needleleaf forest	5, 8			
Cold evergreen needleleaf forest	2	-	-	-
Western U.S.A.				
Warm-temperate evergreen mixed forest	19, 30	801.4	681.12	933.3±316.8
Temperate deciduous broadleaved forest	20	582.1	612	635.0±180.0
Temperate schlerophyll woodland and shrubland	18	985.5	912.5	900.0±100.0
Temperate xerophytic shrubland	21, 23	499.3	555.5	762
Cool temperate mixed forest	25	454.8	478.2	1206.5±63.5
Eastern U.S.A.				
Warm-temperate evergreen mixed forest	46, 47	1104.5	1005.8	1270.0
Europe				
Warm-temperate evergreen mixed forest	103, 104, 105, 119, 120, 140, 148, 151, 153, 157, 159, 161, 165, 170	734.4±34.9	1146.60±691.6	1141.9±100.6
Temperate deciduous broadleaved savanna	163	500.4	541.8	659.5±100.5
Turkey				
Warm-temperate evergreen mixed forest	180	594.7	477.7	1198.5±375.5
Temperate deciduous broadleaved savanna	179	533.2	535.7	1203.5±316.5
South-east China				
Tropical evergreen broadleaved forest	283	1053.4	1005.8	1029.2
Warm-temperate evergreen mixed forest	284	1611.6	974.2	1427.0±212.0
Indonesia				
Tropical evergreen broadleaved forests	302			
Australia				
Warm-temperate evergreen mixed forests	312	804.83	1534.83	1500.0
Temperate schlerophyll woodland and shrubland	303, 307	427.4±155.1	329.8±77.2	1212.0±163.0

Table 4.2. *Cont.* Climate data derived from palaeobotanical evidence. Mean annual temperature (°C) and mean annual precipitation (mm/year) is presented for various regions of the world subdivided by biome type. The palaeo data is from Table 3.4 and is compared to the average Mioc5 climate for each region and the average modern climate.

4.3.3. Tropical zones

The tropical zones (23.5°S – 23.5°N) have good data coverage. Notable exceptions are southern Africa, Central America, eastern South America and northern Australia. In general there is an opening up of the tropical forests of South America, an expansion of tropical vegetation into the Sahara Desert in Africa, extensive tropical forests in India and southeast Asia and open biomes in Australia.

In Central America, palaeobotanical data show the presence of a warm-temperate evergreen and mixed forest (Site T48) at Jalapa, Mexico (Graham, 1975) where a warm *Liquidambar* – *Quercus* forest bordered mangroves. Further south, near Rio Honda, Mexico (Site T49) a tropical evergreen broadleaf forest occupied the region during the Tortonian (Graham, 1998). Apart from these sites the rest of Central America is predicted by BIOME4 (Fig. 4.3, 4.4). In the north, tropical xerophytic shrubland and temperate sclerophyll woodland and shrubland continued into the tropical zone from the temperate zone. Below 20°N a patchwork mixture of tropical savanna, tropical deciduous woodland and tropical semi-evergreen forest is predicted to have existed. At the Panama Seaway, BIOME4 predicts a tropical evergreen broadleaved forest (Fig. 4.3, 4.4). The limited palaeobotanical data for Central America make a comprehensive data-model comparison difficult, but based on the available evidence the model appears to simulate vegetation here well.

In northern South America, a broad expanse of predominantly tropical evergreen broadleaved forest (Sites T53, T58, T54-T55, T60, T62-63) with some isolated areas of tropical deciduous woodland (Sites T56-T57, T59) was present. Along the edges of this forest BIOME4 predicts tropical semi-evergreen forest and tropical deciduous woodland . This forest opened up into tropical savanna (Sites T61, T66-T67) which continued east across South America to between 46°W-38°W where, in an absence of data, BIOME4 predicts tropical xerophytic shrubland (Fig. 4.3, 4.4). Some evidence for tropical evergreen broadleaved forest along the coast is present on Outeiro Island, Brazil (Site T65). Near 23.5°S on the east side of South America there is a lack of data and BIOME4 predicts an area of tropical deciduous woodland within the extensive tropical savanna. In eastern South America, at this latitude there is evidence for tropical deciduous woodland (Sites T71-T72). The eastern tropical deciduous forest biome is estimated to have a MAT of 19.8±3.7°C – 21.5±2.5°C and a MAP of 550±180 mm at Upper Jakokkota (Gregory-Wodzicki, 2002). This is an increase of 9-10°C when compared to the modern MAT, but a reduction in MAP of about 570 mm. The BIOME4 model generated biomes and palaeobotanical data for tropical South America compare very well. The majority of the palaeobotanical data are grouped in the west and shows the extent of the tropical forest successfully predicted by the model to be accurate. It also clearly indicates the areas with tropical savanna and tropical deciduous forest predicted by the model and supported by the palaeobotanical data. In the east of tropical South America there is only a single, coastal data point. This pollen record however shows the model is anomalously dry in this region and the model generated biomes required modification for the hybrid reconstruction.

The tropical zone of Africa, south of the Sahara was an extensive tropical xerophytic shrubland during the Tortonian (Fig. 4.3, 4.4). This turned into tropical savanna at between 15-20°N (Site T192), except on the Arabian Peninsula where xerophytic shrubland is the dominant biome with minor amounts of tropical grasslands along rivers and the coast (Site 120). In West Africa, tropical forests began at 16°N (Sites T185-T186) but were mainly restricted to coastal grid squares and tropical savanna is found as far south as 6°N (Site T191). In central Africa, the tropical forests occupied a region comparable to the modern forests. Data for this comes from the Niger Delta in the west (Sites T188-T189) and Kenya in the east (Site T200) with BIOME4 supporting the data and showing the extent of the forest (Fig. 4.3, 4.4). Climatic estimates for the tropical forest in Kenya give a MAT of 21.7±2°C and a MAP of 1045±200 mm (Jacobs and Deino, 1996); this is comparable to modern levels. Around Ethiopia and Sudan, an area of tropical evergreen forest was present (Site T196) surrounded by tropical savanna (Site T199) and tropical grassland (Sites T197-T198). Apart from the sites mentioned, there is an absence of other data points for tropical Africa and so the reconstruction relies on BIOME4. Between 1°S and 6°S, the tropical forests opened up into tropical savanna with isolated patches of tropical deciduous woodland. At around 19°S this gave way to tropical xerophytic shrubland and a small Namib Desert. Along the east coast of Africa BIOME4 predicts tropical xerophytic shrubland (Fig. 4.3, 4.4). From the palaeobotanical data available for tropical Africa it is clear that the data and model compare closely. Modifications to the model-predicted biomes was mainly restricted to the savanna-xerophytic shrubland boundary which mammalian sites showed was too far south by the distance of a grid cell.

In tropical India, palaeobotanical data are confined to the south and northeast of the subcontinent and indicate the presence of a tropical evergreen broadleaved forest (Sites T271-T280). Away from these regions the vegetation is predicted by BIOME4 (Fig. 4.3, 4.4). The biomes predicted show a mixture of tropical evergreen, semi-evergreen and deciduous forests along the coast and tropical savanna inland. Moving east, data from Vietnam show the warm-temperate evergreen and mixed forest as far south as 18°N (Sites T285-T291). This forest opened up to tropical savanna and tropical grassland (Site T294) along the west of the southeast Asian peninsula. On the east side, a mixture of warm-temperate evergreen and mixed forest (Sites T295, 297) and tropical evergreen broadleaved forest (Site T296) existed. Below 11°N, an absence of data means the vegetation is predicted by BIOME4. From 11°N to 5°N, the model predicts an area of semi-evergreen tropical forest with isolated tropical savanna, below 5°N BIOME4 predicts the presence of tropical evergreen broadleaved forest (Fig. 4.3, 4.4). This is supported by a pollen assemblage from Brunei (Site T300). As in the temperate zone, the model predicted tropical zone of India and southeast Asia compares well to palaeobotanical data requiring only minor modifications for the hybrid reconstruction.

Palaeobotanical sites for the Australian tropical zone are exceedingly sparse. ODP 765 (Site T303), located immediately off the west coast, suggests the presence of a temperate sclerophyll woodland with an estimated MAP of 1050±450 mm (Martin and McMinn, 1994; MacPhail, 1997). On the east coast, there was a coastal temperate needleleaf forest (Site T305), which continued south into the temperate zone. The rest of tropical Australia is predicted by BIOME4 to be coastal tropical savanna and tropical xerophytic shrubland until the temperate zone (Fig. 4.3, 4.4). Limited data for the tropical zone of Australia means the hybrid reconstruction relies on the model defined biomes. The available palaeobotanical data shows that, as with the temperate zone of Australia, the tropical zone is too dry in places.

4.4. Discussion

4.4.1. Tortonian vegetation and climate

The Tortonian palaeobotanical data show agreement with the predictions of the BIOME4 model, with higher than pre-industrial SSTs and atmospheric CO_2 levels at 395 ppmv. The reconstruction of Tortonian biome distribution shows significant differences compared to the present-day potential natural vegetation, in the high latitudes and temperate realms (Fig. 4.4). Differences are also seen in the tropics but these involve the change in distribution of modern tropical biomes, rather than the movement of biomes into regions where they do not exist today. Of these significant vegetation shifts, the northwards shift of boreal taiga, temperate deciduous forest and temperate grasslands are the most pronounced. Potential natural (i.e. without human influence) present day biome distribution (Fig. 1.6) shows the boreal forests (cold evergreen needleleaf and cold deciduous forests of BIOME4) have a southern limit of ca. 45°N in east Eurasia and a northern limit of ca. 70°N in northern Russia and Canada (Kaplan, 2001). During the Tortonian, the evergreen boreal forests reached at least 77°N (Site T101) and in the reconstruction it extends to 80°N. Reconstructing the southern limit is difficult due to a lack of data from the polar region. In Alaska it is at 61°N (Site T3) and minimally at 70°N in Russia (Site T210). In the hybrid reconstruction, the BIOME4 model indicates the lowest occurrence of the boreal taiga forests is in east Eurasia at 55°N.

This dramatic shift of the boreal taiga by up to 10° indicates significant high latitude warming relative to today. Accompanying this northward shift of the boreal taiga was a loss of tundra biomes (Fig. 4.4). The northward shift of the boreal forests has been shown to be a vegetation–climate positive feedback; with the treeline moving north altering the surface albedo and carbon budget of the high latitudes (de Noblet *et al.* 1996; Sturm *et al.* 2001). Inclusion of this Tortonian vegetation reconstruction, as a boundary condition in future modelling studies, may help to increase high northern latitude MATs and the simulation of a reduced pole to equator gradient. In this study the HadAM3-driven BIOME4 vegetation model was able to predict the northward shift of forest biomes but this required a significant increase in SSTs (Table 4.1). These high SSTs could also be responsible for making model-predicted biomes for areas of western Europe, western USA, Australia, South Africa and eastern South America too dry, when compared to the biomes reconstructed from the palaeobotanical data. Although higher SSTs will create a more active hydrological cycle, the Mioc5 AGCM experiment has a global MAP increase of only 126.7 mm/year relative to the pre-industrial scenario. From the number of regions showing model-generated biomes that are too dry compared to palaeobotanical data, the increase in global precipitation is either not enough or is occurring in the wrong regions. These discrepancies in regions that current experiments make too dry will form part of future model simulations. These future simulations will include the Tortonian vegetation reconstruction presented here as a boundary condition instead of the global shrublands used by Lunt *et al.* (2008). This should show to what extent a “best fit” global vegetation reconstruction can impact on precipitation.

Following the cold taiga forests northwards were the temperate forests and temperate grassland biomes (Fig. 4.3, 4.4). The extensive temperate grasslands predicted by BIOME4 are not supported by any palaeobotanical data points. The data and BIOME4 model predictions agree on the presence of a warm-temperate evergreen and mixed forest in Europe bordering the Paratethys Sea, however in western Europe BIOME4 predicts a much more fragmentary biome pattern than indicated by palaeobotany. In places, the model predicts temperate evergreen needleleaf forests and tropical xerophytic shrublands. This suggests the model interprets western Europe as too dry, and is most likely related to the increased MATs from the higher SSTs. This is because there is only a slight difference in the modelled MAP between the Late Miocene and the pre-industrial model experiments (Fig. 4.5). Considering the differences in climate between the Late Miocene model and those derived from palaeobotanical data for this biome; the model predicts slightly higher MATs (within the range of the fossil data) and a MAP comparable to that estimated from the data (Table 4.2). The climatic data suggests the Tortonian MAT in Europe was at least 5-8°C warmer than the pre-industrial age and received around 400 mm/year more precipitation. This warm-wet climate across Europe during the Tortonian is in agreement with studies using other proxies (Böhme *et al.*, 2008).

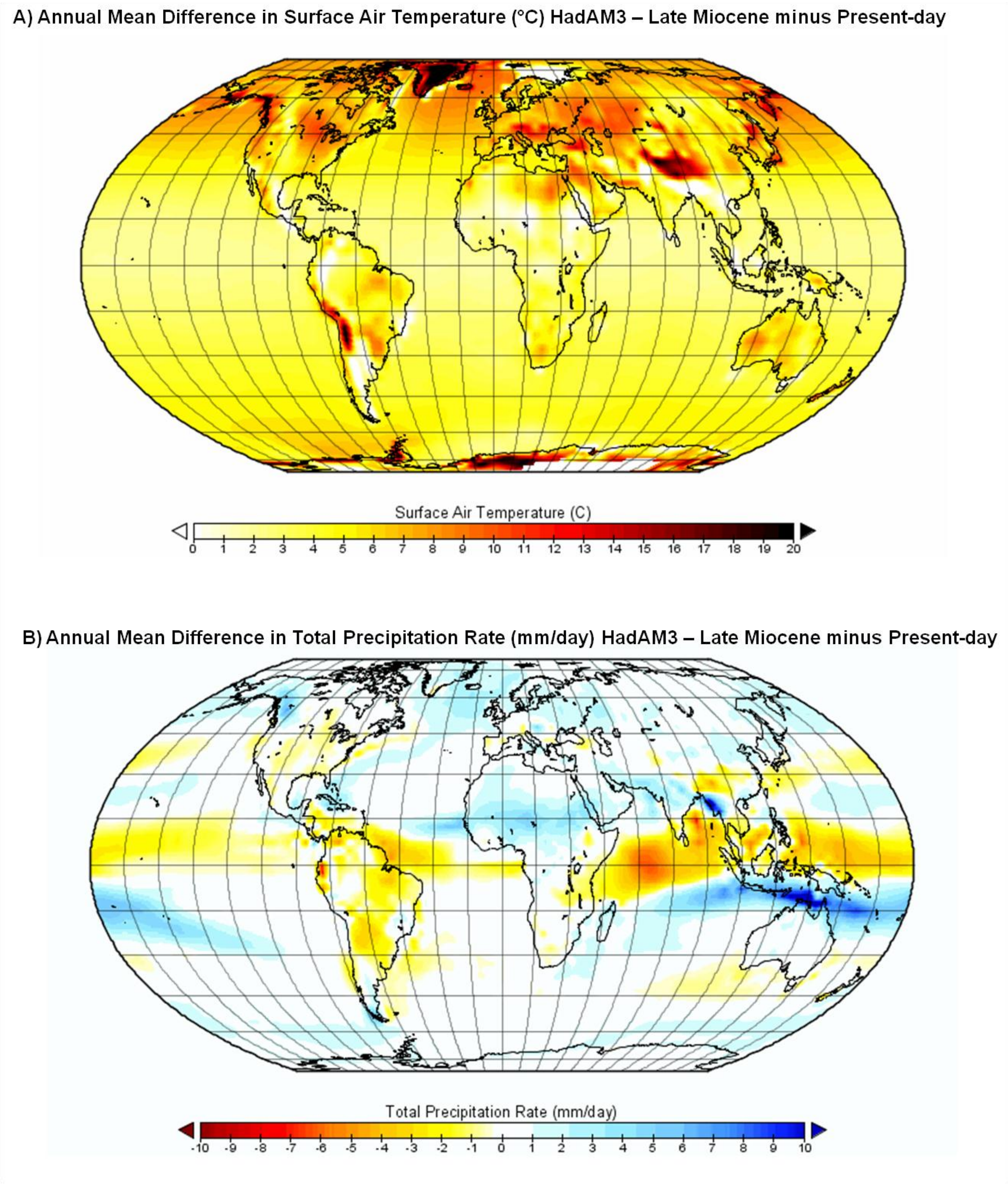


Figure 4.5. Climate maps for the Mioc5 AGCM experiment minus the present day, shown on modern geography. A) Mean annual temperature (°C), B) Mean annual precipitation (mm/day). Both plots show the difference with the pre-industrial.

The palaeobotanical data and BIOME4 predictions for the western USA differ. In this region, the model predicts a mixture of temperate grassland, temperate xerophytic shrubland and temperate needleleaf forest. The palaeobotanical data also suggests a mixture of biomes;

warm-temperate evergreen and mixed forest, temperate deciduous broadleaved savanna, temperate sclerophyll woodland and shrubland and temperate deciduous broadleaved forest. The differences between BIOME4 and the data relates to the orography. It is a common problem for model-data discrepancies in mountainous regions due to both the model resolution and preservation bias of the fossil record (Salzmann *et al.*, 2008). In the BIOME4 model, each 2.5° x 3.75° grid cell has its biome calculated based on the climate generated by the AGCM and the average altitude of the cell. In comparison, the palaeobotanical data comes from a single locality. This locality is within an area of deposition, typically lowland areas such as valley bottoms, which means that the palaeobotanical evidence for mountain regions is often biased towards valley and low altitude habitats and not the regional vegetation. This hampers a meaningful data-model comparison within mountainous regions (Salzmann *et al.*, 2008).

In the reconstruction, there is a relatively small Sahara Desert, mainly based on the BIOME4 reconstruction. The model predicts an expansion of tropical xerophytic shrubland across most of the modern Sahara and the Arabian Peninsula; desert areas were restricted to the north and northeast of the modern Sahara region (Fig. 4.4). The palaeobotanical and mammalian evidence shows that along the Mediterranean coast, a mixture of temperate sclerophyll woodland and shrubland and tropical savanna existed. Tropical grasslands are reconstructed for the east coast of the Arabian Peninsula and tropical savanna was present along the modern southern margin of the Sahara desert. Evidence for desert conditions in North Africa comes from sedimentological evidence in Chad. Here wind-blown sandstones conformably underlie a mammal-bearing horizon dated as 7.4-6 Ma (Schuster *et al.*, 2006a; Vignaud *et al.*, 2002). Across the Sahara region there are however vertebrate fossil sites that suggest more vegetated conditions. Fossil bushbabies (*Galago farafraensis*) from Egypt provide evidence of a habitat with trees and an estimated rainfall of 500-1200 mm/year (Pickford *et al.*, 2006); crocodiles from Tunisia also indicate more humid conditions (Agrasar, 2003; Pickford, 2000).

In South America, southeast Asia and tropical Africa the palaeobotanical data and BIOME4 predictions are consistent (Fig. 4.2). However in the Amazonian basin and Africa south of the equator, the absence of palaeobotanical data means the reconstruction relies entirely on BIOME4 (Fig. 4.2). In East Africa south of the equator the model predicts tropical xerophytic shrubland, this is the same biome predicted for this region in the Piacenzian (Salzmann *et al.*, 2008). The difference between this Tortonian reconstruction and the Piacenzian reconstruction is the presence of palaeobotanical data in this region during the Piacenzian, allowing the reconstruction of tropical savanna rather than tropical xerophytic shrubland. The difference for the Piacenzian between the AGCM and palaeobotanical data was due to the modelling of rainfall patterns possibly related to the Somali Jet, which controls precipitation in this region today (Salzmann *et al.*, 2008). If this is a problem in the model then the same error may exist in the Tortonian simulations, further palaeobotanical exploration in the Horn of Africa and south along the east side may help to prove or disprove the Tortonian vegetation reconstruction.

Of the available Tortonian AGCM experiments from Lunt *et al.* (2008), Mioc5 compared most favourably to the 326 palaeobotanical data points. Statistically Mioc4 compared more favourably in the full biome scheme, but this model predicted a desert in the Amazonian Basin. Mioc5 achieved a higher Kappa score for the mega biome scheme and did not predict the desert in Amazonian Basin. Choosing the experiment with the best megabiome score increases our confidence in the statistical test applied since; having a large number of categories with a low sample in each is less robust than having fewer categories with more samples in each. A minimum of 50 samples per category should be used, and 75-100 samples for more than 12 categories (Congalton and Green, 1999; Jenness and Wynne, 2005). This is difficult for palaeontological studies where sample sizes are restricted by many factors such as deposition, taphonomy, preservation and limited exposure. This makes the mega biome Kappa scores more statistically robust than that for the full biome classification. Combining the palaeobotanical data with the Mioc5-driven BIOME4 vegetation model required some model defined areas to be modified (Fig. 4.2). These include western USA, western temperate South America, western Europe, central Asia, South Africa and Australia. All these regions are in the temperate zone which may indicate the SST gradient used in the experiment was unsuitable. Some of the regions are also heavily influenced by orography which, as previously discussed, confounds palaeobotanical data and model comparisons. Areas that compared favourably included eastern and central USA, tropical South America, central Europe, tropical Africa and southeast Asia. These areas also include regions in the temperate zone but mainly those in the tropics, showing that the SSTs for the tropical zone were correctly defined. The limited palaeobotanical data available in the polar zone provides evidence that the prescribed SSTs for this climatic zone were well-defined, perhaps even too warm around Alaska where the Mioc5 driven BIOME4 model predicts temperate to warm-temperate biomes. Palaeobotanical data for this region shows the presence of a cool mixed forest, a biome that is colder than those predicted by the model. Overall, the prescribed SST gradient for the Mioc5 GCM experiment that generated the model-defined biome distribution best matches the available palaeobotanical data. However, the areas of data-model discrepancy show that further work is required to correctly simulate the Tortonian climate.

4.4.2. A comparison of the vegetation of the Late Miocene and the Pliocene

Examining trends in vegetation patterns of a warmer world, the Tortonian reconstruction presented here is compared with the vegetation of the Piacenzian (3.6-2.6 Ma), created using the same methodology (Salzmann *et al.*, 2008). Both reconstructions show boreal forests migrating towards the poles, followed by temperate forests and grasslands. The spread of warm-temperate evergreen mixed forests in Europe and southeast Asia are evident in both reconstructions, though this biome spreads more in North America in the Late Miocene than in the Piacenzian. Both reconstructions show a reduction in the extent of the Sahara Desert, though more-so in the Late Miocene. Both reconstructions show an opening up of the tropical forest in South America when compared to present day natural vegetation. In temperate South America however the reconstructions differ, with the Late Miocene having drier conditions than those of the Piacenzian. In tropical Africa the biome distribution is comparable with slightly more tropical evergreen broadleaved forest in the Tortonian. Below the equator, the Piacenzian reconstruction benefits from better data coverage and thus the reconstructed biomes differ. Similar biomes are predicted in both reconstructions for Asia behind the Himalayan Front. In the Piacenzian a mixture of temperate grasslands, temperate xerophytic shrubland and temperate forests existed, whilst in the Tortonian temperate savanna dominates with patches of temperate forests and temperate xerophytic shrublands. South of the Himalayan Front, both reconstructions show a mixture of warm-temperate forest, tropical forests and tropical savanna in Southeast Asia. In Australia both reconstructions show much wetter vegetation than that of the present-day potential vegetation; the main difference is where the woodland and forest biomes are distributed. In the Piacenzian forests woodland and savanna are distributed in the east of the continent, whereas in the Tortonian a large area of temperate sclerophyll woodland and shrubland is present across the south of the continent (Salzmann *et al.*, 2008).

Both reconstructions, despite the difference in age, show similar patterns of biome changes relating to both being warmer worlds than present. The reconstructions show a spread of boreal forests polewards followed by temperate biomes. Both show an expansion of warm-temperate forests with subtropical taxa in the temperate realms of Eurasia and both show a reduction of deserts. Different continental configuration, orography and ice-sheet extent are most likely to account for differences between the two reconstructions. These broad vegetation patterns are also seen in future climate simulations, as a result of anthropogenic CO_2 emmisions (Salzmann *et al.*, 2009).

4.4.3. Comparison to previously published Tortonian vegetation reconstructions

The Tortonian reconstruction presented here, using a 27 biome classification of 326 palaeobotanical sites and a state-of-the-art AGCM shows similarities and differences to previously published Tortonian vegetation reconstructions (François *et al.*, 2006; Micheels *et al.*, 2007). Both of these studies used an AGCM with a resolution of 3.75°x3.75°. In François *et al.* (2006) a modern palaeogeography was populated with vegetation based on an unpublished palaeobotanical database and predicted vegetation from BIOME1 (Prentice *et al.*, 1992). This 14 biome reconstruction shows the same spread of boreal forests in the high latitudes. However in North America, Iceland, and east Eurasia, the boreal forests extended southwards into regions with palaeobotanical data showing the presence of other biomes (Fig. 4.3, 4.4). In the temperate region both the reconstructions presented here, and that of François *et al.* (2006), indicate a spread of warm-temperate evergreen mixed forests [temperate broadleaved evergreen forest in François *et al.* (2006)] in Europe and the eastern USA. For the rest of North America, the Tortonian reconstructions differ, with palaeobotanical evidence suggesting temperate savanna where François *et al.*, (2006) predicted tropical seasonal forest and temperate forests (Fig. 4.3, 4.4). In Eurasia, both reconstructions predict a patchwork of vegetation on the Himalayan Plateau, François *et al.*, (2006) predicted grassland, semi-desert and minor savanna leading directly into boreal forests at ca. 45°N. The reconstruction herein (Fig. 4.3, 4.4) shows predominantly temperate savanna with minor areas of temperate xerophytic shrubland, temperate deciduous broadleaved forest and temperate evergreen needleleaf forest. This then changed to temperate grassland at 45°N before a transition to boreal forest at ca. 55°N. In South America, the reconstruction of François *et al.* (2006) predicted tropical rain forest extending into the temperate realm to about 40°S and a tropical seasonal forest occupying the Atacama Desert. The palaeobotanical evidence presented here indicates that the temperate zone of South America was a mixture of temperate xerophytic shrubland and tropical savanna with a reduced Atacama Desert (Fig. 4.3, 4.4). These discrepancies in South America may relate to differences in geography, because a seaway was present in much of modern Argentina (Fig. 4.3, 4.4). Differences also occurred in tropical South America where palaeobotanical evidence suggests an opening up of the modern rainforest to create an area of tropical savanna, whereas François *et al.* (2006) presented an extensive area of tropical forest. In Africa, the reconstructions appear comparable except in the Sahara where BIOME4 predicts small areas of desert and in southern Africa where BIOME4 predicts a mixture of tropical savanna and tropical xerophytic shrubland. Again the reconstructions compare favourably in southeast Asia, both predicting tropical forests. On Australia the reconstructions differ again though this may be more related to different classification schemes; as temperate sclerophyll woodland and shrubland is not represented in the scheme used by François *et al.* (2006). Overall, some of the differences between the reconstruction of François *et al.* (2006) and the one presented here may be related to differences in CO_2, geography and the use of a smaller number of biomes.

The reconstruction of Micheels *et al.*, (2007) is again on a modern land-sea mask, and was based on a 36 site proxy dataset (Micheels, 2003) translated into a classification scheme of 13 biomes. Comparing the reconstruction presented here and that of Micheels *et al.* (2007) there are similarities in the poleward shift of boreal forests. However in Micheels *et al.*, (2007), the boreal forest consistently changed into cool conifer forests; in the reconstruction here this is only observed in Alaska (Fig. 4.3, 4.4). Continuing into the temperate realms, the two reconstructions differ significantly in North America. In the west, palaeobotanical data indicate warm-temperate mixed forests at a slightly higher latitude than reconstructed in Micheels *et al.* (2007). At the latitude of the warm mixed forest of Micheels *et al.* (2007), palaeobotanical data show the presence of coastal warm-temperate mixed forest but temperate xerophytic shrubland further inland (Fig. 4.3, 4.4); these differences may be related to spatial resolution. In the central USA, palaeobotany provides evidence of temperate savanna mixed with BIOME4-predicted temperate needleleaf forests; in Micheels *et al.* (2007) this region is completely forested. The eastern coast of the USA compares favourably in both reconstructions.

The Iberian Peninsula in this reconstruction shows a higher vegetational diversity than in Micheels *et al.* (2007) (Fig. 4.3, 4.4). Moving east across Europe, both reconstructions are comparable, although the reconstruction presented here has a greater expanse of warm-temperate forest. This forest occupied significantly less area in southeast Asia; this is comparable to the reconstruction of Micheels *et al.* (2007). On the Himalayan Plateau and north of it, the reconstruction herein shows more vegetational variation, this is due to using a larger biome scheme. The reconstruction of Micheels *et al.* (2007) also presented a polar desert on the Tibetan Plateau, which is not recognised here.

The most significant difference between the Tortonian reconstruction herein (Fig. 4.3, 4.4) and the reconstruction of Micheels *et al.* (2007) is in South America and Australia. In South America, the reconstruction of Micheels *et al.* (2007) shows latitudinal bands of tropical rain forest, tropical seasonal forest and warm mixed forest to 23.5°S, whereas palaeobotanical data shows tropical savanna separating areas of tropical forest (Fig. 4.3, 4.4). In temperate South America, the reconstructions differ mainly in the absence of the Atacama Desert in Micheels *et al.* (2007), whereas sedimentological evidence shows that it was present (Alonso *et al.*, 1991; Clarke, 2006). In Australia, Micheels *et al.* (2007) interpreted vegetation in longitudinal bands becoming more humid to the northeast. In the present reconstruction, the palaeobotanical data show a dominance of temperate sclerophyll woodland and shrubland along the south of the continent and the predictions of BIOME4 indicate that the vegetation became moister to the southeast (Fig. 4.3, 4.4).

In Africa, the reconstruction presented in this chapter and that of Micheels *et al.* (2007) are comparable. The vegetation distributions differ mainly in the areas predicted by BIOME4 in the reconstruction presented herein. Micheels *et al.* (2007) reconstructed the Tortonian Sahara as a mixture of warm grassland and savanna. In this reconstruction, BIOME4 predicts most of the Sahara desert to be tropical xerophytic shrubland with isolated areas of desert (Fig. 4.3, 4.4). BIOME4 also predicts a mixture of savanna and xerophytic shrubland in southern Africa (Fig.6); in the reconstruction of Micheels *et al.*, (2007) savanna changed to warm mixed forest towards the Cape. The differences between the new reconstruction and that of Micheels *et al.* (2007) could be related to the use of a Tortonian land-sea mask and a larger palaeobotanical data set in the study presented here.

This study has refined previous Tortonian vegetation reconstructions. Previous work used limited palaeobotanical data which was not cited (François *et al.*, 2006; Micheels *et al.*, 2007). Here we present a 326 point palaeobotanical and vertebrate-based data set for the Tortonian in a format which is readily compatible with a state-of-the-art mechanistic vegetation model. This allows it to be easily used for data-model comparisons, and permits it to be used as a boundary condition in future modelling studies. The methodology used to generate the global vegetation reconstruction also uses a novel approach, previously only applied to the Piacenzian (Salzmann *et al.* 2008). The 326 point palaeobotanical data set has been merged with a “best-fit” Tortonian model generated biome distribution map. This has meant that areas lacking palaeobotanical data have been filled with vegetation that most closely suits the climate that fits best with regions with a large amount of palaeobotanical data. This is instead of inferring biome distribution or filling gaps with modern vegetation. Hence an advanced Tortonian biome distribution map has been constructed, which will be used in future modelling studies.

4.5. Conclusions

The Tortonian vegetation reconstruction presented in this chapter, created using palaeobotanical data and a mechanistic vegetation model forced by HadAM3, suggests that this interval was warmer and wetter than present. The Tortonian vegetation distribution shows significant differences to the modern, such as a spread of boreal forests and temperate biomes to much higher latitudes than today. An expansion of warm-temperate evergreen mixed forests in Europe, southeast Asia and parts of North America; due to higher temperatures. The replacement of most arid desert regions by shrubland, grassland, savanna and woodland biomes, indicating increased rainfall. There was also a considerable expansion of temperate savanna in Central USA, the Middle East and on and north of the Himalayan Plateau, during the Tortonian.

In the following chapter I will continue to explore Tortonian climate through the use of the AGCM HadAM3 and the mechanistic vegetation model BIOME4. The data-model hybrid global vegetation map, presented in this chapter, will form part of this investigation. This will allow the impact of Tortonian vegetation on climate to be investigated.

Chapter 5
The impact of vegetation on modelling the Tortonian climate

A model is a lie that allows you to see the truth – Robert MacArthur

5.1. Introduction

In the previous chapter I presented a data-model hybrid global vegetation reconstruction for the Tortonian. At the end of the chapter I proposed that this could be used as a boundary condition in modelling experiments and this will be the focus of this chapter. Building on the experiments of Lunt et al. (2008) this chapter will use the atmosphere-only model HadAM3 to explore the impacts of Tortonian vegetation on climate. In Lunt et al. (2008) this GCM was used to generate a suite of Tortonian climates from different SST profiles (Table 4.1), which were then used to drive the BIOME4 mechanistic vegetation model. In the previous chapter these HadAM3-BIOME4 experiments were evaluated with palaeobotanical data (Table 4.1) and the most comparable, to the palaeobotanical data, was used to create the global hybrid vegetation reconstruction (Fig. 4.4). In these experiments (Mioc1 – Mioc5) the initial vegetation, used as a model boundary condition, was kept constant as global shrublands (Lunt et al., 2008). Although the evidence presented within chapters 2 and 3 would suggest this was unsatisfactory, the benefit of homogenous shrublands as a boundary condition is that they have the least biasing effect on climate (Lunt et al., 2008). This meant that in the absence of a suitable Tortonian vegetation reconstruction the climates derived were not influenced by the choice of land cover. Now that a suitable Tortonian reconstruction is available it is possible to explore the effects of vegetation on the Tortonian climate.

The influence of vegetation on Miocene palaeoclimate has been the subject of many modelling studies (e.g. Dutton and Barron, 1997; Lohmann et al., 2006; Micheels et al., 2007). Using the coarse resolution (4.5 x 7.5°) AGCM GENESIS, Dutton and Barron (1997) showed that the change from modern to Early Miocene vegetation (Wolfe, 1985) could provide an additional 2°C warming globally. In a Tortonian modelling study using ECHAM4 and an ocean circulation model it was found that although open ocean gateways (e.g. CAS) reduced North Atlantic equator to pole circulation (Lohmann et al., 2006; Steppuhn et al., 2006), the inclusion of a Tortonian vegetation reconstruction (Micheels, 2003) compensates by altering subtropical winds and increasing evaporation (Lohmann et al., 2006). Using the ECHAM4/ML AGCM the climate of the Tortonian was simulated with a palaeovegetation reconstruction on modern geography (Micheels, 2003; Micheels et al., 2007). The simulated climate was 0.6°C warmer and 0.06 mm/day wetter than the pre–industrial (Micheels et al., 2007). This modest warming, at comparable CO_2 levels, is significantly less than the ca. 4.5°C reported by Lunt et al. (2008) for the Mioc5 simulation, which compared most favourably to palaeobotanical data (Chapter 4). Micheels et al. (2011) modelled the Tortonian using the COSMOS AOGCM and found a global increase in temperature of 1.5°C and an increase in precipitation of 0.12 mm/day. This experiment used the same vegetation reconstruction, CO_2 concentrations and orography as Micheels et al. (2007), but changed the geography to a representative Tortonian one (Micheels et al., 2011). This combination of a fully coupled model and the changes in geography has allowed a further 0.9°C warming on the pre-industrial. The experiments also showed a zonal mean meridional temperature gradient with a shape comparable to their modern control experiment, just with a slight increase in temperature at all latitudes (Micheels et al., 2011). The distribution of bioclimatic zones, presented in Chapter 3, showed that the Tortonian had a weaker than modern latitudinal temperature gradient especially in the northern hemisphere. Recently the impact of vegetation on Tortonian climate has been claimed to resolve the long standing "warmer world – low CO_2 paradox" (Knorr et al., 2011). Using the AOGCM ECHAM5 – MPIOM Knorr et al. (2011) found that with a CO_2 concentration of 278 ppmv the strongest forcing agent on the warming was vegetation. The vegetation reconstruction used was from Micheels (2003), which could mean the modelling study was preconceived to achieve this result. The global biome map of Micheels (2003) was generated using a proxy dataset of 36 points and the output from an AGCM driven BIOME3 model. This climate model used a CO_2 concentration of 360 ppmv, producing a global vegetation in equilibrium with a 360 ppmv earth system (Micheels, 2003). The Micheels(2003) global vegetation map then applied to a low CO_2 AOGCM could produce the required forcing of climate to create a warmer world with low CO_2. If the experiment had allowed the vegetation to adjust to the 278 ppmv earth system of their modelling study the forcing of climate may not have been as strong.

From the previous modelling studies of the Tortonian there is a discrepancy between the experiments with global shrublands (Lunt et al., 2008) and those using Tortonian vegetation (Micheels et al., 2011). This discrepancy suggests that the application of a more realistic palaeovegetation to a modelling study actually reduces the difference in global average MAT between the Tortonian and the pre-industrial. However, in other modelling studies it has been shown that the application of a palaeovegetation increases this difference in MAT (e.g.

Dutton and Barron, 1997). As has been discussed in section 4.4.3, previous Tortonian vegetation reconstructions were not entirely compatible with palaeobotanical data. This was due to a combination of small, geographically restricted datasets and extrapolation to fill areas not covered by data. Could the application of the up to date reconstruction presented in Chapter 4, developed using the extensive palaeobotanical database presented in Chapter 3, provide a more realistic Tortonian climate simulation?

5.2. Methods

5.2.1. The Tort experiment series

Using the atmosphere only GCM HadAM3 introduced in the previous chapter, a suite of experiments were designed and run to explore the role of vegetation on the Tortonian climate. This suite of Tortonian experiments builds on the initial Mioc series of simulations (Mioc1 - Mioc5). Within the Mioc series the vegetation boundary condition was set as global shrublands (Lunt et al., 2008). This limited the amount of vegetation – climate feedbacks (as shrubs are the least biasing land surface cover), allowing the impacts of the various SST profiles to be explored (Lunt et al., 2008). The series of model experiments presented in this chapter are referred to as Tort1 – Tort4 (Table 5.1). The experiments are based on the Mioc5 simulation from Lunt et al. (2008) as this proved to be the most comparable to palaeobotanical data (Chapter 4).

Each of the four new Tort experiments uses identical boundary conditions to Mioc5 (Lunt et al., 2008) with the exception of the land surface scheme, which is changed to investigate the impacts of vegetation on climate. The GCM HadAM3 was introduced in Chapter 4 as were the Mioc5 boundary conditions. The new experiment Tort1 is identical to Mioc5, which allows any differences between computer systems to be understood. Mioc5 was simulated at the University of Bristol, whereas Tort1 – Tort4 were run at the University of Leeds. Different computer systems can produce slightly different climates due to system – specific model fixes and differences in computer architecture (S.J. Hunter, 2012 Pers. Comm.). As Tort1 is a replication of Mioc5 it is initiated with global shrublands and will form the control experiment. All the other experiments can then be compared against this control to understand the impacts on climate of changing vegetation. Tort2 changes the initial vegetation, from the global shrublands of Tort1, to global forests (Table 5.1). This will provide an opposing view to global shrublands as forests should have a strong feedback on climate (Notaro et al., 2006). Tort3 introduces the global vegetation hybrid from Chapter 4 into the model. This experiment seeks to explore the impact of realistic vegetation on modelling the Tortonian climate. Tort4 returns to having global shrublands as the model boundary condition but changes the land surface exchange scheme from MOSES 1 (Cox et al., 1999) to MOSES 2 (Essery et al., 2001). The differences between the two land surface exchange schemes will be presented in the following sub-section.

Experiment	Description
Mioc5	Original (Lunt et al., 2008)
Tort1	Replicant of Mioc5 run on University of Leeds computer
Tort2	Tort1 + global forests
Tort3	Tort1 + Tortonian vegetation reconstruction (Chapter 4)
Tort4	Tort1 + MOSES 2

Table 5.1. The details of AGCM experiments Tort1 – Tort4.

5.2.2. MOSES1 and MOSES2

The Met Office Surface Exchange Scheme (MOSES) calculates the surface to atmosphere fluxes of heat and water (Cox et al., 1999). It also updates the surface and subsurface variables, which influence these fluxes (Cox et al., 1999). MOSES 1 uses a land cover classification scheme of 23 different types (although seven of which are anthropogenic and not applicable to palaeoclimates) and three soil textures: fine, medium and course (Cox et al., 1999). Each land cover classification has nine surface parameters: root depth, snow-free albedo, cold deep-snow albedo, surface resistance, roughness length, canopy water capacity, surface infiltration enhancement factor, leaf area index and canopy height. Whilst the three soil textures are defined by relative fractions of clay, silt and sand. Each soil texture then has eight parameters controlling soil temperature and hydrology (Cox et al., 1999). It is this combination of surface and soil parameters that drives a single surface energy balance for each GCM grid cell through sub-grid cell processes such as surface heat flux, surface runoff and transpiration etc. (Cox et al., 1999). MOSES 2 built on MOSES 1 by introducing heterogeneity (Essery et al., 2001). In MOSES 2 this heterogeneity is achieved by allowing each grid cell to be tiled; containing a fraction of the eight land cover types or ice. Each grid cell contains a proportion of each land cover type and so eight different surface energy balances are calculated and contribute towards the overall grid cell level exchanges with the atmosphere (Essery et al., 2001). Several other improvements were made on MOSES 1, including a better representation of snowfall (Essery and Clark, 2003). Overall the modifications made to MOSES 1 to create MOSES 2 have led to more realistic model simulations of modern climate (Essery and Clark, 2003).

5.3. Results

Overall the Tort1 – Tort4 simulations show a globally warmer and wetter world than the pre-industrial (Table 5.2). Globally the MAT is 4.5 – 4.9 °C warmer than the pre-industrial and 0.31 – 0.38 mm/day wetter (Table 5.2). In the following sub-sections each model simulation will be described in terms of its differences with Tort1 to highlight the impact of vegetation on the climate system. Globally Tort1 is slightly cooler (0.07°C) and drier (0.09 mm/day) than Mioc5. The comparison of Tort2 to Tort1 shows the impacts of initialising a GCM experiment with the climatologically opposite of global shrublands: global forests. Comparing Tort3 to Tort1 shows the effects of including a realistic Tortonian vegetation reconstruction on climate. The comparison of Tort4 to Tort1 shows the differences in simulated climate between MOSES2 and MOSES1. Each experiment will then be compared to the quantitative climate data, reconstructed from palaeobotanical sources (Chapter 3), in an attempt to show any improvements towards the modelling of the Tortonian climate.

Measurement	Unit	Pre-industrial	Mioc5	Tort1	Tort2	Tort3	Tort4
Global Mean	MAT (°C)	13.77	18.21	18.14	18.32	18.26	18.63
	MAP (mm/day)	2.88	3.23	3.19	3.26	3.24	3.19
Land only mean	MAT (°C)	7.18	11.88	11.54	12.16	11.98	13.21
	MAP (mm/day)	2.26	2.57	2.42	2.77	2.62	2.17
Difference with pre-industrial global mean	ΔMAT (°C)	-	4.44	4.37	4.55	4.49	4.86
	ΔMAP (mm/day)	-	0.35	0.31	0.38	0.36	0.31
Difference with pre-industrial land only mean	ΔMAT (°C)	-	4.7	4.36	4.98	4.8	6.03
	ΔMAP (mm/day)	-	0.31	0.16	0.51	0.36	-0.09
Difference with tdaua global mean	ΔMAT (°C)	-4.37	0.07	-	0.18	0.12	0.49
	ΔMAP (mm/day)	-0.31	0.04	-	0.07	0.05	0
Difference with tdaua land only mean	ΔMAT (°C)	-4.36	0.34	-	0.62	0.44	1.67
	ΔMAP (mm/day)	-0.16	0.15	-	0.35	0.2	-0.25

Table 5.2. The climate details (MAT and MAP) of the experiments Tort1 – Tort4. Differences with pre-industrial are based on the same experiment presented in table 4.1.

5.3.1. Tort2 – global forests

Compared to Tort1 the application of global forests in Tort 2 provides an atmospheric warming of 0.18°C globally and 0.62°C over the land (Table 5.2). Annually this warming is mostly restricted to the northern hemisphere, particularly in north eastern North America and north eastern Eurasia where the difference with Tort1 is ≥4°C (Fig. 5.1). Across the rest of the northern hemisphere there is a warming of around 3°C at the high latitudes and 1-2°C in the mid-latitudes (Fig. 5.1). In the southern hemisphere there is a warming of 1-2°C in southern Australia and isolated parts of southern Africa and South America (Fig. 5.1). In the tropics there is mostly little or no difference in global annual MAT, except for areas of a 1-3°C cooling in North Africa and northern South America (Fig. 5.1). Seasonally, December-January-February (DJF) shows areas of up to 4°C warming (North America, north of the Paratethys central and east Asia and Australia) and areas of up to 4°C cooling (Alaska, central high latitude Eurasia, northern South America, North Africa, north India and northern south-east Asia) when compared to Tort1 (Fig. 5.2). There is significant warming in the northern hemisphere during March-April-May (MAM) of up to 11°C, particularly in the north eastern areas of the continents (Fig. 5.3). During June-July-August (JJA) Tort2 continues to show a warming on Tort1, especially at the high latitudes (Fig. 5.4). There is also significant cooling of up to 5°C in isolated parts of the tropics during JJA (Fig. 5.4). The strong warming in the north eastern part of the northern hemisphere continents continues into September-October-November (SON) (Fig. 5.5). There is also warming in southern Australia of up to 3°C (Fig. 5.5).

Most changes in precipitation between Tort2 and Tort1 occur within the tropics (Fig. 5.6). MAP increases globally by 0.07 mm/day and terrestrial MAP by 0.35 mm/day (Table 5.2). The strongest increases in MAP occur; west of Central America, northern South America, across north and west Africa, Arabian Peninsula and northern Australia (Fig. 5.6). Significant decreases in MAP are found offshore west India and either side of the Southeast Asian peninsula (Fig. 5.6). Seasonally there are increases of rainfall of up to 8 mm/day in parts of northern South America, equatorial West Africa and northern Australia during DJF (Fig. 5.7). There is a much more uniform increase in precipitation during MAM across most areas of land, typically of 1-2 mm/day (Fig. 5.8). JJA shows significant increases in precipitation of up to 13 mm/day in isolated regions such as; offshore west Central America and northern India/ Pakistan (Fig. 5.9). Decreases in precipitation, of up to 6 mm/day occur across India and Southeast Asia during SON (Fig. 5.10). Whilst there are increases of up to 6 mm/day across Africa and offshore Central America (5.10).

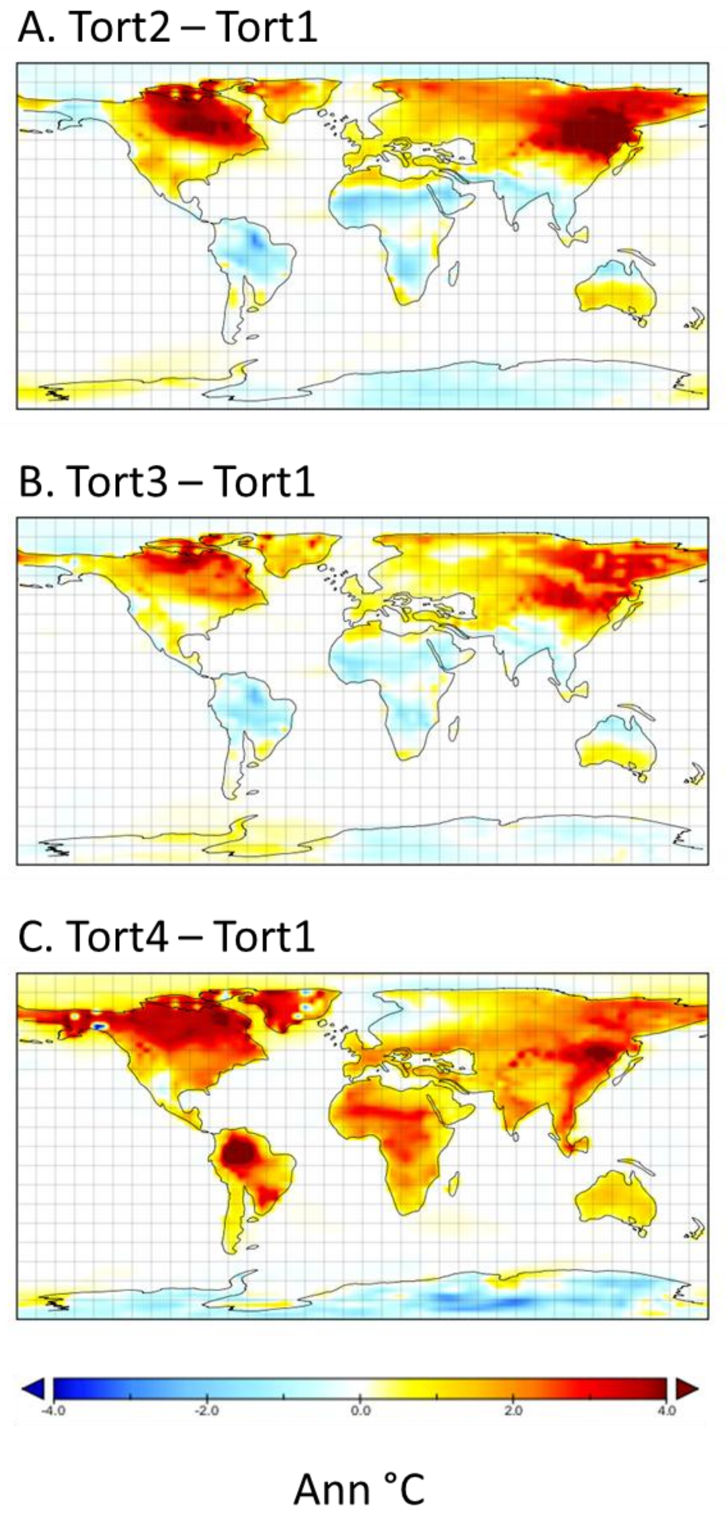


Figure 5.1. Global mean annual surface air temperature anomaly with Tort1.

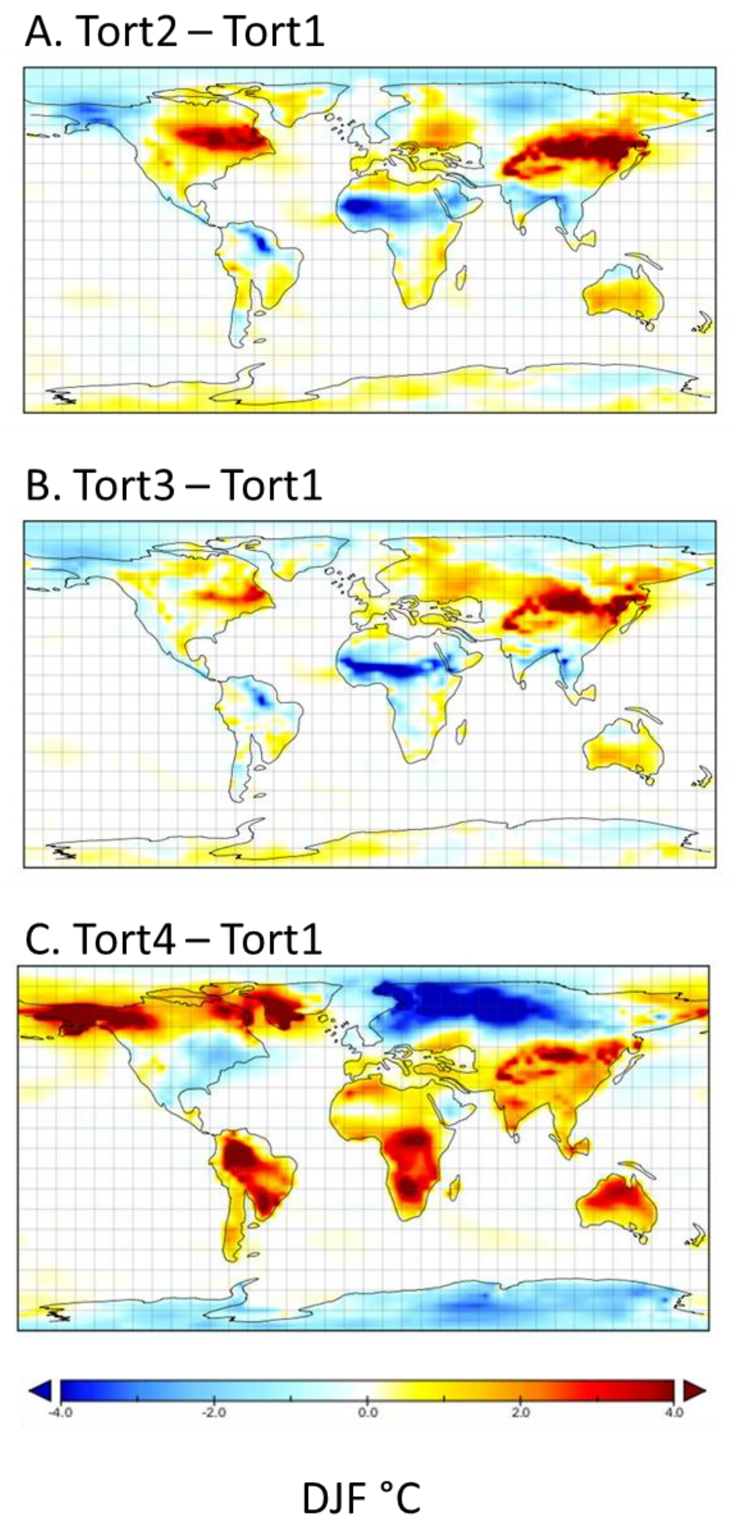
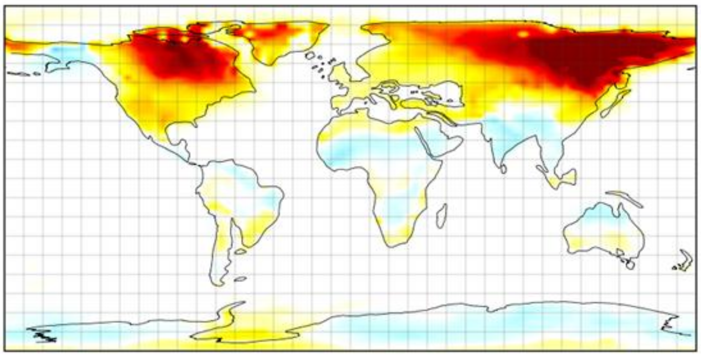
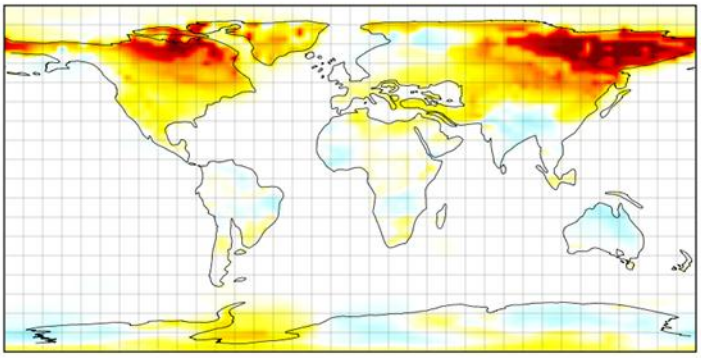


Figure 5.2. Global DJF surface air temperature anomaly with Tort1.

A. Tort2 – Tort1



B. Tort3 – Tort1



C. Tort4 – Tort1

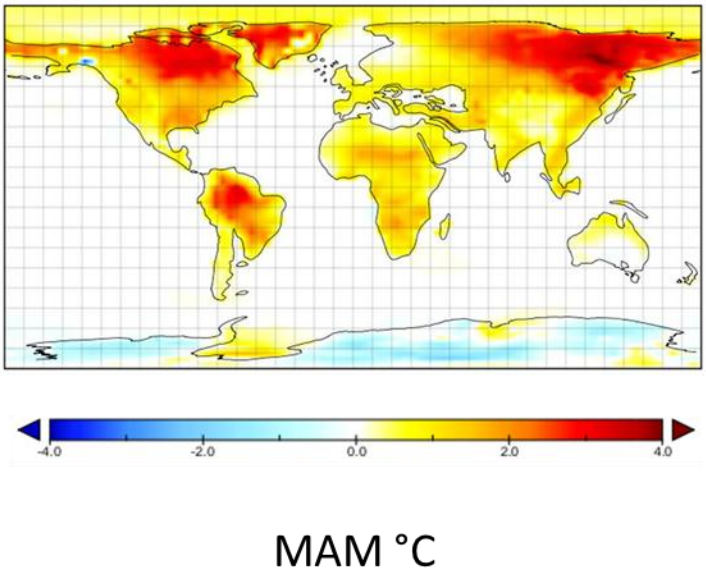
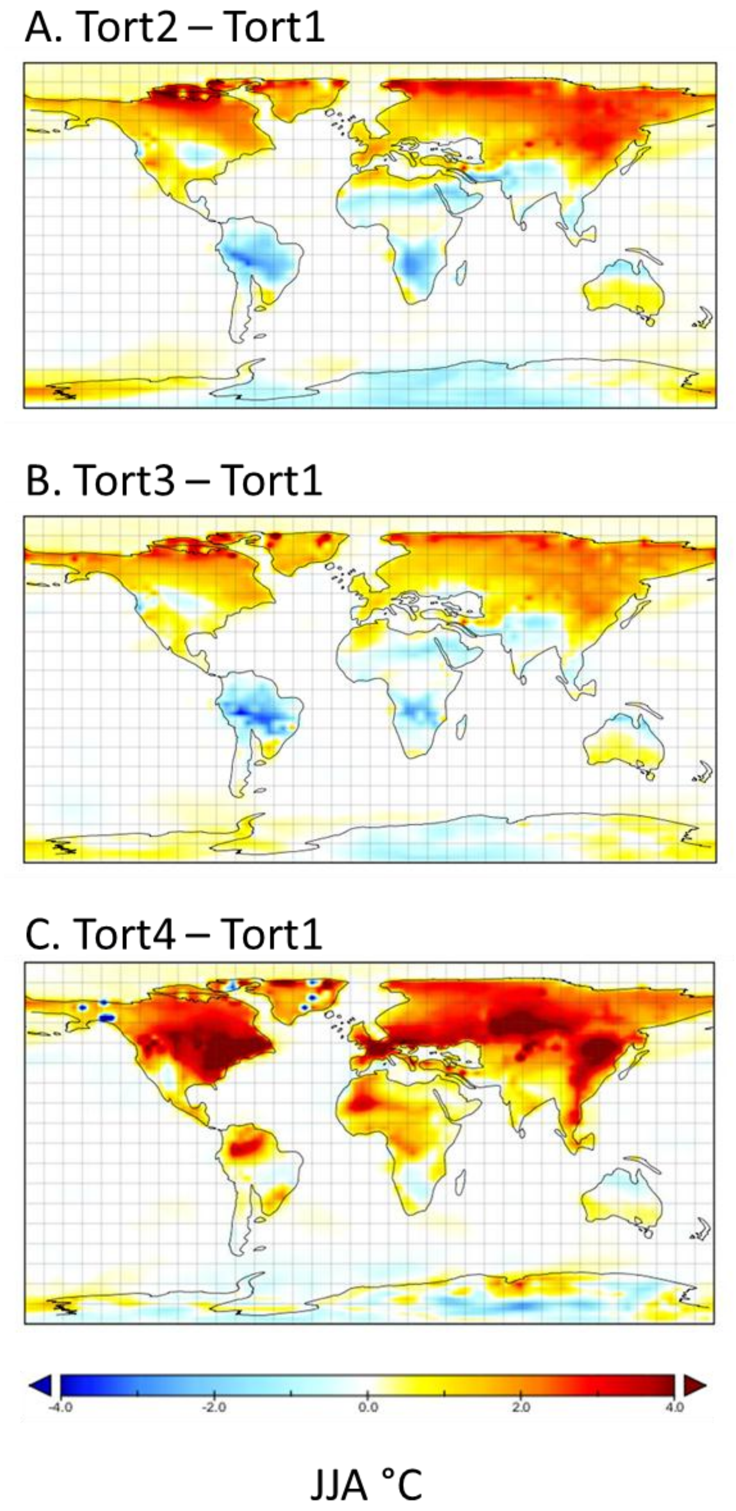


Figure 5.3. Global MAM surface air temperature anomaly with Tort1.



A. Tort2 – Tort1

B. Tort3 – Tort1

C. Tort4 – Tort1

Figure 5.4. Global JJA surface air temperature anomaly with Tort1.

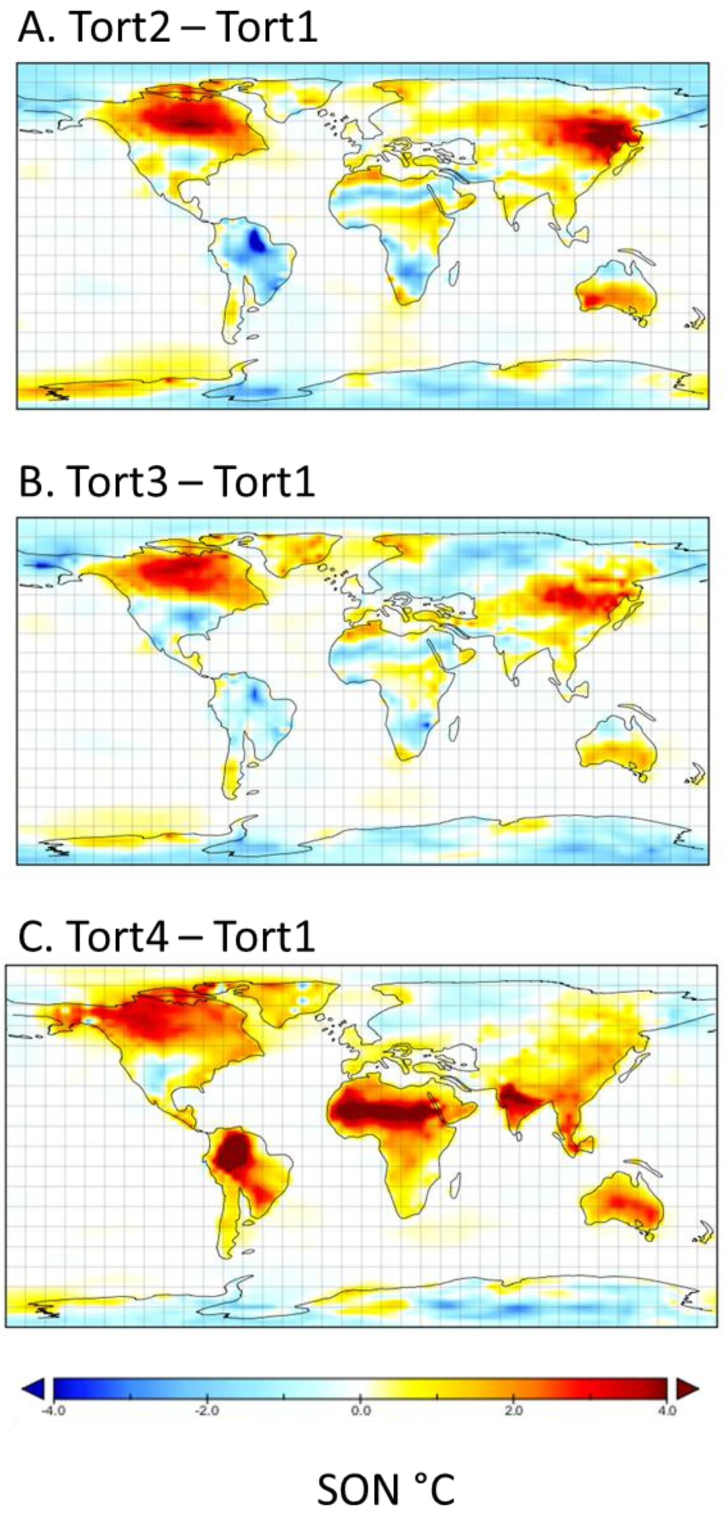


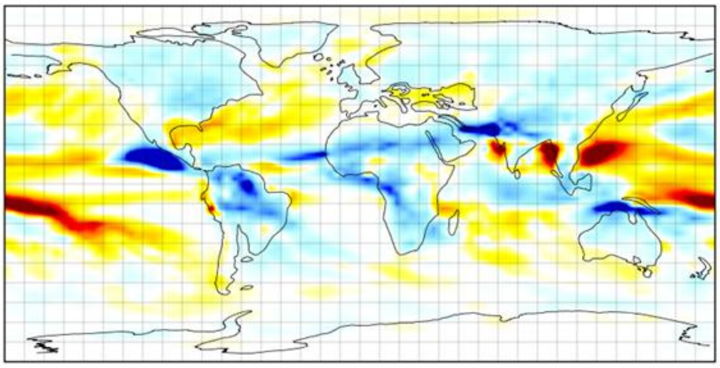
Figure 5.5. Global SON surface air temperature anomaly with Tort1.

5.3.2. Tort3 – Tortonian hybrid vegetation

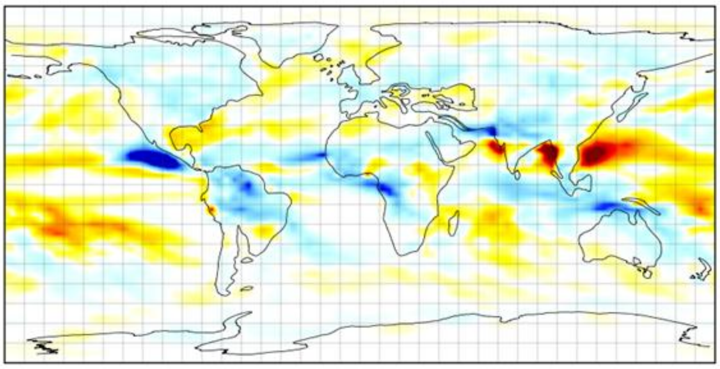
Compared to the global shrublands of Tort1 the application of the Tortonian global vegetation reconstruction (Chapter 4) shows a global increase in MAT of 0.12°C and an increase across the land of 0.44°C (Table 5.2). Geographically, most of this warming occurs in the northern hemisphere especially at the high latitudes, where parts of Arctic North America show an increase in MAT of 4°C (Fig. 5.1). There is also significant warming in north eastern Eurasia and subtle warming across southern Australia (Fig. 5.1). The tropical regions show no change or a slight decrease in MAT, of around 1-2 °C (Fig. 5.1). During DJF the strongest differences in temperature are a strong warming (up to 6.7°C) across central and eastern Eurasia and a warming across north eastern North America (Fig. 5.2). Significant cooling of up to 5°C is found across North Africa and other isolated parts of the tropics (Fig. 5.2). There is a warming in the northern hemisphere of up to 10°C during MAM and up to 9°C during JJA (Fig. 5.3, Fig. 5.4). During JJA there is also significant cooling (up to 6°C) in the tropics (Fig. 5.4). During SON there is a much more mixed warming and cooling pattern, compared to Tort1 (Fig. 5.5). Warming of up to 3°C occurs across northern North America, Greenland and northeast Eurasia, central and eastern Eurasia and southern Australia (Fig. 5.5). Cooling, of up to 3°C, is found in Alaska, mid – latitude North America, central north Eurasia and areas of the tropics (Fig. 5.5).

The application of a more realistic Tortonian vegetation shows an overall increase in MAP of 0.05 mm/day globally and 0.2 mm/day across the land (Table 5.2). Globally there are increases in MAP: offshore west Central America, northern South America, West Africa, northern India and offshore north Australia (Fig. 5.6). Significant decreases in MAP are found offshore of west India and either side of the Southeast Asian peninsula (Fig. 5.6). During DJF increases in precipitation of up to 6 mm/day occur in isolated regions of the tropics (Fig. 5.7). There is very little difference in precipitation during MAM, between Tort3 and Tort1 (Fig. 5.8). During JJA there are large differences in precipitation, with large increases (up to 8 mm/day) offshore west Central America, northern South America and northern India. There are strong decreases in precipitation offshore west India and either side of the Southeast Asian peninsula (Fig. 5.9). These patterns in the differences in precipitation are also seen during SON, but with a larger extent to the area of reduced precipitation in India and Southeast Asia (Fig. 5.10).

A. Tort2 – Tort1



B. Tort3 – Tort1



C. Tort4 – Tort1

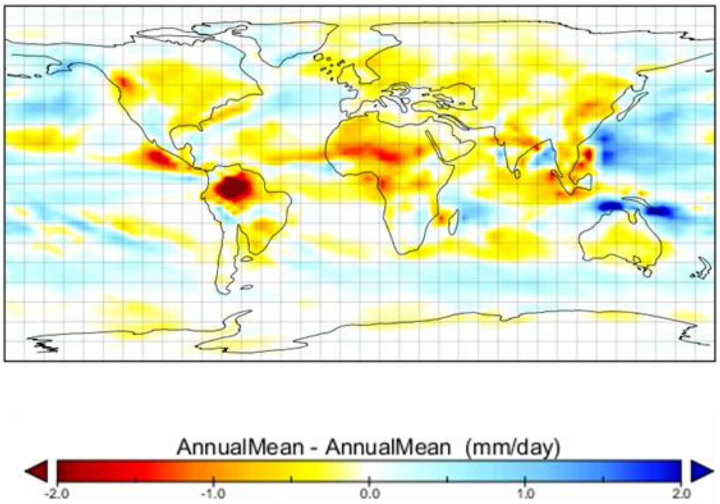
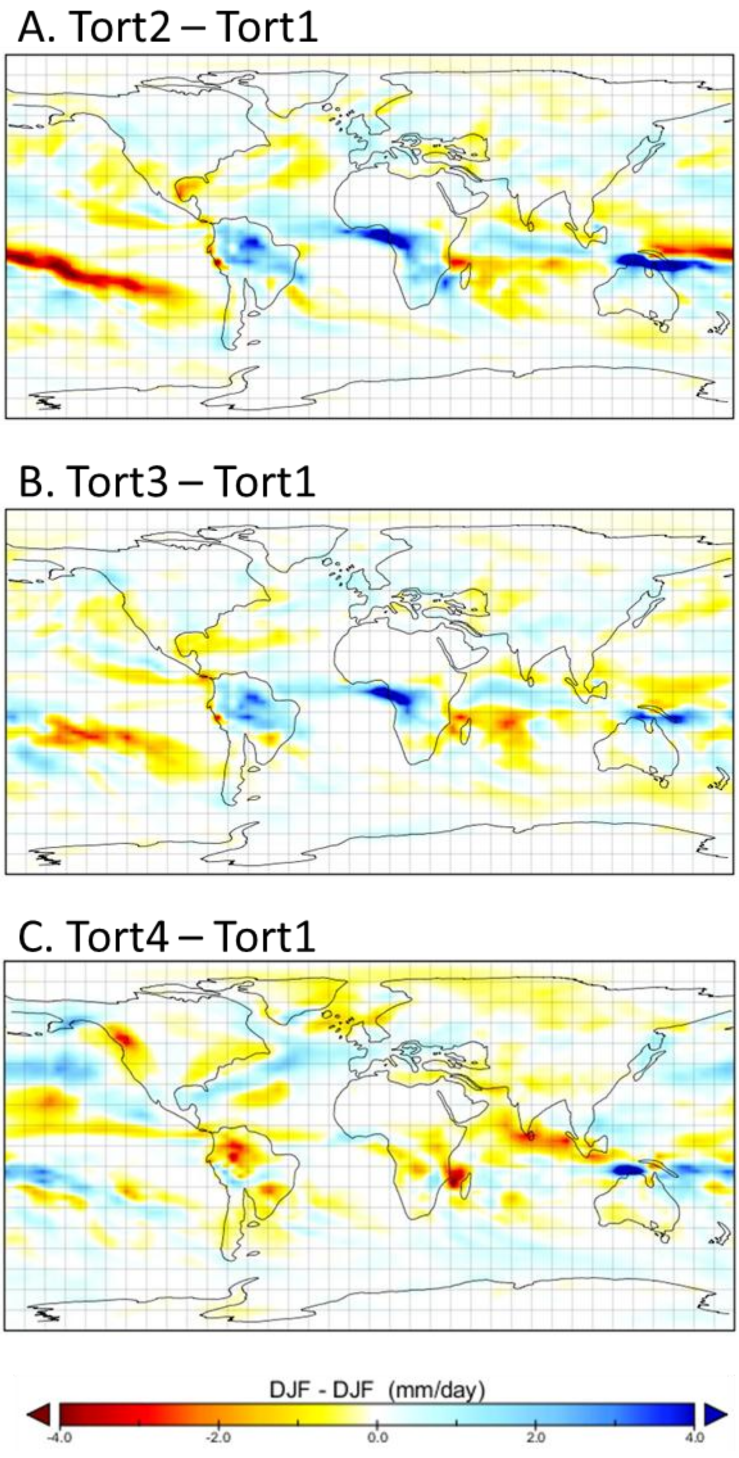


Figure 5.6. Global mean annual precipitation anomaly with Tort1.



A. Tort2 – Tort1

B. Tort3 – Tort1

C. Tort4 – Tort1

Figure 5.7. Global DJF precipitation anomaly with Tort1.

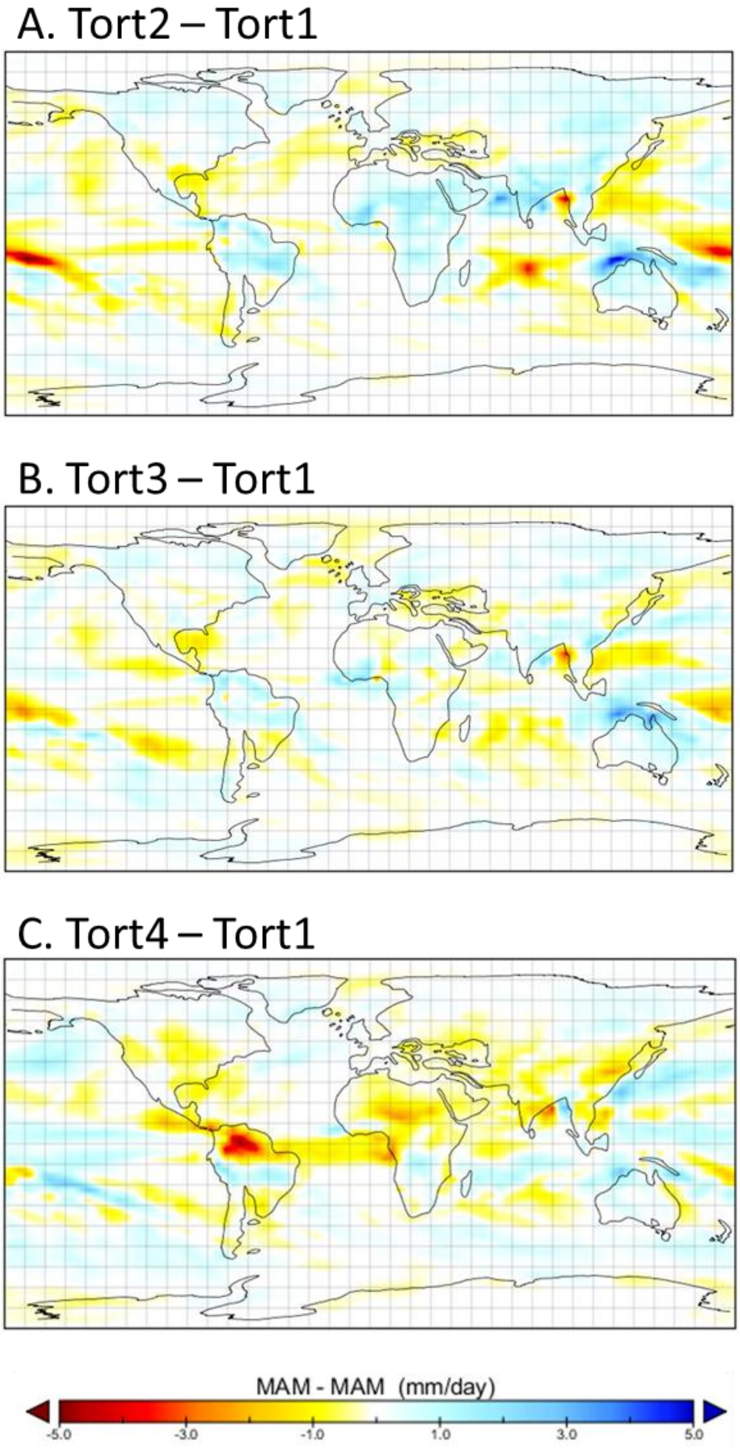
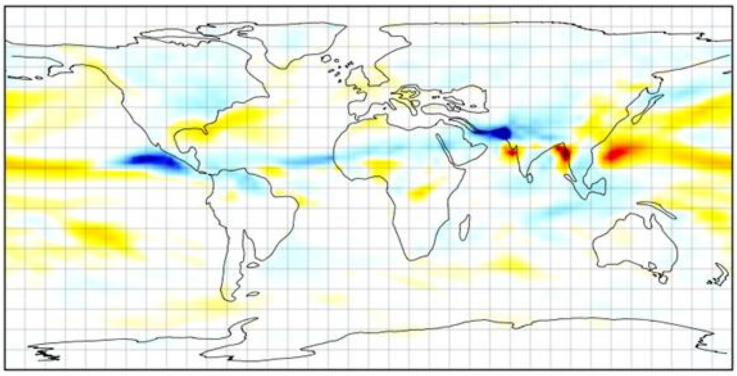
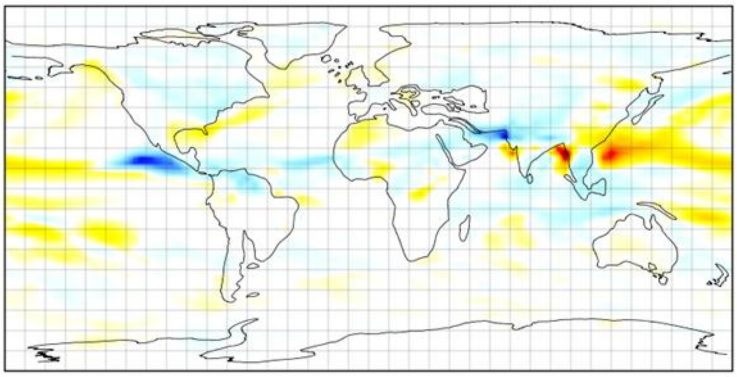


Figure 5.8. Global MAM precipitation anomaly with Tort1.

A. Tort2 – Tort1



B. Tort3 – Tort1



C. Tort4 – Tort1

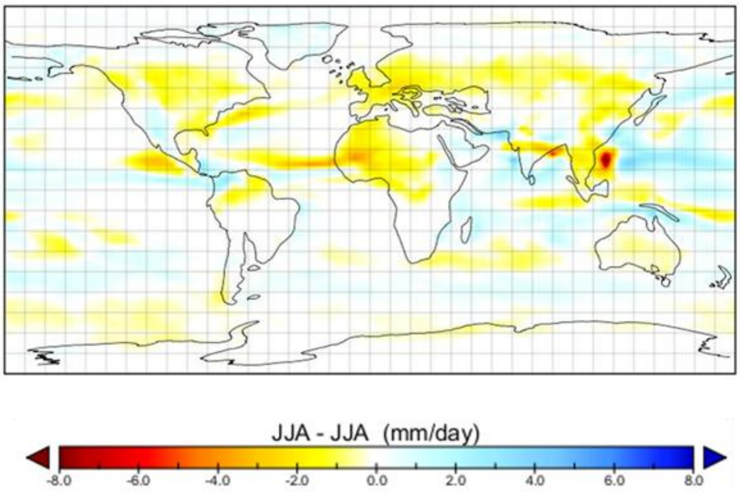
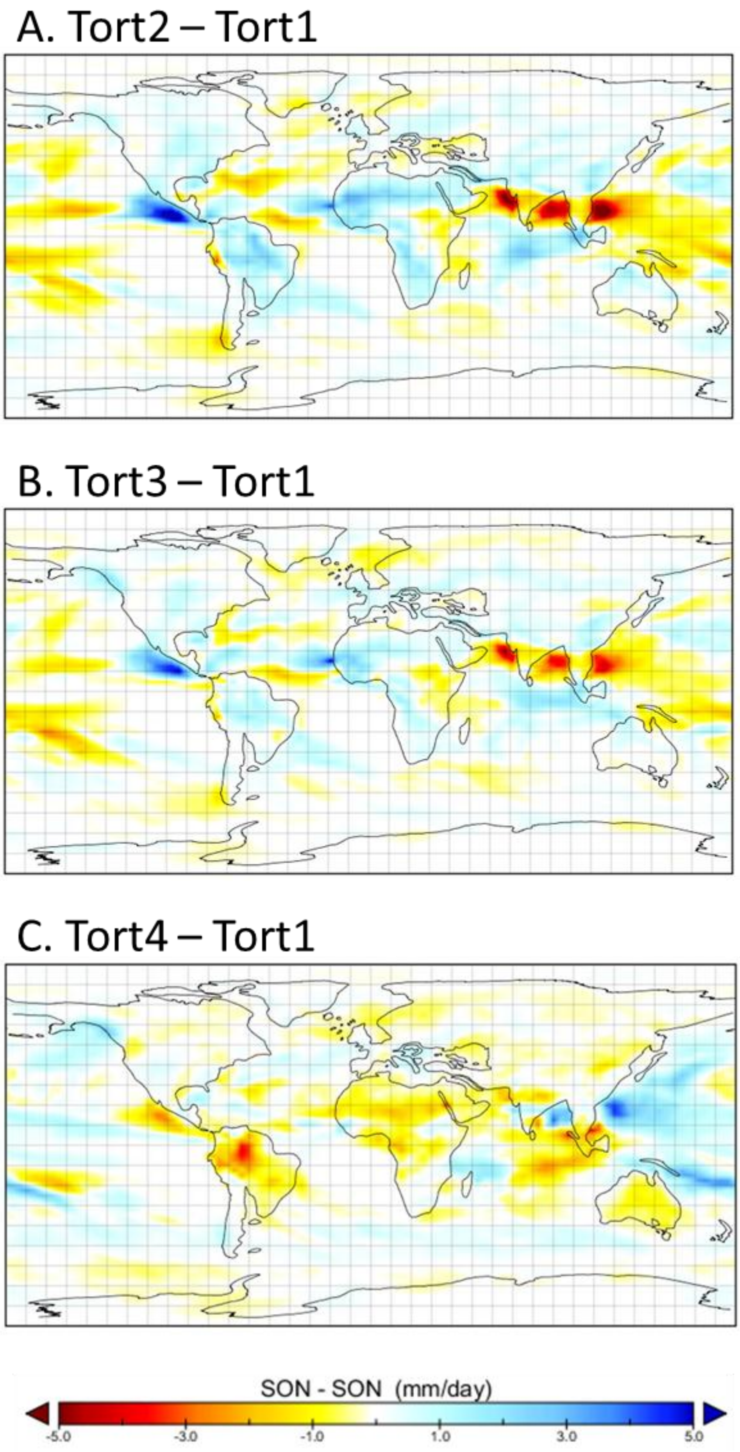


Figure 5.9. Global JJA precipitation anomaly with Tort1.


A. Tort2 – Tort1

B. Tort3 – Tort1

C. Tort4 – Tort1

Figure 5.10. Global SON precipitation anomaly with Tort1.

5.3.3. Tort4 – MOSES2 with global shrublands

Compared to MOSES1, used in Tort1, the implementation of MOSES2 in Tort4 shows a global increase in MAT of 0.49°C and an increase of 1.67°C across the land (Table 5.2). There is warming on all continents of up to 5.8°C, except north western Eurasia and Antarctica (Fig. 5.1). During DJF there is significant cooling, of up to 6°C, on Antarctica and north western

Eurasia (Fig. 5.2). Other areas of the world show considerable warming of up to 10°C (Fig. 5.2). The areas of strongest warming are Alaska, Greenland, northern South America, central and southern Africa, central and eastern Asia and Australia. The difference between Tort4 and Tort1 is large during MAM, with warming of up to 8°C in the high northern latitudes (Fig. 5.3). All continental regions show a warming except Antarctica and Australia (Fig. 5.3). During JJA there is a warming across the northern latitudes, except in regions with prescribed land ice (Fig. 5.4). There is warming of up to 9°C northward of 10°S, particularly in east North America, Europe, east Asia and northern South America (Fig. 5.4). In the southern hemisphere there is little or no change between Tort4 and Tort1 (Fig. 5.4). During SON in Tort4 the northern hemisphere shows a warming of up to 6°C in northern North America and Greenland, but little or no warming in high latitude Eurasia (Fig. 5.5). There is also significant warming in the tropics and the southern hemisphere, when compared to Tort1 (Fig. 5.5). In the southern hemisphere South America and Australia show warming of up to 6°C (Fig. 5.5).

There is no difference in globally averaged MAP, however across the land there is a reduction in precipitation of 0.25 mm/day (Table 5.2). In Tort4 most continental regions show a reduction in MAP of up to 3 mm/day (Fig. 5.6). During DJF there is an increase in precipitation, of up to 7.4 mm/day offshore northern Australia (Fig. 5.7). However, western North America, northern South America and Madagascar show a decrease in rainfall of up to 5 mm/day. There is no significant increase in precipitation across any continental regions during MAM, but considerable decrease in northern South America and North Africa (Fig. 5.8). JJA shows a general reduction in precipitation across the continents of up to 9.6 mm/day (Fig. 5.9). However, there are moderate increases in precipitation across the Arabian Peninsula and the CAS (Fig. 5.9). There is a reduction in precipitation, of up to 9.6 mm/day in North Africa and Southeast Asia (Fig. 5.9). During SON offshore Southeast Asia shows has an increase in precipitation of up to 4.4 mm/day (Fig. 5.10). However, across the continents there is either no increase, or a decrease in rainfall of as much as 3.8 mm/day (Fig. 5.10).

5.3.4. Data – model comparison

Using the data presented in Table 3.4 the experiments Tort1 to Tort4 have been compared to the MAT and MAP estimates from palaeobotanical reconstructions (Table 3.4). To compare temperatures between data and models, the modelled mean annual Surface Air Temperature (SAT) has been used rather than the *surface* temperature (i.e. the *skin* temperature). The SAT is measured at 2m above ground level and should represent the ambient temperature surrounding vegetation. Therefore MAT reconstructions from palaeobotanical data should correspond to this. Comparing the SATs predicted in the Tort series of experiments with the estimates of MAT from palaeobotanical reconstructions, shows that there is a reasonable agreement in MAT for all experiments (Fig. 5.11). The experiment Tort3 shows the highest r^2 value (0.79), whilst Tort2 has the lowest (r^2 = 0.71). Both experiments Tort1 and Tort4 have r^2 values of 0.77 (Fig. 5.11). In all the experiments the palaeobotanical temperature reconstructions compare well to the model predicted SATs in the tropics (Fig. 5.12). There is considerable variability in performance in the mid-latitudes, with examples of sites where either the models are either too warm or too cold (Fig. 5.12). At the high latitudes the SATs simulated by the models are too cold when compared to the reconstructions from palaeobotancial data (Fig. 5.12).

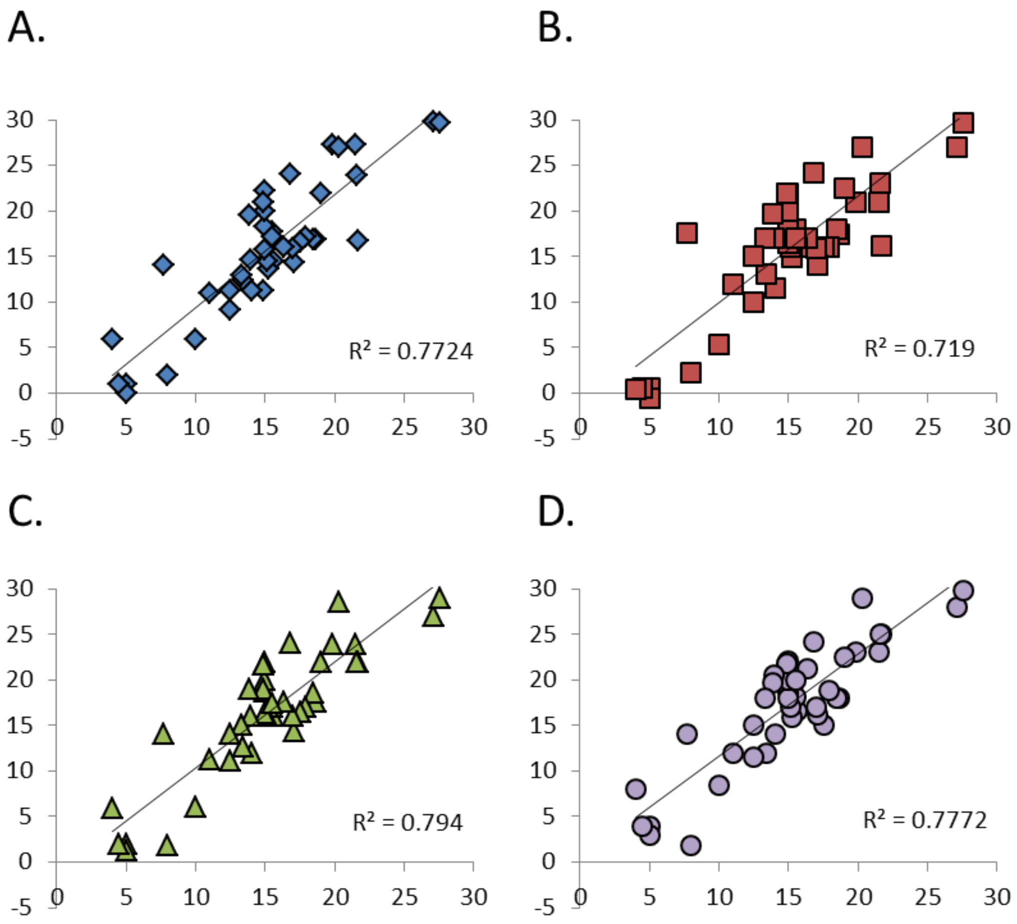


Figure 5.11. Comparison of model predicted mean annual SAT (Y-axes) with reconstructions from palaeobotanical data (X-axes) (Table 3.4). A. Tort1, B. Tort2, C. Tort3, D. Tort4.

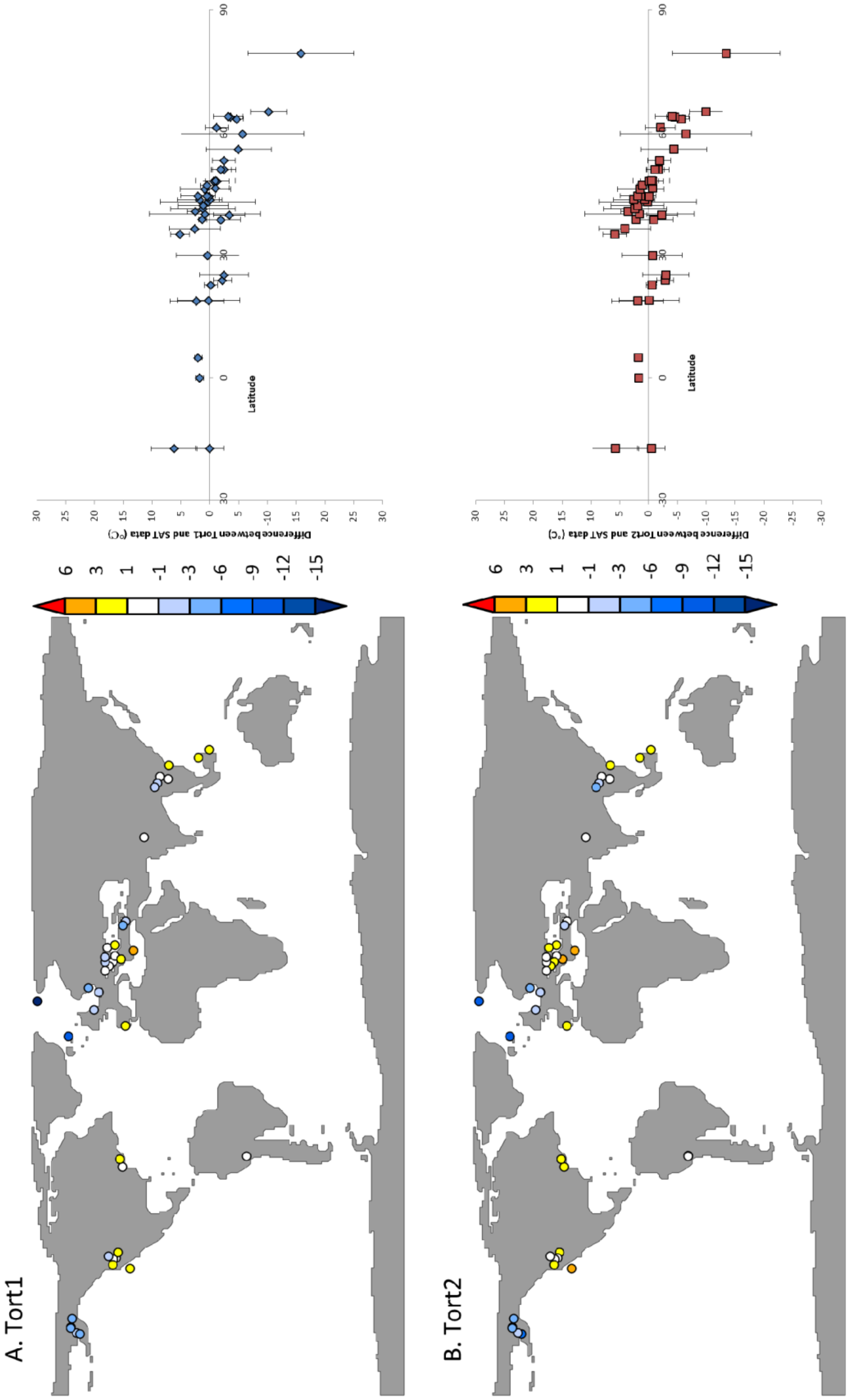


Figure 5.12. The geographical and latitudinal SAT differences between model and data. The circles on the map represent palaeobotanical data points with numerical MAT estimates. These circles are coloured based on the difference between the model and the data, where red shows the model was ≥6°C warmer and dark blue shows the model was ≤15° colder than the data. The graphs show the latitudinal distribution of SAT differences including any errors associated with the palaeobotanical estimates. A. Tort1, B. Tort2, C. Tort3, D. Tort4.

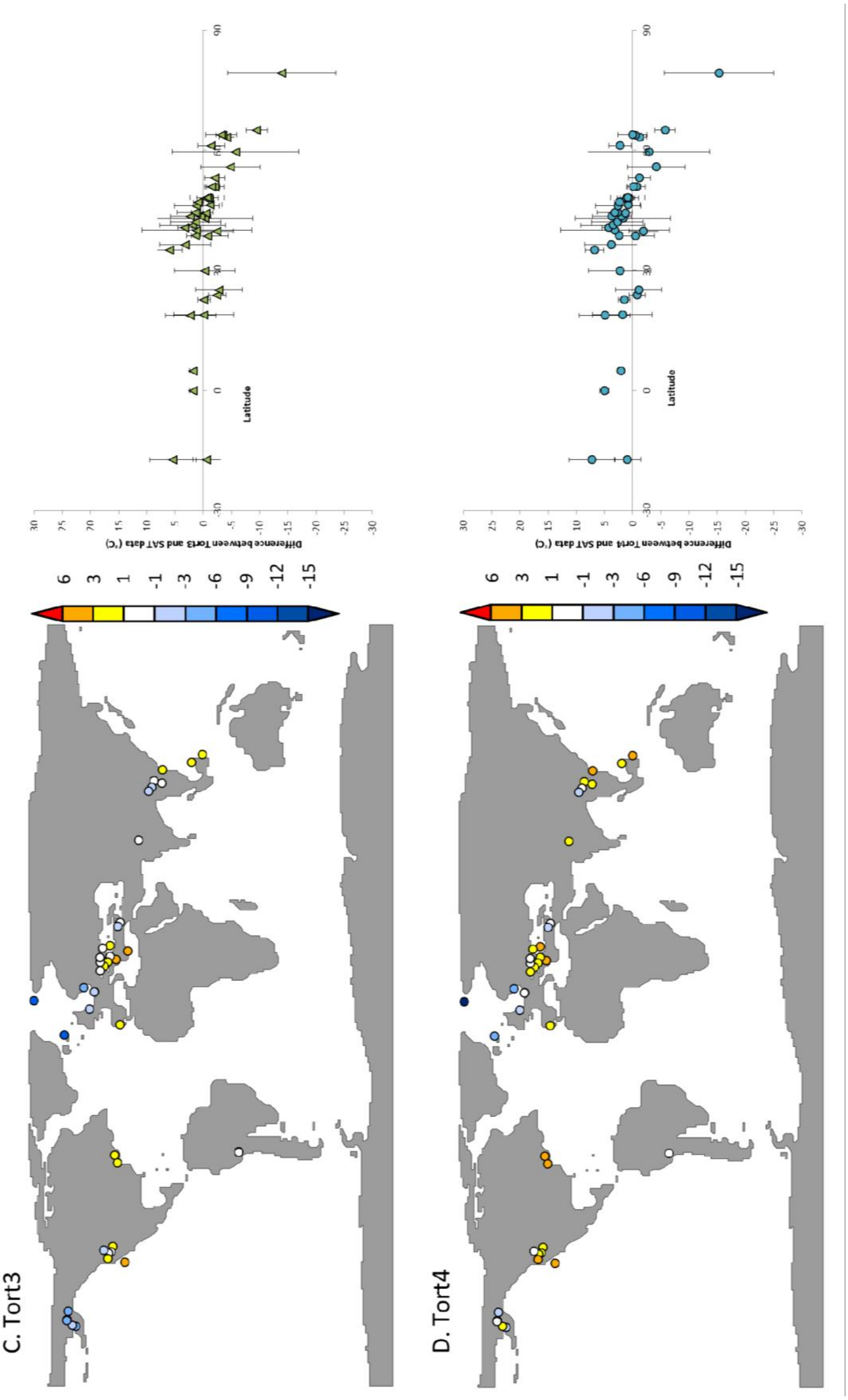


Figure 5.12. cont**.** The geographical and latitudinal SAT differences between model and data. The circles on the map represent palaeobotanical data points with numerical MAT estimates. These circles are coloured based on the difference between the model and the data, where red shows the model was ≥6°C warmer and dark blue shows the model was ≤15° colder than the data. The graphs show the latitudinal distribution of SAT differences including any errors associated with the palaeobotanical estimates. A. Tort1, B. Tort2, C. Tort3, D. Tort4..

There are differences in the SAT data – model comparison between each of the Tort experiments. Comparison of SATs in Tort1 to palaeobotanical data shows that the high latitudes, northwest Europe and south of the Paratethys Sea were simulated as being too cold (Fig. 5.12a). The high latitude sites in the North Atlantic shows that the model generated SATs are 10.0 – 15.8°C too cold, in Alaska the model is 1 - 6°C too cold and in northwest Europe the model is 2 - 6°C too cold(Fig. 5.12a). In the mid – latitudes of North America, the Iberian Peninsula, Greece-Turkey region and Southeast Asia the model generates SATs 1 - 6°C higher than those predicted by palaeobotanical data (Fig. 5.12a). There are sites of good model – data agreement in the mid and low latitudes. When the error margins on the data and the standard deviation of the experiment is taken into account it can be seen that the greatest data – model mismatch is at the high latitudes (Fig. 5.12a). In experiment Tort2 the high latitudes again show the largest data model mismatch, but it is not as great as in Tort1 (Fig. 5.12b). In the North Atlantic the model generated SATs are 10.0 – 13.5°C colder than reconstructed from the palaeobotanical vegetation (Fig. 5.12b). Taking into account the error margins on the data reconstructions does not make these SATs comparable (Fig. 5.12b). In Alaska there is greater disparity between the SATs modelled in Tort2 and those reconstructed from data than there was in Tort1 (Fig. 5.12b). In Europe the pattern in temperature difference is similar between Tort1 and Tort2, with the exception of southeast Europe where Tort2 is slightly warmer (Fig. 5.12b). This greater warmth in southeast Europe brings some areas closer to the data reconstructed MATs, but makes others too warm (Fig. 5.12b). Southeast Asia also shows little improvement when compared to Tort1 (Fig. 5.12). Tort3 shows a comparable pattern of data – model temperature differences to Tort2 (Fig. 5.12c). Comparing the SATs from Tort4 to the MATs reconstructed from palaeobotanical data, shows that most sites in the low and mid – latitudes were simulated as too warm (Fig. 5.12d). This over-warming of the low and mid - latitudes ranges from: 0.7 – 3.8°C in North America, 0.6 – 6.7°C in Europe and up to 6°C in Southeast Asia (Fig. 5.12d). The higher latitudes are still too cold in Tort4 but the degree of miss-match is highly variable. In Alaska two data sites are colder than the SATs predicted by Tort4 by up to 2.2°C and three palaeobotanical sites are warmer than model derived SATs by as much as 2.9°C (Fig. 5.12d). However, when the error on the data reconstructions is taken into account Tort4 performs well in the Alaska region (Fig. 5.12d). In the North Atlantic the model generated SATs are too cold to compare favourably to the data, even when the errors are taken into account (5.12d). The model SATs are too cold in Northwest Europe as well, but when the range of possible MATs reconstructed by palaeobotanical data is taken into account the temperatures are comparable (Fig. 5.12d). Figure 5.13 shows that for experiments Tort2 and Tort3 57% of data model comparisons show between 0 and ±2°C difference. This drops to 54% for Tort1 and 47% for Tort4 (Fig. 5.13). Looking at the extreme differences (greater than ±4°C) between data and model generated SATs Tort2 has the highest proportion of large data model differences: 23% (Fig. 5.13). Tort4 has 19% of data-model comparisons greater than ±4°C, Tort1 and Tort3 both have 16% of the model predicted SATs showing a large difference with MATs reconstructed from palaeobotanical data (Fig. 5.13).

Comparison between model-predicted MAP and those reconstructed from palaeobotanical data shows considerably less agreement (Fig. 5.14). Experiment Tort3 shows the highest r^2 value however, this is only 0.08 and not significant. The other experiments have r^2 values of ≤0.07 showing very little comparability between model-predicted MAP and the estimates from palaeobotanical data (Fig. 5.14). All the Tort experiments are too dry, when compared to the reconstructed MAP from palaeobotanical data. There are exceptions to this where exceptionally wet regions of the simulated world do not compare to drier proxy reconstructions (Fig. 5.14).

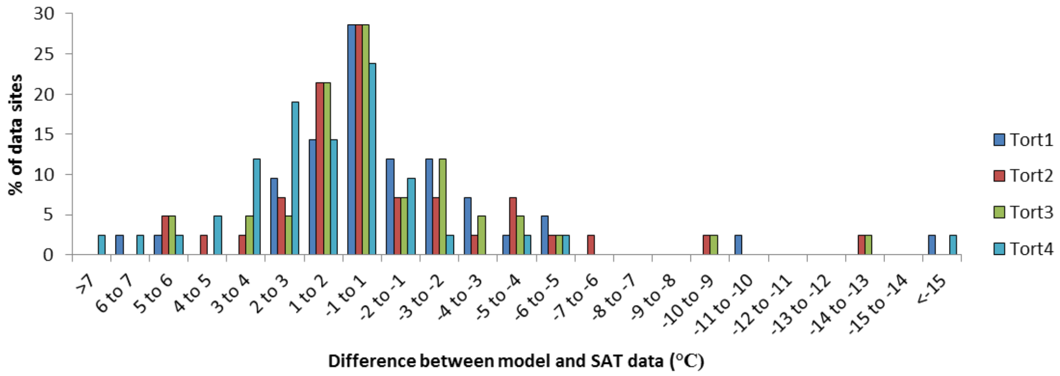


Figure 5.13. The percentage of data sites grouped into difference with model temperature increments.

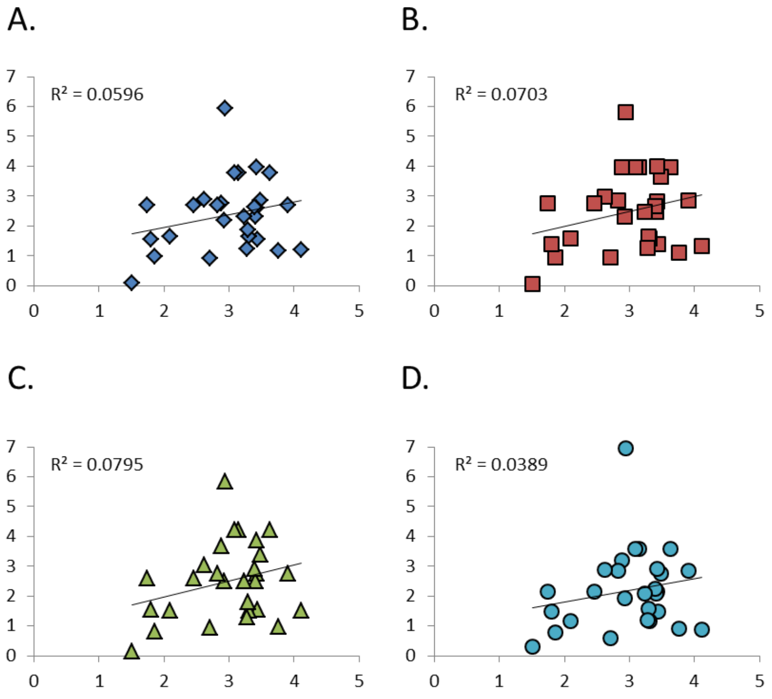


Figure 5.14. Comparison of model predicted MAP (Y-axes) with reconstructions from palaeobotanical data (X-axes) (Table 3.4). A. Tort1, B. Tort2, C. Tort3, D. Tort4.

5.4. Discussion

5.4.1. The impacts of changing the land surface boundary conditions on Tortonian climate

The GCM experiments presented in this chapter show that changing the initial global vegetation and using a different land surface scheme warms the global Tortonian climate by 0.18 - 0.49°C and warms SAT over the land by 0.44-1.67°C (Table 5.2). The greatest change in global and land-only MAT is achieved by applying the MOSES2 land surface scheme, whilst keeping the initial vegetation as global shrublands (Tort4) (note that the Tortonian hybrid vegetation was not incorporated into MOSES2). Experiment Tort2, which used MOSES1 and global forests had the second greatest warming (Table 5.2). Finally the experiment using the hybrid global vegetation reconstruction presented in Chapter 4 (Tort3) had the smallest increase in MAT when compared to Tort1. However, despite having the smallest increase in MAT on Tort1, Tort3 compares best to the reconstructed MATs presented in Chapter 3 (Fig. 5.11). Experiment Tort4 also shows an improvement in the fit to proxy reconstructions, whilst Tort2 compares less well to the palaeobotanical based MAT reconstructions than Tort1 (Fig. 5.11). Compared to Mioc5 all but experiment Tort2 compare more favourably to proxy based MAT reconstructions (Fig. 5.11; Table 4.1).

The strong warming in Tort4, when compared to Tort1, will be due to the improved snow albedo, snow hydrology and snow interaction with vegetation canopy parameters in MOSES2

(Essery and Clark, 2003). The global warming has allowed MATs at the high latitudes to get closer to those reconstructed from palaeobotanical data (though many are still too cold), but has also warmed the tropical and warm-temperate zones above the temperatures suggested from palaeobotanical data (Fig. 5.12). However, this warming is not present globally in every season. During the northern hemisphere winter (DJF) there is a strong cooling signal in high latitude Eurasia, which is likely the result of albedo from the improved snowfall scheme in MOSES2 (Essery and Clark, 2003). Both Tort2 and Tort3 show annual MAT increases at the high latitudes compared to Tort1 (Fig. 5.1). As Tort1, Tort2 and Tort3 all used MOSES1, this warming in Tort2 and Tort3 is related to the presence of trees decreasing surface albedo (Notaro et al., 2006). This signal is especially pronounced in Tort3, where high latitude zones of temperate grassland are clearly visible as areas with smaller MAT differences compared to Tort1, highlighting the strong warming of high latitude forests (Figs. 4.4, 5.1). In general, the patterns in the MAT difference with Tort1 are comparable between Tort2 and Tort3 (Fig. 5.1). This is related to the change from homogenous shrub PFTs, used in Tort1, to having trees globally in Tort2 and realistically distributed in Tort3. These results, as well as the improvement in the data-model comparison between the palaeobotanical data in Chapter 3 and the climate of Tort3 shows the importance of vegetation boundary conditions in promoting high latitude temperature increases whilst having little impact on tropical climates (Fig. 5.1). Overall, the initialisation of a Tortonian AGCM experiment with a realistic vegetation generates a climate most comparable to estimates reconstructed from palaeobotanical data. This shows that the model is interpreting the forcings from a realistic vegetation in a beneficial way. Therefore if the Tortonian hybrid was incorporated into MOSES2 then the data-model fit would be expected to improve. However, it should be noted that in an AGCM the primary control on temperature is the SSTs prescribed to the model. This means that any further improvement in the data – model comparison is likely to come from a better understanding of Tortonian SST distributions (Wood et al., 2012).

In the Tort series of experiments there is little similarity between the GCM generated MAP and those reconstructed from palaeobotanical data (Fig. 5.14). The most comparable experiment is Tort3 (MOSES1; Hybrid vegetation) and the least comparable is Tort4 (MOSES2; global shrublands). This shows the benefit of implementing a Tortonian modelling study with an accurate vegetation boundary condition. Interestingly the large MAT increase in Tort4 co-occurs with no change in global MAP (Table 5.2). This may relate to both Tort1 and Tort4 being initialised with global shrublands, whereas the experiments Tort2 and Tort3 contained more forested regions and experienced an increase in global MAP (Table 5.2). This could be the converse result from previous studies that showed the replacement of forests by more open vegetation types reduces precipitation (Notaro and Liu, 2008; Shukla et al., 1990). When comparing model generated precipitation to proxy reconstructed values we should be mindful that it is a well reported problem that GCMs struggle to reproduce precipitation quantities recorded in the fossil record (Haywood et al., 2009). This however, could stem from multiple problems including model boundary conditions such as soils, lakes and orography.

5.4.2. Comparison to other Tortonian modelling studies

In the introduction to this chapter it was suggested that the inclusion of Tortonian vegetation as a boundary condition into GCM experiments actually led to a smaller increase in MAT compared to pre-industrial. This was based on published Tortonian AOGCM modelling studies such as Micheels et al. (2011) where the inclusion of a Tortonian vegetation reconstruction (from Micheels, 2003) led to a 1.50°C warming compared to their pre-industrial simulation. Using the same global vegetation but an AGCM, Micheels et al. (2007) created a Tortonian climate 0.6°C warmer than their pre-industrial control experiment. Whereas, the Mioc5 simulation with global shrublands, rather than Tortonian vegetation, had a +4.44°C MAT difference with pre-industrial (Lunt et al., 2008). These differences may be related to prescribed CO_2 differences, the Micheels et al. (2011) study used 360 ppmv, whilst the Mioc5 experiment had CO_2 set to 395 ppmv (Lunt et al., 2008). In a separate study Micheels et al. (2009a) simulated Tortonian climate at different atmospheric concentrations of CO_2 using boundary conditions similar to Micheels et al. (2011). Using an Earth Simulator of Intermediate Complexity (EMIC) Micheels et al. (2009a) performed CO_2 sensitivity studies using atmospheric concentrations of 360 and 460 ppmv; these yielded MAT increases on pre-industrial of 3.00 and 3.70°C respectively. These MAT increases on pre-industrial are greater than Micheels et al. (2011) but still lower than reported for Mioc5 (Lunt et al., 2008). A recent modelling study using an AOGCM and a dynamic vegetation model simulated a climate with a MAT 2.88°C warmer than the pre-industrial (Bradshaw et al., 2012). This model was also initiated with global shrublands like the Mioc5 simulation (Lunt et al., 2007). This experiment with an AOGCM used an atmospheric CO_2 concentration of 400 ppmv (Bradshaw et al., 2012), which shows that using global shrublands does not always produce MATs significantly greater than when using a Tortonian global vegetation (e.g. Micheels et al., 2009a). Within this chapter the three experiments Tort2 – Tort4 all produced climates substantially warmer than the pre-industrial (Table 5.2). These experiments were run with global forests, global shrublands and the hybrid global vegetation presented in Chapter 4. Of the three experiments designed to test the impact of vegetation on climate, the experiment with the realistic Tortonian global vegetation (Tort3) produced the lowest MAT difference with pre-industrial (Table 5.2). Tort3 however compared most favourably to MAT and MAP values reconstructed from palaeobotanical data (Chapter 3). Interestingly, changing the land surface scheme from MOSES1 to MOSES2 can have a large impact on global temperatures comparable to changing the actual prescribed vegetation cover. However, as has been previously stated, the main driving force on MAT in an AGCM is the prescribed SSTs. It could be that these prescribed SSTs are artificially generating the higher MAT differences with the pre-industrial. Further to this all of the previously mentioned modelling experiments use different models; COSMOS (Micheels et al., 2011), ECHAM4 (Micheels et al., 2007), HadAM3 (Lunt et al., 2007; this study), HadCM3L (Bradshaw et al., 2012) and Planet Simulator (Micheels et al., 2009a). To properly understand these differences in simulated Tortonian climate, especially those using realistic Tortonian vegetation, a proper model intercomparison project would be required where the models are initialised with comparable boundary conditions (Haywood et al., 2010).

5.5. Conclusions

From the data model comparison it is clear that the inclusion of realistic Tortonian vegetation into an atmosphere-only GCM provides a more robust fit to the palaeobotanical MAT reconstructions. This chapter has also shown that a considerable warming on pre-industrial can be achieved through using a different land surface scheme with global shrublands, but this may be detrimental to global precipitation. It can also be concluded that using global shrublands provides a reasonable fit to proxy data when global vegetation is unknown. However, when a suitable global vegetation reconstruction is available this should be included in future modelling studies.

Further experiments should repeat Tort3 with MOSES2 rather than MOSES1 to see what affects the more up-to-date land surface scheme would have on the data-model comparison. A more comprehensive data model comparison could be achieved by using the biomes presented in Chapter 3 and using the climates of the Tort series to produce biome maps using BIOME4. This would provide a more meaningful comparison as it inadvertently takes into account multiple climate parameters such as the degree of seasonality. The importance of this can be best explained by considering two hypothetical areas of the Earth, both of which have an MAT of 10°C. However, area one is highly seasonal and fluctuates from -15°C in the winter to 25°C in the summer. Whereas area two has limited seasonal fluctuation in temperature and only changes from a low of 8°C in the winter to a summer temperature of 12°C. These two areas would have totally distinct vegetation types but this wouldn’t be apparent in the MAT. By comparing the biomes presented in Chapter 3 to BIOME4 output a more thorough data – model comparison could be achieved.

Chapter 6
The global biogeography and biome specialisation of Late Miocene mammals

Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare? – Charles Darwin, 1859

6.1. Introduction

In the previous four chapters I have shown Middle to Late Miocene global vegetation and climate from palaeobotanical data (Chapters 2 and 3), data – model hybridisation (Chapter 4) and climate modelling (Chapter 5). This has provided an unequalled view of global vegetation, which can now be used to explore the ecology and biogeography of Late Miocene mammals (this Chapter). In particular this chapter will focus on the biome preferences of mammals during the Late Miocene. Most modern mammals are restricted to one or two biomes (Cantalapiedra et al., 2011; Hernández Fernández & Vrba, 2005; Moreno Bofarull et al., 2008). If this was also true of mammals during the Late Miocene then understanding their palaeoecology in terms of biome preferences, will enable mammal faunas to be used to reconstruct vegetation biomes (Chapter 7). This would allow mammal faunas to be used to improve the geographic spread of biomes, providing more complete data maps (Fig. 3.5) and improved data-model hybrid maps (Fig. 4.4). The ultimate aim over the next two chapters is to expand our knowledge of Late Miocene global vegetation using mammals. The current chapter will explore whether the geographic distribution of Late Miocene mammal taxa is related to the distribution of biomes.

Today the distribution of life is not uniform, but varies in a non-random and often predictable manner (Lomolino et al., 2006). The present day distribution and diversity of mammals is the result of ambient environmental conditions and the evolutionary and geographical history of each taxon (Bush, 1994; Lomolino et al., 2006; Moreno Bofarull et al., 2008). It has long been established that many abiotic and biotic factors form ecological gradients within the environment; these are n-dimensional ecological spaces where the axes are resources or environmental variables (Hutchinson, 1957; Futuyma & Moreno, 1988). Every species can survive within an envelope of environmental conditions. Some species have narrow envelopes (stenotopic), whilst others are more tolerant (eurytopic). These ranges of environmental conditions are bordered by areas of physiological stress, where a species survival is more difficult (Lehman & Fleagle, 2006). Where n-dimensional ecological spaces are defined for many species within a habitat they are defined as niches (Hutchinson, 1957). For example, two hypothetical nut eating rodents live in the same forest. The first rodent has powerful jaws but lacks the ability to climb, whilst the second rodent can climb but has weak jaws. Plotting canopy height against thickness of nut shells consumed would show these two rodents occupy different envelopes within n-dimensional space: The two rodents occupy different niches in this hypothetical forest. This type of resource partitioning has been observed in modern mammals and allows animals to have different life strategies to avoid competition (Dueser and Shugart Jr., 1978). Reconstructing a fossil mammals ecological niche is complex and often relies on a proxy such as range size (DeSantis et al., 2012). Reconstructing fossil niches is further complicated by the observation that one modern taxon can occupy multiple niches (Foley et al., 2010; Kerosky et al., 2008). Using Late Miocene mammal niches to facilitate the reconstruction of vegetation would be complex, potentially very fine scale (reconstructing habitats rather than biomes) and require multiple steps of interpretation.

Macroevolutionary habitat theory (Vrba, 1992; 1995; 1999) states that the main promoters of speciation and extinction are physical and environmental changes. Part of this theory is the resource use hypothesis, which stresses the degree of specialization to within biome specific resources (Vrba, 1980; 1987). Biome resources include moisture, temperature, substrate, vegetation cover, food items and any other environmental components that can be utilized by an organism (Vrba, 1987; Moreno Bofarull et al., 2008). The resource use hypothesis allows the identification of stenobiomic (inhabits a particular biome) and eurybiomic (inhabits multiple biomes) species (Hernández Fernández and Vrba, 2005; Moreno Bofarull et al., 2008). It is thought that stenobiomic species, being specialist and more susceptible to removal of a resource, have a higher speciation and extinction rate than eurybiomic species (Hernández Fernández and Vrba, 2005; Moreno Bofarull et al., 2008). From this Hernández Fernández and Vrba (2005) made four predictions based on the resource use hypothesis: (1) specialists should be more numerous than generalists, i.e. there should be a higher degree of stenobiomic species than eurybiomic; (2) certain taxonomic groups of animals should be more eurybiomic than others, as their resources are more widespread; (3) biomes that have been fragmented due to past climatic changes should contain a higher proportion of stenobiomic species than those that have not undergone extensive fragmentation; and finally (4) from the previous prediction, it should be expected that certain combinations of biomes are more commonly inhabited than others. These combinations must be those that include few biomes (Hernández Fernández & Vrba, 2005; Moreno Bofarull et al., 2008). The first prediction of Hernández Fernández and Vrba, (2005): that biome specialists should be more numerous than biome generalists, would allow fossil mammals to be used as a new proxy for biomes. If the geographic distribution of a mammal can be overlain onto a biome map then the Biome Specialisation Index (BSI) can be calculated and compared to others (Hernández Fernández & Vrba, 2005; Moreno Bofarull et al., 2008). The BSI is a simple metric that counts the number of biomes that a taxon inhabits and allows stenobiomic (BSI of 1 or 2) and eurybiomic (BSI >5) taxa to be defined (Hernández Fernández and Vrba, 2005). Work on modern mammal faunas has shown that the majority of mammals are stenobiomic, with most only inhabiting a single biome (Cantalapiedra et al., 2011; Hernández Fernández & Vrba, 2005; Moreno Bofarull et al., 2008). This is despite Monte Carlo statistics predicting that most species should inhabit two or three biomes (Cantalapiedra et al., 2011; Moreno Bofarull et al., 2008). When looking at the order level there are greater differences. For example the Rodents and Lipotyphla show a high proportion of strongly stenobiomic taxa (Moreno Bofarull et al., 2008), whereas the Carnivora contains a higher than expected number of eurybiomic species (Hernández Fernández & Vrba, 2005; Moreno Bofarull et al., 2008). It is postulated that the reason the Rodents and Lipotyphla contain a greater number than predicted of stenobiomic species, is due to the typically small body size which limits dispersal (Moreno Bofarull et al., 2008). The Carnivora probably contains a higher than expected number of eurybiomic taxa because the availability of prey is unlikely to be controlled by a biome (Hernández Fernández & Vrba, 2005; Moreno Bofarull et al., 2008). Herbivores show mixed results, some orders are stenobiomic others are eurybiomic (Cantalapiedra et al., 2011; Hernández Fernández & Vrba, 2005; Moreno Bofarull et al., 2008). Mean BSIs of 2 – 3.5 are typical for modern herbivore orders (Cantalapiedra et al., 2011; Hernández Fernández & Vrba, 2005; Moreno Bofarull et al., 2008). Eurybiomic herbivore orders are typically those with low numbers of species such as the Proboscidea (Hernández Fernández & Vrba, 2005). So far this work has focussed on modern faunas and has yet to be applied to the palaeontological record, despite the conclusion of Hernández Fernández and Vrba (2005) that the key to macroecological patterns is to be found in the past.

Part of the reason that global scale mammal palaeoecology studies have not been attempted is a long held view that the terrestrial fossil record is more incomplete than the marine, but this is contentious (Benton, 2001; Benton et al., 2011; Lloyd et al., 2011). Global completeness studies on the Late Miocene mammal fossil record are not reported in the literature. However, work on the Neogene basins of the Iberian Peninsula has shown that with extensive sampling and favourable preservation conditions the mammalian fossil record can be 90% complete at the generic level (Alba et al., 2001). Conversely recent work on the Chiroptera has estimated that over the whole Cenozoic only 12% of bat genera are preserved as fossils (Eiting & Gunnell, 2009). Studies on sediment successions have shown that some of the most complete successions are terrestrial (Sadler, 1981; Schindel, 1982). Reviewing the literature on the completeness of the terrestrial fossil record led Benton (2001) to conclude that: diversity and macroecological studies are possible from the terrestrial fossil record.

This chapter undertakes a macroecological study of global Late Miocene mammals to discover if they fit into the first prediction of the resource use hypothesis: more taxa should be biome specialists than generalists. If this can be shown then Late Miocene mammals can be used as a proxy for vegetation. Through the combination of a 407 locality mammal dataset, and the global biome data presented in Chapter 3, the Biomic Specialisation Index (BSI) has been calculated for Late Miocene mammals.

6.2. Methods

6.2.1. The mammal data

Using published literature, the Neogene Old World Mammal database (Fortelius, 2011) and the Paleobiology database (Alroy, 2011) 407 mammal localities have been synthesised in a new database termed MAD (Miocene Animal Database; Appendix C). This database records palaeo-rotated vertebrate fossil sites and the original author's inferred habitat as well as taxonomic data. MAD also records information about the sedimentary facies, age and dating method, nearest living relative life habit, specimen completeness and any taphonomic information provided. The 407 localities have an almost global distribution although there is only one reported Late Miocene terrestrial mammal site in Australia (Alroy, 2011; Myers *et al.*, 2001) and no fossil localities at latitudes north of 55°N or south of 40°S (Fig. 6.1). The 407 localities contain 5370 terrestrial mammal occurrences. These occurences are divided into 1576 named species, in 969 genera, within 119 families, contained within 23 orders. There are also 568 accounts of known genus but unidentifiable species; if a fossil's genus was uncertain then it was not recorded in MAD. The taxonomy within MAD has been made internally consistent using the recent taxonomic revisions of McKenna and Bell (1997) and Alroy (2011).

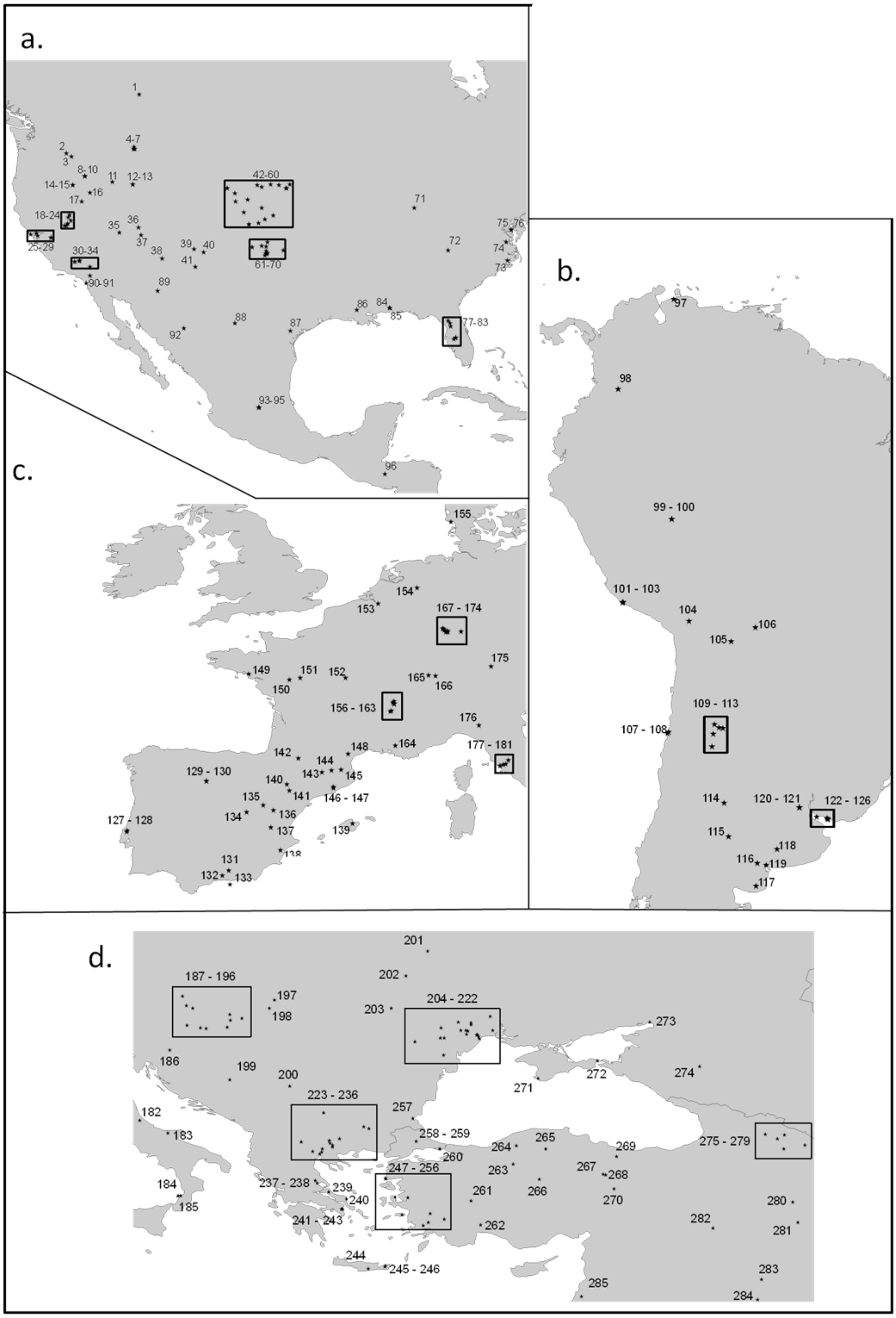


Figure 6.1. The distribution of the 407 Late Miocene mammal localities. A. North America, B. South America, C. Western Europe, D. Eastern Europe, E. Africa and F. Asia. Numbers refer to Appendices C and D.

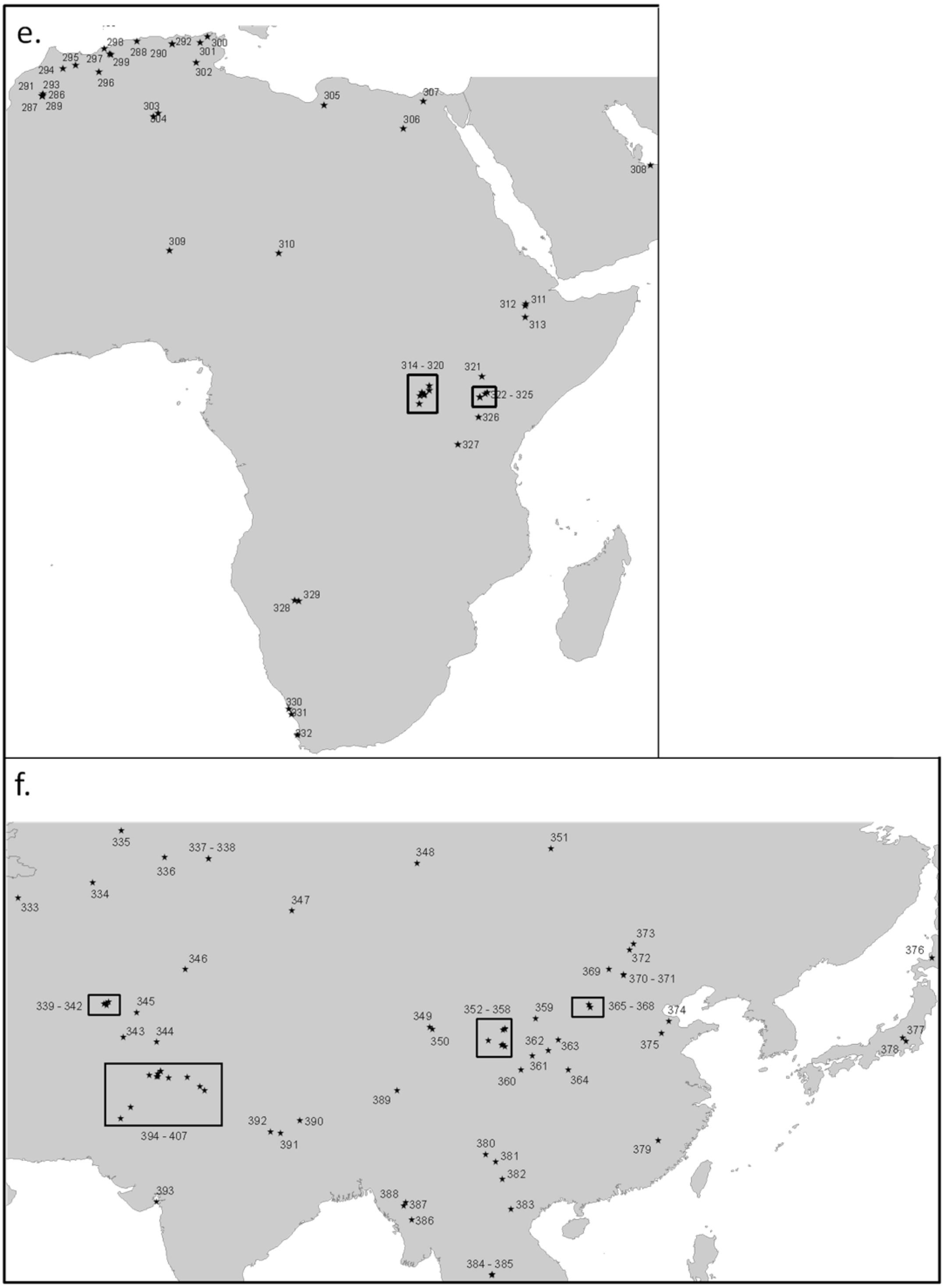


Figure 6.1. *Cont.* The distribution of the 407 Late Miocene mammal localities. A. North America, B. South America, C. Western Europe, D. Eastern Europe, E. Africa and F. Asia. Numbers refer to Appendices C and D.

6.2.2. The vegetation data

The Late Miocene vegetation dataset is taken from Chapter 3 providing 326 biome localities for the Tortonian and 252 for the Messinian. As each data point represents an isolated flora, whether it came from a borehole or a widely distributed sedimentary unit, comparing the mammalian fossil sites with the palaeobotanical fossil sites requires some degree of extrapolation. Except where a palaeobotanical assemblage is found at the same locality as a mammalian fauna (e.g. Combémorel *et al.*, 1970). From the palaeobotanical sites, gridded vegetation maps of the world were generated for roughly two million year intervals (Fig. 6.2). These time interval maps are: the early Tortonian (11.6 – 9 Ma), late Tortonian (9 – 7.25 Ma) and the Messinian (7.25 – 5.33 Ma).To grid the palaeobotanical data the continents have been divided up into grid cells that are 2.5° X 3.75° in size, this size is commonly used in palaeoclimate modelling studies (e.g. Lunt *et al.*, 2008). This large grid size does mean that some grid cells contain multiple palaeobotanical sites. In some cases these multiple sites in a single grid cell are of different biomes. In this event a grid cell has been assigned multiple possible biomes, though the location of the biome within a grid cell does not relate to the position of the data site within the grid cell. This has been done to not bias the gridcells. For example one grid cell in India contains four palaeobotanical sites each indicating the presence of a different biome. Rather than bias the methodology by choosing which of these multiple biomes a mammal inhabited, any mammal occurring in a multiple biome grid cell was recorded as potentially residing in any of the biomes. This might have been avoided with smaller grid cells, but this proved to limit the comparisons between mammals and palaeobotanical data. It was decided that a larger dataset for comparisons, that might artificially create more eurybiomic taxa, was more desirable than a limited dataset. The gridded palaeobotanical data shows the occurrence of 18 different biomes from tropical evergreen broadleaf forest to desert (Fig. 6.2).

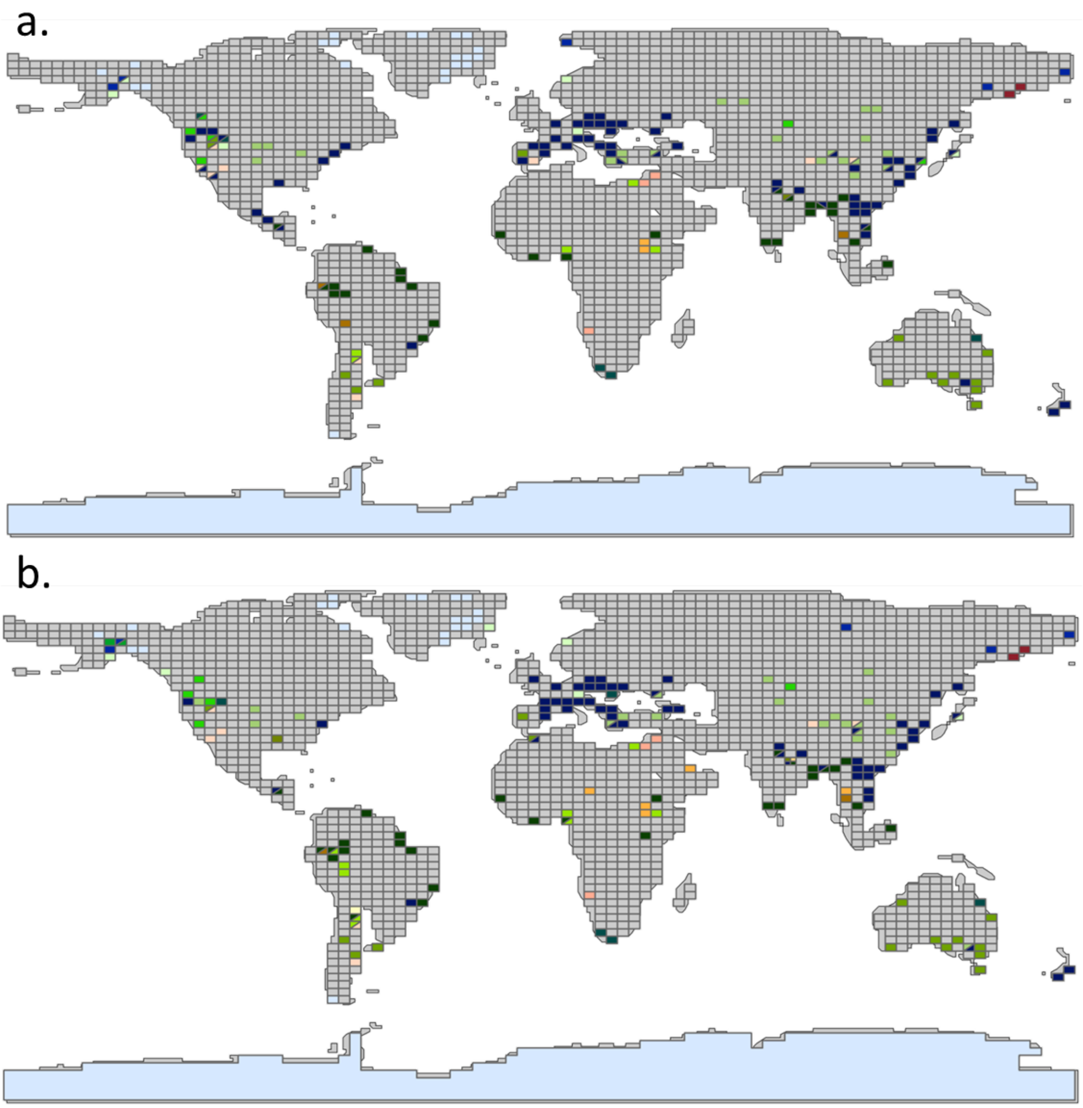


Figure 6.2. The gridded vegetation of the Late Miocene, from Chapter 3. a) early Tortonian, b) late Tortonian and c) Messinian.

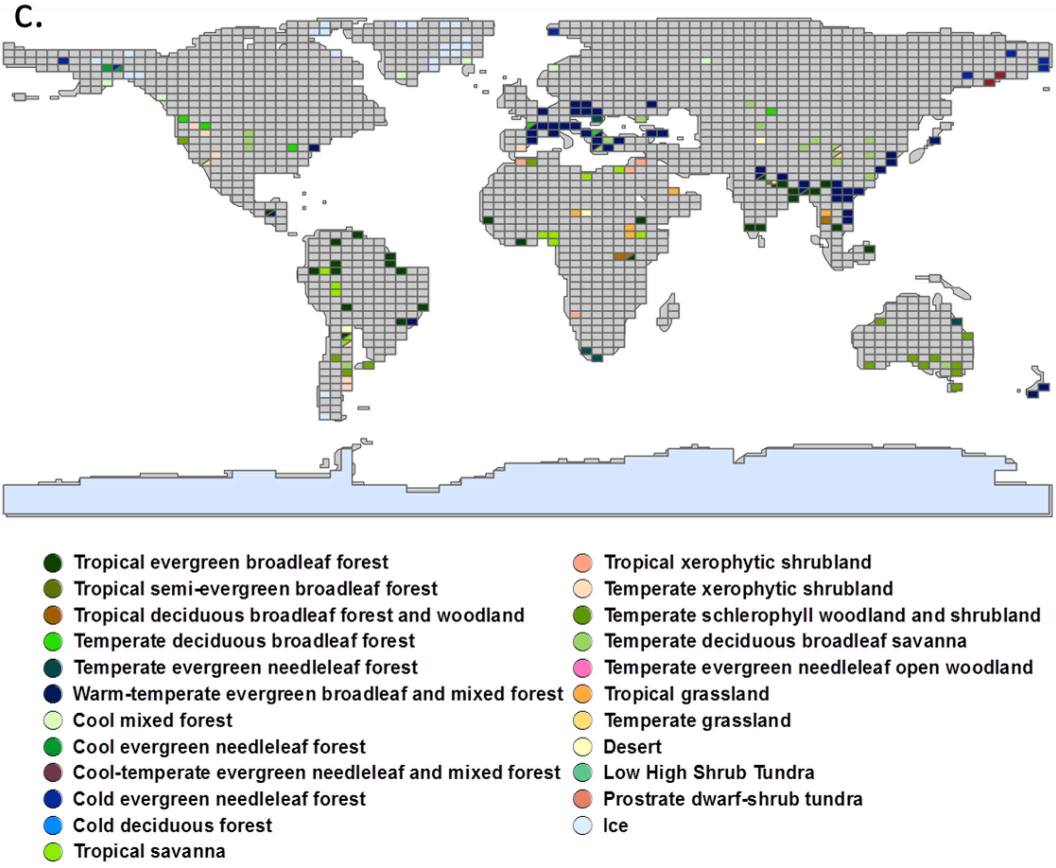


Figure 6.2. Cont. The gridded vegetation of the Late Miocene, from Chapter 3. a) early Tortonian, b) late Tortonian and c) Messinian.

6.2.3. Calculating the biome preferences of Late Miocene mammals

Using the palaeobotanical based vegetation maps (Fig. 6.2) and the 407 faunal localities (Fig. 6.1) the biome preferences of Late Miocene mammals have been evaluated. A Late Miocene mammal's biome preferences were decided using the BSI (Hernández Fernández & Vrba, 2005; Moreno Bofarull *et al.*, 2008). Each mammal species and genus was evaluated for their distribution across the vegetation maps (Fig. 6.2). Using the genus level overcomes the difficult question of what is a species in the fossil record, when it is reportedly difficult to identify an extant one (Hey, 2001; Kamilar, 2006; Sites & Marshall, 2003). Species level BSI data will be presented in Section 6.3, but not discussed at length. The BSI is a simple but powerful tool that rates a taxon based on the number of biomes it inhabits, where a score of one is a strongly stenobiomic mammal only able to survive in a single biome type. Whereas a BSI score of five or more means that the animal in question is a biome generalist and able to tolerate a diverse array of vegetation types and/or climate zones (Hernández Fernández & Vrba, 2005).

With a BSI score applied to each of the 969 genera in MAD, the data were filtered for single occurrence taxa. A single occurrence taxon is a mammal that even after exhaustive data mining currently only appears once in the Late Miocene fossil record. In total, 29.1% of mammal genera in MAD only occur once. For each mammal order, the value is typically between 20 – 35% of genera only occurring once in MAD. Some orders in MAD contain considerably more genera that only occur once, Late Miocene South American orders contain a high proportion (>70%) of genera that have only ever been reported once from the fossil record. The Primates also contain a high proportion of genera only reported once (58%). Genera that only occur once in MAD could skew the BSI to show more stenobiomic mammals than actually existed during the Late Miocene. For example if a genus only occurs once in the entire MAD database, and it is located in a grid cell containing only a single biome, then it would receive a BSI score of 1. When a genus occurs many times in MAD, and is only found in grid cells containing the same biome, then it can be stated with more confidence that this genus is a stenobiomic and contains only stenobiomic species. To avoid this possible skewing of the BSI scores, it was decided to omit both genera and species that only occur once. In general if single occurrence taxa had been included, the proportion of stenobiomic mammals would have been much higher in all orders.

6.3. Late Miocene mammalian BSI

A comparision of 407 Late Miocene mammalian faunas with the palaeobotanical biome data suggests that the majority of Late Miocene mammals inhabited only one or two biomes (69.7%) (Fig. 6.3; Tab. 6.1). Further 15.8% of Late Miocene genera occupied three biomes and 13.1% are found in four to six biomes (Tab. 6.1). Only 1.41% of Late Miocene mammalian genera could occupy 7 or more biomes. Finally, 16% of the genera have a BSI of zero because they do not occur in a grid cell containing palaeobotanical data. The data shows that during the Late Miocene the Mammalia had a mean BSI at the genus level of 2.23 and 1.73 at the species level (Fig. 6.3; Tab. 6.1). In the following sub-sections the BSI results for each mammalian order will be presented and the biome preferences of individual genera will be reported. This will provide evidence that individual mammal taxa can be used to infer biomes and present new information on an aspect of Late Miocene mammal palaeoecology.

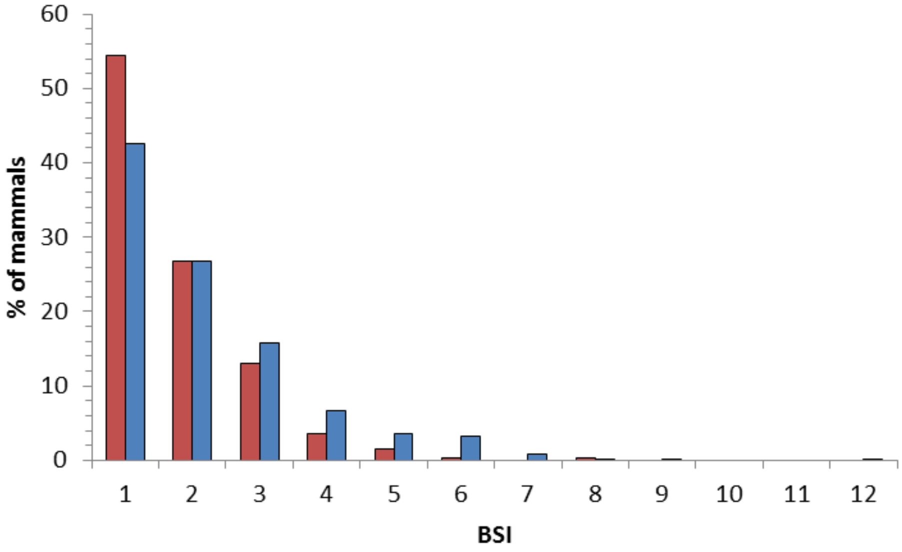


Figure 6.3. The Biomic Specialisation Index (BSI) of Late Miocene Mammals. Showing the percentage of mammal genera (blue) and species (red) inhabiting each BSI classifiaction.

	Late Miocene (Global)				Modern	
BSI	Species Number	%	Genera Number	%	South America %	Africa %
1	392	54.52	205	42.53	41.54	34.29
2	192	26.70	129	26.76	24.40	33.06
3	94	13.07	76	15.77	21.34	13.88
4	26	3.62	32	6.64	8.29	5.71
5	11	1.53	17	3.53	1.14	7.76
6	2	0.28	16	3.32	1.70	1.63
7	0	0.00	4	0.83	0.45	3.27
8	2	0.28	1	0.21	0.68	0.41
9		0.00	1	0.21	0.45	0.00
10		0.00	0	0.00	0.00	0.00
11		0.00	0	0.00	0.00	0.00
12		0.00	1	0.21	0.00	0.00

Table 6.1. The Biomic Specialisation Index (BSI) of the Mammalia for the Late Miocene (Global), modern South America (Moreno Bofarull et al., 2008) and Africa (Hernández Fernández & Vrba, 2005). The modern values have been calculated based on species distribution whilst the Late Miocene values are from the distribution of mammals at the genus level excluding single occurrence taxa.

6.3.1. The Rodentia

The Late Miocene Rodentia is the most taxonomically diverse group in MAD (Number of fossil occurrences in MAD [N] = 1306) (Tab. 6.2). The order has a mean BSI of 1.89 showing it is strongly stenobiomic. It has a maximum BSI of 6 (Fig. 6.4a) from the genera *Hystrix* (N = 28) and *Myocricetodon* (N = 26). Both of these are found in a variety tropical to temperate forests, woodlands and more open biomes. In contrast to the previously mentioned eurybiomic genera a total of 76.5% of Late Miocene rodents only inhabit one or two biomes (Fig. 6.4a).

At the family level the Rodentia show a preference for two or fewer biomes (Tab. 6.3). The family with the most diverse number of genera in MAD is the Cricetidae (N = 318), which were a stenobiomic family (mean BSI = 1.83), although the family does include the eurybiomic genus *Myocricetodon*. The Hystricidae (N = 36) had a mean BSI of 3.33 showing the family to be eurybiomic. The families Castoridae (N = 94), Eomyidae (N = 42), Heteromyidae (N = 28), Muridae (N = 229) and Zapodidae (N = 17) also show a mean BSI of over two (Tab. 6.3). Within the Castoridae, the genera show a preference for warm – temperate to temperate forests, woodlands, savannas and shrublands, except for the genus *Monosaulax* (N = 4) which may have inhabited tropical evergreen forests. The genus *Dipoides* (N = 25) shows the most eurybiomic distribution (BSI = 5) inhabiting warm – temperate to temperate forests, woodlands, shrublands and savannas. Within the Eomyidae the genera *Keramidomys* (N = 12) and *Leptodontomys* (N = 9) have a BSI of 3. These genera were found in forest and savanna biomes in the tropical and warm – temperate regions, whilst *Eomyops* (N = 15) only inhabited warm – temperate mixed forests. The Heteromyidae show a preference for more open biomes in the temperate realm, though some taxa may have inhabited warm – temperate and temperate forests. The Muridae are the second most diverse rodent family recorded during the Late Miocene (Tab. 6.3). The family has a mean BSI of 2.29 and a maximum BSI of 4 for the genera *Apodemus* (N = 34), *Occitanomys* (N = 26) and *Paraethomys* (N = 11). *Apodemus* and *Occitanomys* inhabited warm – temperate forests, savanna and shrubland, whilst *Paraethomys* also inhabited tropical shrublands. Other Muridae genera were stenobiomic and found in only one or two of biomes (Fig. 6.2A). The Zapodidae contains only five Late Miocene genera (Tab. 6.3) and only two of these, *Eozapus* (N = 9) and *Pliozapus* (N = 5), occur at more than one location, both of these had a preference for temperate to warm – temperate forests, woodlands and savanna. The other genera, although only recorded at a single locality, each show a similar biome preference.

The third most taxonomically diverse rodent family in MAD is the Sciuridae (N = 183), which have a mean BSI of 1.93. Within the family most genera were stenobiomic, inhabiting only one biome (e.g. *Spermophilinus* (N = 31), which is only recorded in warm – temperate mixed forests), two biomes (e.g. *Albanesia* (N = 7) and *Sciurotamias* (N = 4), both of which inhabited tropical and warm – temperate forests) or three biomes (e.g. *Atlantoxerus* (N = 10) and *Pliopetaurista* (N = 15), both of which inhabited forests, savannas and shrublands). Only the North American *Spemophilus* (N = 33) shows a strong degree of eurybiomic distribution, inhabiting five biomes ranging through warm – temperate to temperate forests, woodland, shrubland and savanna.

6.3.2. The Lagomorpha

The Lagomorpha (N = 139) of the Late Miocene are a relatively small group with only 22 genera in MAD, of which only 11 occur more than once. The Lagomorpha has a mean BSI of 2.00 (Tab. 6.2) and a maximum BSI of 5 from the genera *Alilepus* (N = 14) and *Hypolagus* (N = 40). *Alilepus* inhabited forests, woodlands and savannas in the tropical and temperate realm, whilst *Hypolagus* was abundant in most warm – temperate to temperate biomes. At the genus level the Lagomorpha show an unusual pattern of BSI: 72.7% are strongly stenobiomic, being found in only a single biome type. The remainder of the Lagomorpha were eurybiomic and inhabited four or five different biomes (Fig. 6.4b). The two Lagomorph families Leporidae (N = 71) and Ochotonidae (N = 68) are both represented by 11 genera in MAD (Tab. 6.3). During the Late Miocene the Ochotonidae were more stenobiomic than the Leporidae (Tab. 6.3). Within the Ochotonidae only *Prolagus* (N = 35) was eurybiomic (BSI = 4).

Order	Late Miocene				Modern	
	Global				South America	Africa
	No. species	Mean BSI	No. Genera	Mean BSI	Mean BSI	Mean BSI
Rodentia	183	1.62	147	1.91	1.81	0.00
Lagomorpha	19	1.84	11	2.00	5.00	0.00
Lipotyphla	55	1.38	38	1.89	2.00	0.00
Carnivora	128	1.91	88	2.47	3.83	3.10
Proboscidea	30	2.10	16	3.06	0.00	6.00
Tubulidentata	2	2.00	1	3.00	0.00	5.00
Artiodactlyla	165	1.85	114	2.26	3.33	2.10
Primates	6	1.50	5	2.00	1.41	1.80
Hyracoidea	2	1.50	2	1.50	0.00	3.20
Perissodactyla	101	1.66	37	2.78	2.67	2.30
Chiroptera	5	2.00	5	2.20	2.73	0.00
Litopterna	0	0.00	2	1.00	0.00	0.00
Xenarthra	17	1.41	22	1.36	2.48	0.00
Notoungulata	4	1.00	5	1.60	0.00	0.00
Didelphimorpha	2	1.00	1	1.00	2.00	0.00

Table 6.2. The Biomic Specialisation Index (BSI) of the Mammalia at the order level for both species and genera. The number of species and genera is for taxa with more than one occurrence in MAD. The values for modern South America and Africa are provided for comparison (Hernández Fernández & Vrba, 2005; Moreno Bofarull et al., 2008).

6.3.3. The Lipotyphla

The Late Miocene Lipotyphla (N = 333) had a mean BSI of 1.89, showing this order is strongly stenobiomic (Tab. 6.2). At the genus level 73.7% of the Lipotyphla inhabited only one or two biomes (Fig. 6.4c). During the Late Miocene the order had a maximum BSI of 5 from two genera *Scapanus* (N = 11) and *Sorex* (N = 11). *Scapanus* was found throughout temperate biomes in North America, whilst *Sorex* inhabited temperate and tropical biomes. These two eurybiomic genera were also the only members of the Lipotyphla that inhabited arid shrublands. At the family level the Soricidae (N = 109) have the highest mean BSI of 2.07, this highlights the strongly stenobiomic nature of the Lipotyphla (Tab. 6.3). Within the Soricidae the Eurasian genus *Paenelimnoecus* (N = 12) shows an occurrence only in warm – temperate mixed forests. Apart from this genus the majority of genera in the Soricidae inhabited two or three biomes. The Soricidae inhabited temperate to warm – temperate forests, woodlands and savannas; *Anourosorex* (N = 5), *Blarinella* (N = 3) and *Crocidura* (N = 5) were also found in tropical evergreen forests. The Talpidae (N = 105) had a mean BSI of 2.00 (Tab. 6.3) and apart from *Scapanus* most of the genera inhabited three or less forest, woodland, shrubland or savanna biomes. The Erinaceidae (N = 87) is strongly stenobiomic with a mean BSI of 1.86 (Tab. 6.3). Within the Erinaceidae the highest BSI score is 3 for *Erinaceus* (N = 5) and *Schizogalerix* (N = 18), both of which inhabited warm – temperate and temperate forest and savanna biomes. Most of the genera in the Erinaceidae inhabited one or two tropical or warm – temperate forest biomes during the Late Miocene. The Dimylidae (N = 14), though not taxonomically diverse, were strongly stenobiomic (Tab. 6.3). Both the genera *Metacordylodon* (N = 2) and *Plesiodimylus* (N = 12) were only found to occur in grid cells containing warm – temperate mixed forests. A similar pattern is observed in the Heterosoricidae (N = 12); *Dinosorex* (N = 10) was only found in warm – temperate mixed forests, whilst *Heterosorex* (N = 2) was only found to occur in tropical evergreen forests.

6.3.4. The Carnivora

The Carnivora (excluding the Phocidae) (N = 864) of the Late Miocene had a mean BSI of 2.47 calculated at the genus level showing this order was moderately eurybiomic (Tab. 6.2). Despite this 64.8% of all Carnivora genera were only recorded inhabiting one or two biomes (Fig. 6.4d). The strongest eurybiomic genera during the Late Miocene were *Machairodus* (BSI = 9; N = 52), *Plesiogulo* (BSI = 7; N = 24), *Adcrocuta* (N = 42), *Borophagus* (N = 37), *Felis* (N = 24), *Hyaenictitherium* (N = 22), *Indarctos* (N = 29), *Metailurus* (N = 22) and *Simocyon* (N = 11) (all of which had a BSI of 6). These genera were found in a variety of biome types. At the family level the Ailuridae (BSI = 4.00; N = 15), Felidae (BSI = 3.23; N = 170) and Ursidae (BSI = 3.20; N = 72) are all strongly eurybiomic, whereas the Amphicyonidae (BSI = 1.60; N = 21), Barbourofelidae (BSI = 1.50; N = 12) and the Procyonidae (BSI = 1.25; N = 11) were all strongly stenobiomic families (Tab. 6.3). The Ailuridae contains only four genera in MAD and only two of these *Protursus* (N = 2) and *Simocyon* are found at more than one fossil locality. *Protursus* was associated with tropical to warm temperate forests, whilst *Simocyon* was much more eurybiomic inhabiting tropical to temperate forests, woodlands, shrublands and savannas. The Felidae is strongly eurybiomic with 63.6% of genera occupying three or more biomes. Most genera in the Felidae show no preference for any biome type, a notable exception to this is the genus *Nimravides* (N = 12) which may have been a savanna specialist. The Ursidae contains five genera that occur in grid cells with palaeobotanical data. Three of these five genera have a BSI of greater than three; *Agriotherium* (BSI = 4; N = 18), *Indarctos* (BSI = 6) and *Ursavus* (BSI = 3; N = 16). Much like the Felidae the Ursidae appear to have no preference for any biome type.

The Amphicyonidae has a maximum BSI of 4 from the genus *Amphicyon* (N = 12), although this is related to the grid cell on the Indian subcontinent with four possible biomes in it. This means that the relatively high BSI of *Amphicyon* might be related to the uncertainties in the palaeobotanial reconstruction. This is further supported by the rest of the Amphicyonidae, whom show a preference for tropical evergreen forests or warm – temperate mixed forests. The Barbourofelidae contains three genera, of these only two genera occur in grid cells with palaeobotanical data; *Barbourofelis* (N = 7) and *Sansanosmilus* (N = 4). *Sansanosmilus* shows a preference for warm – temperate mixed forests, whilst *Barbourofelis* shows preference for an unusual combination of biomes; warm – temperate mixed forests and temperate xerophytic shrubland. The Procyonidae shows a preference for open biomes such as temperate savanna and temperate xerophytic shrubland.

The other Carnivora families have a mean BSI between 2 and 3. The Hyaenidae (N = 202) has a mean BSI of 2.93 and has 41.2% of eurybiomic genera. Its stenobiomic genera such as: *Crocuta* (N = 6) preferred warm – temperate mixed forests; *Miohyaenatherium* (N = 4) was found in warm – temperate to temperate forests; whilst *Plioviverrops* (N = 8) and *Protictitherium* (N = 17) are found occurring where palaeobotanical data reconstructs warm – temperate mixed forests or temperate savanna. The Mustelidae (N = 212) is the most taxonomically diverse Carnivora family recorded in MAD (Tab. 6.3). The family had a mean BSI of 2.03 showing that although it contains strongly eurybiomic genera such as *Plesiogulo*, as a family it is more stenobiomic. Of all the Mustelidae genera recorded in MAD 80% only occupy one or two biomes. However, the Mustelidae suffer from a poor fossil record due to their small size and low population densities (Pasitschniak-Arts and Larivière, 1995). This poor fossil record is also seen in MAD as there appears to be a positive correlation between the number of occurrences in MAD and the number of inhabited biomes. The other “small carnivore family” the Viverridae (N = 25) had a mean BSI of 2.20 during the Late Miocene showing the group to be stenobiomic (Tab. 6.3). However, like the previously discussed Mustelidae, the Viverridae may suffer from a poor fossil record: the most common genera are only found at six localities in MAD. Despite this, as a family the Viverridae show a preference for tropical biomes and warm – temperate to temperate forests. The Canidae (N = 111) during the Late Miocene had a mean BSI of 2.50 (Tab. 6.3). The Canidae shows a strong preference for the temperate savanna biome. It is only the more eurybiomic genera *Borophagus*, *Epicyon* (N = 25) and *Eucyon* (N = 12) that are found in a diverse array of tropical to temperate biomes.

6.3.5. The Proboscidea

At the order level the Proboscidea (N = 280) have the highest mean BSI score, both for species (2.10) and genera (3.06) showing the group as strongly eurybiomic (Tab. 6.2). The maximum BSI in the Proboscidea is 8 for the genus *Deinotherium* (N = 54) and 7 for the genus *Anancus* (N = 20). There is also a relatively even spread through the BSI scores of one to four at the genus level, showing a mixture of stenobiomic and eurybiomic taxa. Whilst looking at the species level the Proboscidea as an order are more stenobiomic (Fig. 6.4e).

At the family level the Deinotheridae (N = 57) and Mammutidae (N = 32) have a BSI greater than 4 (Tab. 6.3). The Late Miocene Mammutidae comprises of two genera: *Mammut* (BSI = 5; N = 21) and *Zygolophodon* (BSI = 3; N = 11). The genus *Zygolophodon* inhabited tropical evergreen forests, warm – temperate mixed forests and temperate savannas, whilst *Mammut* was found in tropical and temperate forests, shrublands and savannas. The Late Miocene Gomphotheridae (N = 153) has a mean BSI of 3.86 (Tab. 6.3). Within the Gomphotheridae 85.7% of genera occupied 3 or more biomes ranging from forests, woodlands, shrublands and savannas in the tropical and temperate realm. The Elephantidae (N = 38) during the Late Miocene had a mean BSI of 2.00 (Tab. 6.3). The most eurybiomic genera were *Stegodon* (N = 8) and *Stegotetrabelodon* (N = 9), both of which inhabited three biomes. *Stegodon* and *Stegotetrabelodon* both inhabited tropical deciduous woodlands, warm – temperate forest and grasslands. The other genera inhabited tropical, warm – temperate and temperate forests, woodlands and grasslands.

6.3.6. The Tubulidentata

The Late Miocene Tubulidentata (N = 19) order only contains a single genus that occurs at more than one locality (Tab. 6.2, 3, Fig. 6.4f). *Orycteropus* (N = 18) had a BSI of 3.00 and was found in warm – temperate mixed forest, temperate savanna and tropical grassland biomes. The diversity of biome types from closed forests to open grasslands shows the genus to be eurybiomic, much as it is today (Vrba, 1987).

6.3.7. The Artiodactyla

The Late Miocene Artiodactyla (N = 1217) (Fig. 6.4g) had a mean BSI of 2.26 at the genus level, a maximum BSI of 7 (*Gazella* (N = 89) and *Samotherium*(N = 26)) and contains 66.7% strongly stenobiomic genera (BSI of one or two). At the family level only Gelocidae (N = 7) and Tragulidae (N = 40) were eurybiomic with a mean BSI over 3.00 (Tab. 6.3). Four families were strongly stenobiomic with mean BSI scores below 2.00; Hippopotamidae (N = 19), Merycoidodontidae (N = 6), Moschidae (N = 17) and Palaeomerycidae (N = 28).

Within the Gelocidae there are only two reported genera during the Late Miocene. Of these two genera only *Pseudoceras* (N = 6) occurs at more than one locality. The genus *Pseudoceras* inhabited tropical to warm – temperate forests and temperate savannas. The Tragulidae contains three genera during the Late Miocene (Tab. 6.3). Only two of these, *Dorcabune* (N = 8) and *Dorcatherium* (N = 31), are found at more than one locality. Both *Dorcabune* and *Dorcatherium* were eurybiomic with BSI scores of 4 and 6 respectively. However, *Dorcabune* and *Dorcatherium* both occur in the grid cell on the Indian subcontinent with four biomes in it. The Tragulidae as a family inhabited tropical to warm – temperate forests, woodlands and temperate savanna. Both the Gelocidae and Tragulidae may be eurybiomic due to the low number of genera in the families and in the case of the Tragulidae, the complex vegetation pattern preserved in the Himalayan foothills.

The Hippopotamidae contains three genera *Hexaprotodon* (N = 13), *Hippopotamus* (N = 3) and *Kenyapotamus* (N = 3) (Tab. 6.3). All three genera prefered open biomes and especially occur where palaeobotanical data reconstructs the tropical savanna biome. However, as all three were aquatic herbivores (Alroy, 2011; Pickford, 1983) the presence of suitable water bodies may have been more important than a biome type. The Merycoidontidae family contains two genera during the Late Miocene *Merychus* (N = 4) and *Ustatochoerus* (N = 2), both of which have a BSI score of 1 and inhabited temperate savanna. The Family Moschidae contains five genera of which three occur at more than one locality (Tab. 6.3). *Hispanomeryx* (N = 2), *Micromeryx* (N = 11) and *Moschus* (N = 2) all show a preference for tropical to temperate forests. Whilst *Blastomeryx* (N = 280) and *Longirostromeryx* (N = 280) only occur once in MAD, they show that the family may have also inhabited temperate savanna. The Palaeomerycidae contains five genera in MAD (Tab. 6.3), all of which occur at more than one fossil site. Unfortunately two of the genera do not occur in a grid cells containing palaeobotanical data. Despite this the remaining genera show that *Cranioceras* (N = 3) and *Pediomeryx* (N = 10) preferred open biomes (temperate xerophytic shrubland and temperate savanna), whilst *Palaeomeryx* (N = 6) preferred forested biomes.

The Anthracotheriidae (N = 14) contains four genera, three of which have more than one occurrence in MAD and the family has a mean BSI of 2.67 (Tab. 6.3). *Libycosaurus* (N = 4) and *Merycopotamus* (N = 5) were stenobiomic, inhabiting tropical savanna and grassland. The genus *Hemimeryx* (N = 4) is more eurybiomic (BSI = 5) and inhabited tropical forests, tropical savanna, tropical grassland, warm – temperate forest and temperate grassland. The Antilocapridae (N = 37) has a mean BSI of 2.20 and contains seven genera with more than one occurrence in MAD (Tab. 6.3). The family is mainly stenobiomic apart from the genus *Plioceros* (N = 5). *Plioceros* has a BSI score of 4 and inhabited warm temperate to temperate forests, woodlands and shrublands.

The Bovidae (N = 485) contains the greatest number of Late Miocene Artiodactyla genera in MAD (Tab. 6.3). The family is strongly stenobiomic with 71.7% of genera inhabiting only one or two biomes. Eurybiomic members of the Bovidae include *Gazella* (BSI = 7), *Miotragocerus* (BSI = 6; N = 33), *Pachyportax* (BSI = 5; N = 6), *Palaeoryx* (BSI = 5; N = 25) and *Prostrepsicerus* (BSI = 6; N = 25) all of which could inhabit a diverse range of tropical and temperate forests, woodlands, shrublands and savannas. The Camelidae (N = 95) has a mean BSI of 2.43 and a total of ten genera during the Late Miocene (Tab. 6.3). Unfortunately only seven of these occur at more than one fossil locality. The Camelidae is moderately stenobiomic with no genera inhabiting more than three biomes. The genera *Alforjas* (N = 9) and *Hemiauchenia* (N = 33) inhabited warm – temperate mixed forests, temperate savanna and temperate xerophytic shrublands. *Megacamelus* (N = 3) also had a BSI score of 3 occupying temperate sclerophyll woodland, savanna and shrubland. Whereas *Megatylopus* (N = 25), *Procamelus* (N = 12) and *Protolabis* (N = 2) were more typically found in tropical evergreen forests, warm – temperate mixed forests and in the case of *Megatylopus* and *Procamelus* temperate savanna as well.

The Cervidae (N = 109) had a mean BSI of 2.17 showing the group to be stenobiomic. The most eurybiomic genera were *Metacervulus* (N = 6) and *Muntiacus* (N = 10), which both had a BSI of 4 and inhabited tropical and warm – temperate forests, temperate savanna and temperate grassland. The other Cervidae genera were mainly found in warm – temperate mixed forests and temperate savanna. The Giraffidae (N = 159) has a mean BSI of 2.83 and contains a relatively even mix of stenobiomic and eurybiomic genera (Tab. 6.3). The eurybiomic genera include *Samotherium* (BSI = 7), *Palaeotragus* (BSI = 5; N = 62), *Bohlinia* (N = 13) and *Giraffokeryx* (N = 6) (both had a BSI score of 4). Overall the Giraffidae show no preference for particular biome types: inhabiting forests, woodlands, savannas, shrublands and savannas. The Suidae (N = 173) contains 17 genera that occur in more than one fossil assemblage. The family has a mean BSI of 2.31 and 69.2% of genera occur in only one or two biomes. The most eurybiomic genera were *Nyanzachoerus* (N = 28) and *Propotamochoerus* (N = 21), both of which had a BSI of 6 and inhabited a variety of forest, woodland, shrubland, savanna and grassland in the tropical and temperate realm. *Chleuastochoerus* (N = 8) was slightly eurybiomic (BSI = 4), but was restricted to warm – temperate to temperate biomes. The Tayassuidae (N = 28) had a mean BSI of 2.33 during the Late Miocene (Tab. 6.3). The family contains seven genera unfortunately only four are known from more than one locality. *Prosthennops* (N = 14) is the only eurybiomic genus and has a BSI score of 5; it was found in tropical and temperate forests, woodland and savanna. *Catagonus*(N = 5) and *Platygonus* (N = 3) were both stenobiomic genera, inhabiting temperate savannah.

6.3.8. The Primates

The Primate order (N = 64) during the Late Miocene had a mean BSI of 2.00 (Tab. 6.2).This low mean BSI score shows that the Primates were stenobiomic, with 60% of genera inhabiting two or less biomes (Fig. 6.4h). MAD records eight Primate families during the Late Miocene four of these: the Adapidae, Atelidae, Cebidae and Galagidae have such poor fossil records that they could not be used in the BSI study. The Cercopithecidae (N = 27) are the most eurybiomic of the Late Miocene Primates (BSI = 3). However, the family contains only one genus which occurs in multiple fossil assemblages and within grid cells containing palaeobotanical data. This genus: *Mesopithecus* (N = 16) inhabited warm – temperate to temperate forests and savanna. Other Cercopithecidae genera that only occur at single sites include *Libypithecus*, which was found in tropical savanna and *Paracolobus* found in tropical evergreen forests.

The Homindae (N = 30) has a mean BSI of 2.00 and contains 12 genera during the Late Miocene (Tab. 6.2). Unfortunately only a quarter of these are found at more than one fossil locality. *Dryopithecus* (N = 10) is the most eurybiomic genus with a BSI score of 3; it inhabited warm – temperate mixed forests, temperate savanna and temperate grassland biomes. *Sivapithecus* (N = 7) and *Udabnopithecus* (N = 2) were more stenobiomic and were only found in forest biomes. *Udabnopithecus* was only found in warm – temperate mixed forests, whilst *Sivapithecus* occurred in tropical evergreen forests and warm – temperate mixed forests.

The Pliopithecidae (N = 7) has a mean BSI of 1.00 and contains three genera during the Late Miocene (Tab. 6.3). As a family the Pliopithecidae show a preference for forest biomes. *Anapithecus* (N = 4) was found in warm – temperate mixed forests and *Laccopithecus*, though only occurring once in MAD, inhabited tropical evergreen forests. The genus *Pliopithecus* (N = 2) does not co-occur in any grid cell with palaeobotanical data. The Sivaladapidae family also has a mean BSI of 1.00 but only two genera are recorded in MAD for the Late Miocene (Tab. 6.3). Of these two genera only *Sinoadapsis* occurs more than once in MAD, but at the same locality. This locality co-occurs in a grid cell containing palaeobotanical evidence for a tropical evergreen forest.

6.3.9. The Hyracoidea

The Hyracoidea order (N = 14) is strongly stenobiomic showing a mean BSI of 1.50 during the Late Miocene (Tab. 6.2; Fig. 6.4i). The order contains two families, the Pliohyracidae (N = 9) and the Procaviidae (N = 5). The Pliohyracidae is the slightly more eurybiomic with a mean BSI of 2.00 from a single genus; *Pliohyrax* (N = 8), which occurs at multiple fossil localities co-occurring with palaeobotanical evidence for warm – temperate mixed forests or temperate savanna. The Procaviidae had a mean BSI of 1.00 again from a single genus *Procavia* (N = 2). The genus *Dendrohyrax* conversely occurs at a single locality but has a BSI score of 2, due to the grid cell containing palaeobotanical evidence for both the tropical evergreen forest biome and the tropical deciduous woodland biome. A limited fossil record (14 recorded occurrences in MAD, many of which are single occurrences of taxa) inhibits much to be resolved from the distribution of Late Miocene Procaviidae, today the family are found throughout sub - Saharan Africa in a diverse range of biomes (Wilson & Reeder, 2005).

Order & family	No.	Mean	No.	Mean	Order & family	No.	Mean	No.	Mean
Rodentia					**Proboscidea**				
Abrocomidae	1	2.00	1	2.00	Deinotheridae	8	2.33	2	4.50
Anomalomyidae	4	1.00	1	1.00	Elephantidae	22	1.13	7	2.00
Aplodontidae	5	0.00	3	1.00	Gomphotheriidae	35	2.40	12	3.86
Castoridae	29	1.46	12	2.13	Mammutidae	8	2.75	2	4.00
Caviidae	6	1.25	5	1.33	**Tubulidentata**				
Chinchillidae	2	2.00	2	2.00	Orycteropodidae	9	2.00	2	3.00
Cricetidae	160	1.57	59	1.83	**Artiodactlyla**				
Ctenodactylidae	8	1.00	3	1.00	Anthracotheriidae	8	2.33	4	2.67
Dinomyidae	10	1.50	6	1.67	Antilocapridae	18	2.00	8	2.20
Dipodidae	28	1.50	11	1.33	Bovidae	196	1.79	87	2.11
Echimyidae	4	1.00	3	1.00	Camelidae	22	1.73	10	2.43
Eomyidae	18	1.33	6	2.25	Cervidae	52	1.76	22	2.17
Geomyidae	11	1.50	7	1.40	Gelocidae	3	1.50	2	3.00
Gerbillidae	8	0.00	5	2.00	Giraffidae	43	2.24	21	2.83
Gliridae	48	1.25	20	1.36	Hippopotamidae	14	2.00	3	2.00
Heteromyidae	18	1.67	6	2.60	Merycoidodontidae	2	1.00	2	1.00
Hydrochoeridae	3	0.00	3	0.00	Moschidae	10	1.00	5	1.33
Hystricidae	10	2.75	4	3.33	Palaeomerycidae	11	1.50	5	1.67
Muridae	102	1.69	43	2.29	Suidae	64	1.68	23	2.31
Mylagaulidae	7	2.00	3	2.00	Tayassuidae	11	2.25	7	2.33
Neoepiblemidae	6	0.00	2	1.00	Tragulidae	13	2.67	3	5.00
Nesomyidae	3	2.00	3	2.00	**Primates**				
Octodontidae	5	2.00	4	1.50	Cercopithecidae	12	1.67	9	3.00
Sciuridae	75	1.64	33	1.93	Hominidae	23	1.50	12	2.00
Siphneidae	4	1.00	1	1.00	Pliopithecidae	5	1.00	3	1.00
Spalacidae	8	1.00	5	1.50	Sivaladapidae	3	1.00	2	1.00
Thryonomyidae	8	2.00	4	2.00	**Hyracoidea**				
Zapodidae	7	2.50	5	2.50	Pliohyracidae	5	2.00	2	2.00
Lipotyphla					Procaviidae	4	1.00	3	1.00
Dimylidae	4	1.00	2	1.00	**Perissodactyla**				
Erinaceidae	34	1.20	13	1.86	Chalicotheriidae	14	2.00	5	3.33
Heterosoricidae	6	1.00	2	1.00	Equidae	122	1.55	15	2.92
Soricidae	51	1.59	30	2.07	Rhinocerotidae	78	1.82	27	2.55
Talpidae	42	1.59	22	2.00	Tapiridae	12	1.67	4	4.00
Lagomorpha					**Chiroptera**				
Leporidae	26	2.00	11	2.60	Hipposideridae	2	0.00	2	0.00
Ochotonidae	27	1.63	11	1.50	Rhinolophidae	4	1.00	1	2.00
Carnivora					Vespertilionidae	17	2.67	11	2.25
Ailuridae	9	2.67	4	4.00	**Litopterna**				
Amphicyonidae	11	1.75	7	1.60	Macraucheniidae	3	0.00	3	0.00
Barbourofelidae	6	1.00	3	1.50	Proterotheriidae	6	0.00	5	1.00
Canidae	29	1.57	11	2.50	**Xenarthra**				
Felidae	50	2.50	20	3.23	Dasypodidae	26	1.50	15	1.55
Hyaenidae	65	2.08	18	2.93	Glyptodontidae	14	1.25	11	1.14
Mustelidae	111	1.63	55	2.03	Megalonychidae	10	1.50	4	1.50
Percrocutidae	8	1.50	2	2.00	Mylodontidae	15	1.00	10	1.00
Procyonidae	10	2.00	4	1.25	**Notoungulata**				
Ursidae	22	1.69	7	3.20	Hegetotheriidae	6	1.00	4	2.00
Viverridae	13	2.25	7	2.20	Mesotheriidae	3	1.00	2	1.50
Didelphimorpha					Toxodontidae	14	1.00	14	1.00
Didelphidae	9	1.00	7	1.00					

Table 6.3. The number of species, number of genera and mean BSI for each Late Miocene mammal family recorded in MAD.

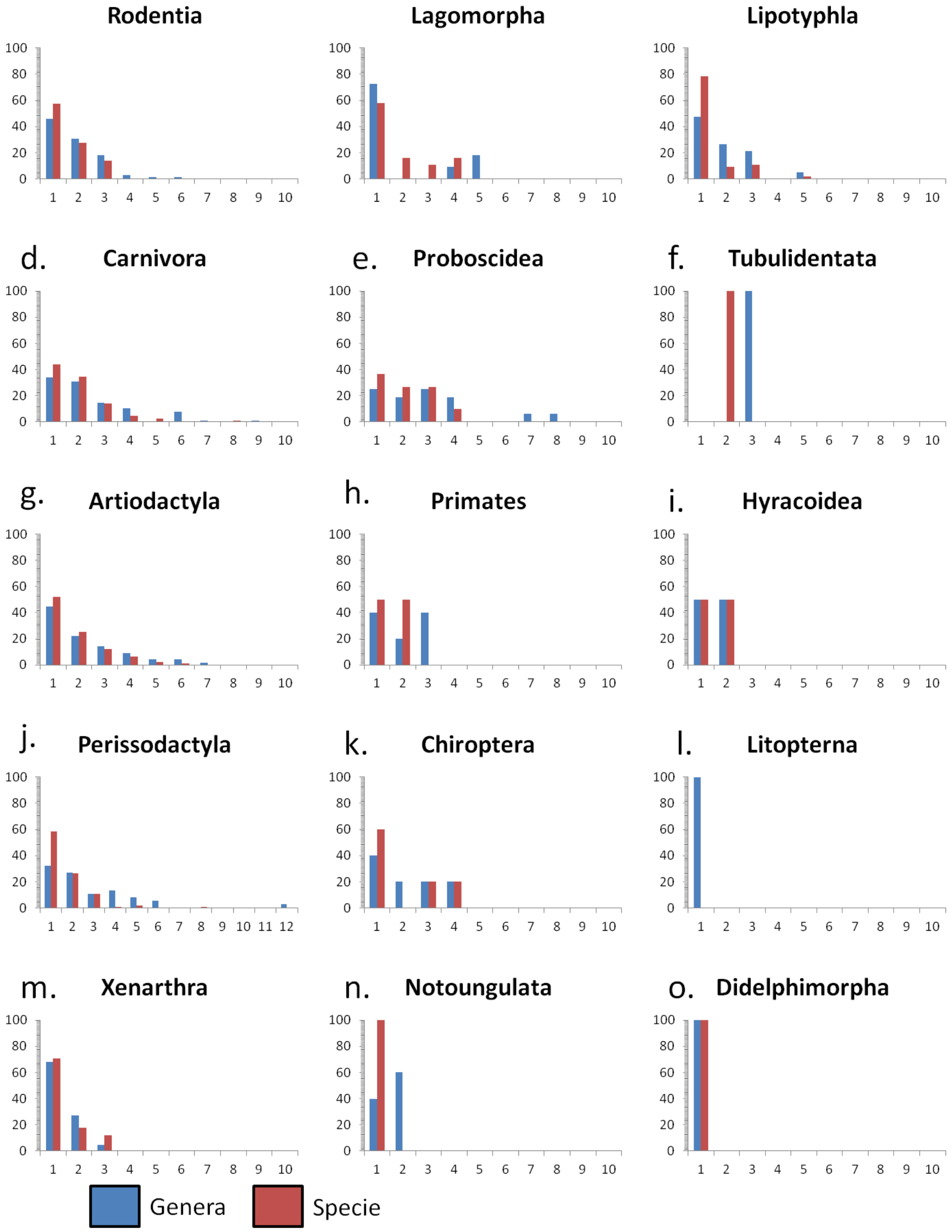


Figure 6.4. The Biomic Specialisation Index scores of mammal orders. The blue represents the proportion of genera in each biome score and the red represents the proportion of species. The x-axis is the BSI score and the y-axis is the percentage of taxa.

6.3.10. The Perissodactyla

The Late Miocene Perissodactyla (N = 780) (Fig. 6.4j) had a mean BSI of 2.78 (Tab. 6.2) and a large proportion of stenobiomic genera - 52.5% inhabiting only one or two biomes. However the Perissodactyla does contain the most eurybiomic genus in the study: *Hipparion* (BSI = 12; N = 166). However, this genus contains 53 named species, of which 26 occur more than once in MAD and 50% of these inhabited only a single biome. The Late Miocene Perissodactyla contains four families: Chalicotheridae (mean BSI = 3.33; N = 47), Equidae (mean BSI = 2.92; N = 420), Rhinocerotidae (mean BSI = 2.55; N = 283) and the Tapiridae (mean BSI = 4.00; N = 30).

The Chalicotheriidae contains five genera during the Late Miocene (Tab. 6.3). Two of these *Kalimantsia* and *Metaschizotherium* are each only known from a single fossil occurrence, though both of the fossil localities are found within warm – temperate mixed forests. *Anisodon* (N = 2) was a stenobiomic genus also found in warm – temperate mixed forests. *Ancylotherium* (N = 16) and *Chalicotherium* (N = 27) were eurybiomic genera with BSI scores of 5 and 4 respectively. *Ancylotherium* inhabited tropical to temperate forests and temperate savanna, whilst *Chalicotherium* inhabited warm – temperate to temperate forests, savanna and grassland. This slight difference in biomes inhabited also means that *Ancylotherium* and *Chalicotherium* are only found co-occurring at a single fossil locality at Hadjidimovo, Bulgaria (Fortelius, 2011; Kostopoulos *et al.*, 2001).

The Equidae contains 15 genera, of which two (*Plesihipparion* and *Sivalhipparion*) are each only known from a single locality. *Anchitherium* (N = 5), though known from multiple fossil localities, does not occur in a grid cells containing palaeobotanical data. As previously mentioned *Hipparion* is the most eurybiomic genus within the Equidae and occurred in most biomes in the study. *Cremohipparion* (BSI = 4; N = 18) and *Dinohippus* (BSI = 5; N = 36) were also eurybiomic, the former inhabited tropical savanna, warm – temperate mixed forests, temperate deciduous forests and temperate savanna, whilst the latter was found to occur in warm – temperate to temperate forest, woodland, shrubland or savanna. *Pliohippus* (N = 11) has a BSI score of 3 showing that it was fairly eurybiomic and was found in tropical evergreen forests, warm – temperate mixed forests or temperate savanna. The other Equidae genera are stenobiomic with *Astrohippus* (N = 10), *Hippotherium* (N = 59), *Nannipus* (N = 32) and *Neohipparion* (N = 37) inhabiting warm – temperate mixed forests and temperate savanna. *Calippus* (N = 13), *Protohippus* (N = 9) and *Pseudhipparion* (N = 10) are only found in grid cells which contain palaeobotanical evidence for temperate savanna. *Eurygnathohippus* inhabited tropical evergreen forest and tropical deciduous biomes.

The Rhinocerotidae contains 27 genera recorded in MAD, of this total five genera only occur in a single fossil assemblage and another two do not co-occur in grid cells with palaeobotanical data. Excluding these seven genera, the Rhinocerotidae contains 57.9% of genera that only occur in one or two biomes. Common vegetation occurrences for strongly stenobiomic genera include: temperate savanna; *Aphelops* (N = 19), *Ningxiatherium* (N = 2), *Shansirhinus* (N = 2) and *Stephanorhinus* (N = 4) and warm – temperate mixed forest; *Diceros* (N = 7) and *Lartetotherium* (N = 3). Other stenobiomic genera occur in two biomes, such as *Dicerorhinus* (N = 17) which inhabited warm temperate mixed forests and temperate deciduous forests, *Sinotherium* (N = 5) which occurred in temperate savanna and grasslands and *Hoploaceratherium* (N = 3) which was found in tropical deciduous woodland and warm – temperate mixed forests. *Aceratherium* (BSI = 5; N = 42), *Brachypotherium* (BSI = 6; N = 18) and *Teleoceras* (BSI = 6; N = 40) represent the most eurybiomic genera within the Rhinocerotidae. *Aceratherium* inhabited tropical to temperate forests, woodland and savanna, whilst *Brachypotherium* occupied these and tropical to temperate grasslands. *Teleoceras* was found to occur in tropical to temperate forests, woodland, savanna and shrubland.

The Tapiridae, during the Late Miocene, contained four genera (Tab. 6.3), two of which (*Protapirus* and *Tapiravus*) only occur once in MAD and another genus (*Tapiriscus*; N = 3) does not co - occur with vegetation data. This leaves *Tapirus* (N = 25) as the sole genus in MAD with sufficient data coverage to provide biome preference information on the Tapiridae. The genus *Tapirus* has a BSI of 4 suggesting the genus is eurybiomic. These biomes include tropical to temperate forests and temperate savanna. This is in agreement with the modern Lowland Tapir (*Tapirus terrestris*) in South America (Bodmer & Brooks, 1997; de Thoisy *et al.*, 2010). However, it should be noted that it is only an occurrence of *Tapirus* sp. in North America that co-occurs with palaeobotanical evidence for temperate savanna (Voorhies, 1990). The Eurasian species; *T. balkaniscus* (N = 1), *T. jeanpiveteaui* (N = 1), *T. priscus* (N = 13) and *T. yunnanensis* (N = 2) were only found in forested habitats, which has been their established palaeoecology for some time (Guerin & Eisenmann, 1993).

6.3.11. The Chiroptera

The Chiroptera order (N = 42) during the Late Miocene had a mean BSI of 2.20, showing the order to be stenobiomic (Fig. 6.4k, Tab. 6.2). MAD records three Chiroptera families for the Late Miocene (Tab. 6.3) the Hipposideridae (mean BSI = 0; N = 3), Rhinolophidae (BSI = 2.00; N = 8) and the Vespertilionidae (BSI = 2.25; N = 31). The Rhinolophidae, recorded in MAD, contains only a single genus *Rhinolophus* (N = 8), which has been recorded occurring in warm – temperate mixed forest and temperate xerophytic shrubland. The Vespertilionidae is represented by 11 genera (Tab. 6.3), of which only four genera occur at more than one fossil locality. The genus *Eptesicus* (N = 6) is the most eurybiomic with a BSI score of 4, - occurring in tropical evergreen forests, warm – temperate mixed forests, temperate conifer forests and temperate xerophytic shrubland. *Myotis* (N = 14) is recorded in tropical evergreen forest, warm – temperate mixed forest and temperate xerophytic shrubland. *Paleptiscus* (N = 2) and *Plecotus* (N = 2) are both only recorded from a single biome, the former from warm – temperate mixed forests and the latter from tropical evergreen mixed forests.

6.3.12. The Litopterna

The Late Miocene mammals of the Litopterna order (N = 10) have a mean BSI of 1.00 (Tab. 6.2) and are strongly stenobiomic (Fig. 6.4l). However, the order is not very well represented in MAD with eight genera and only two of these occurring at more than one fossil locality. One of these genera, *Promacrauchenia* (N = 2) of the Macraucheniidae, does not occur in a grid cell containing palaeobotanical data. The only Macraucheniidae genus to be found in the same grid cell as palaeobotanical data was *Culinia* (N = 1), which inhabited tropical savannas. The Proterotheriidae contains five genera and only *Proterotherium* (N = 2) is found at more than one fossil locality containing tropical savanna. *Diadiaphorus* (N = 1) also inhabited tropical savanna but, as it is only recorded at a single locality it is not possible to say if it occurred in other biomes.

6.3.13. The Xenarthra

The Xenarthra order (N = 98) had a mean BSI of 1.36 during the Late Miocene (Tab. 6.2). The order was strongly stenobiomic with 95.5% of genera inhabiting one or two biomes (Fig. 6.4m). The most eurybiomic genus, within the Xenarthra, was *Proeuphractus* (N = 5) with a BSI of 3. The Dasypodidae (N = 39) had a mean BSI of 1.55, during the Late Miocene. This family contains 15 genera, four of which are only recorded in MAD at a single fossil locality. The Dasypodidae show a preference for open biomes with all genera being found in one of, or a combination of, tropical savanna, temperate savanna and temperate xerophytic shrubland.

The Glyptodontidae (N = 18) contained 11 genera (Tab. 6.3) during the Late Miocene, seven of which occur more than once in MAD. The family has a mean BSI of 1.14 showing it is strongly stenobiomic, only a single genus *Eosclerocalyptus* (N = 2) is found in two biomes. Like the Dasypodidae family the Glyptodontidae show a preference for open biomes, with genera inhabiting tropical savanna, temperate savanna and temperate xerophytic shrubland.

The Megalonychidae (N = 23) had a mean BSI of 1.50 during the Late Miocene (Tab. 6.3). The family contains four genera, two of which, *Megalonyx* (N = 11) and *Pliomorphus* (N = 2), are found in grid cells containing palaeobotanical evidence. *Megalonyx* had a BSI of 2 inhabiting temperate xerophytic shrubland and temperate savanna, whereas *Pliomorphus* only occurred in tropical savanna.

The fourth and final Xenarthra family recorded in the Late Miocene MAD is the Mylodontidae (N = 15). The Mylodontidae contained ten genera and had a mean BSI of 1.00, showing the group to be strongly stenobiomic (Tab. 6.3). Of these ten genera, five only occur once and a further three do not occur in grid cells containing palaeobotanical data. The other two genera: *Elassotherium* (N = 2) and *Urumacotherium* (N = 2) only inhabited a single biome. *Elassotherium* inhabited temperate savanna, whereas *Urumacotherium* occurred in tropical savanna.

6.3.14. The Notoungulata

The Notoungulata order (N = 28) had a mean BSI of 1.60 during the Late Miocene (Tab. 6.2; Fig. 6.4n). Three families are recorded in MAD: the Hegetotheriidae (N = 8), Mesotheriidae (N = 4) and the Toxodontidae (N = 16). The Hegetotheriidae contains four genera and is the least stenobiomic of the three Notoungulata families, with a mean BSI of 2.00 (Tab.3). Of the four genera *Pseudohegetotherium* and *Tremacyllus* are only recorded at a single fossil locality each. *Hemihegetotherium* (N = 2) and *Paedotherium* (N = 4) are both recorded at multiple fossil sites and both have a BSI of 2. *Hemihegetotherium* inhabited tropical savanna and temperate xerophytic shrubland, whereas *Paedotherium* occurred in both tropical and temperate savanna.

The Mesotheriidae contained two genera in the Late Miocene and had a mean BSI of 1.50 (Tab. 6.3). *Pseudotypotherium* (N = 2) occurred in tropical savanna and temperate xerophytic shrubland and is the more eurybiomic genus (BSI = 2). The other genus in the Mesotheriidae, *Typotheriopsis* (N = 2), was only found in tropical savanna (BSI = 1).

The Toxodontidae, during the Late Miocene, had a mean BSI of 1.00 and has 14 genera recorded in MAD (Tab. 6.3). However, only one of these 14 genera occurs at multiple fossil sites and within grid cells containing palaeobotanical data. *Xotodon* (N = 2) had a BSI of 1 and inhabited tropical savanna. A preference for tropical savanna can be seen in the genera that are only recorded from a single fossil site, except for *Calchaquitherium* which is found within a grid cell containing palaeobotanical data for both tropical evergreen forest and tropical savanna.

6.3.15. The Didelphimorpha

The Didelphimorpha order (N = 11) had a mean BSI of 1.00 for the Late Miocene (Tab. 6.2). The order is strongly stenobiomic (Fig. 6.4O). However, this may be an artefact of a group with a poor fossil record. The order contains a single family the Didelphidae, which in turn contains seven genera (Tab. 6.3). Of these seven genera only *Thylatherium* (N = 5) occurs at more than one fossil site and is associated with temperate savanna only.

6.4. Could mammals be used to reconstruct biomes?

The aim of this chapter was to investigate whether Late Miocene mammal distributions were controlled by biomes.The combination of a 407 locality mammal data set with a gridded version of the palaeobotanical data presented in Chapter 3, has shown that the global distribution of Late Miocene mammals was controlled by the distribution of biomes. Overall 69.7% of Late Miocene mammal genera inhabited only one or two biomes and a further 15.8% were found to co-occur with three biomes. These results match the first prediction of Hernández Fernández & Vrba (2005); that stenobiomic taxa should be more numerous than eurybiomic ones. This high proportion of stenobiomic taxa is comparable to the results of modern studies (Fig. 6.4). Although modern studies have focussed on Africa and South America the general proportion of taxa in each BSI classification is comparable to this current global study of the Late Miocene (Fig. 6.4). At the species level the Late Miocene shows a greater proportion of taxa inhabiting one biome than either of the modern studies (Fig. 6.4). Whether this is an artefact of the fossil record or related to sampling a larger geographic area will require future research.

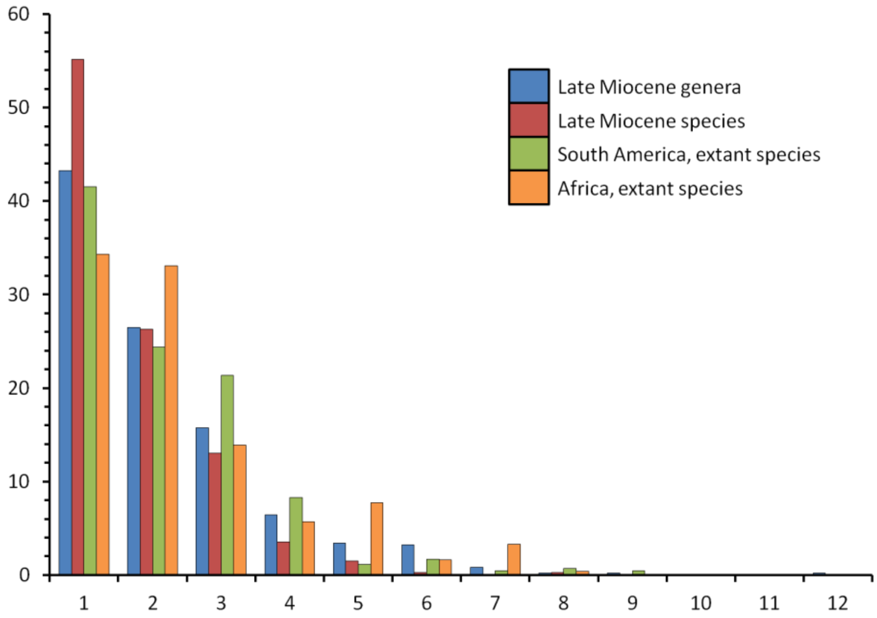


Figure 6.5. The percentage of mammals in each Biomic Specialisation Index category for the Late Miocene genera, species and for modern extant species. The extant species data is re plotted from Moreno Bofarull *et al.* (2008) and Hernández Fernández and Vrba (2005).

As most Late Miocene mammals are stenobiomic, to differing degrees, they have a good potential to be a new proxy for biomes. Some taxa will be more useful than others in reconstructing biomes. Based on the results presented in Section 6.3 members of the Artiodactyla, Lagomorpha, Lipotyphla, Primates, Rodentia and Xenarthra will be the most useful in reconstructing biomes, as these orders contain the greatest proportion of stenobiomic taxa. Within these orders certain families will be more useful in reconstructing biomes than other families. For example in the Rodentia the Cricetidae and Gliridae will probably be the most useful due to their low mean BSI scores and high number of taxa (Table 6.3). Whereas the Muridae has a large number of taxa but a slightly higher mean BSI score, implying that this family might not be as useful as others. At the opposite end of the BSI are taxa from the Carnivora, Perissodactyla and Proboscidea orders. These will probably be less definite in reconstructing biomes due to them containing more eurybiomic taxa (Table 6.2).

The results of undertaking a BSI survey of Late Miocene mammals suggests that it should be possible to use them to reconstruct biomes where palaeobotanical data does not exist. This is due to the high number of taxa specialised to one or two biomes. However, the degree of usefulness of using mammals to reconstruct biomes needs to be evaluated. For example if all the strongly stenobiomic taxa are specialised to the warm – temperate mixed forest. Then it is likely that using this data will result in a greatly improved geographic spread of the warm – temperate forest, but limited improvement towards our knowledge of other biome distributions. Overall the results presented in this chapter show there is a strong preference for mammals to only occupy a single biome (Table 6.4, Fig. 6.5). Of all the biomes the warm – temperate mixed forest contains the most stenobiomic genera (18.6%) followed by temperate savanna (15%), which is probably partly related to the excellent mammal and palaeobotanical data available from Eurasia and North America (Fig. 6.1, Fig. 6.2A). There is also a high proportion of stenobiomic taxa in the tropical savannah biome (Table 6.4). It should be expected that a higher proportion of stenobiomic genera would be present in tropical evergreen forest than were found in this study (Hernández Fernández & Vrba, 2005). Only 1.2% of all the global genera are restricted to tropical evergreen forest and only 6.3% of genera that inhabit this biome are restricted to it (Tab. 6.4). This is certainly an artefact of the fossil record. Within the Late Miocene mammalian fossil record there is a strong bias towards latitudes between 26°N and 55°N (Fig. 6.6). This means that of the current 407 localities in MAD only 10.5% occur between 25°S and 25°N, which represents the area occupied by the majority of the tropical biomes (Fig. 6.6). Thus the current Late Miocene mammalian fossil record is under – sampled in the tropical realm. However, the vast majority of Late Miocene mammal sites occupied a latitudinal belt between 26°N and 55°N, which contains a high number of biomes (Fig. 6.6). The only biomes not found in this latitudinal belt are the high latitude forests, tropical deciduous woodland and desert biomes (Fig. 6.7). Since the proportions of stenobiomic to eurybiomic taxa, in the Late Miocene, are comparable to the modern studies then this shows that the distribution of Late Miocene mammals were, partly, controlled by vegetation distribution (Fig. 6.5). This suggests that although the tropical realm is currently under-sampled, the results from this study are robust especially between the latitudes of 26°N and 55°N. In the next chapter a methodology will be developed to use these results to reconstruct Late Miocene biomes.

Biome combinations	**% of mammal genera**
Tropical evergreen forest	1.19
Tropical evergreen forest, Tropical deciduous woodland	2.57
Tropical evergreen forest, Warm - temperate mixed forest	2.77
Tropical evergreen forest, Warm - temperate mixed forest, Temperate deciduous broadleaf savanna	1.78
Tropical savanna	5.73
Tropical savanna, Temperate xerophytic shrubland	1.98
Tropical savanna, Temperate deciduous broadleaf savanna	2.17
Temperate xerophytic shrubland, Temperate deciduous broadleaf savanna	2.96
Temperate deciduous broadleaf savanna	15.02
Tropical grassland	0.99
Temperate deciduous forest, Temperate sclerophyll woodland, Temperate deciduous broadleaf savanna	1.38
Temperate deciduous forest, Warm - temperate mixed forest	0.99
Temperate deciduous forest, Warm - temperate mixed forest, Temperate deciduous broadleaf savanna	3.95
Temperate needleleaf forest	0.99
Warm - temperate mixed forest	18.58
Warm - temperate mixed forest, Temperate xerophytic shrubland	1.19
Warm - temperate mixed forest, Temperate xerophytic shrubland, Temperate deciduous broadleaf savanna	2.37
Warm - temperate mixed forest, Temperate deciduous broadleaf savanna	7.71
Warm - temperate mixed forest, Temperate deciduous broadleaf savanna, Temperate grassland	1.19

Table 6.4. Common biome combinations of Late Miocene mammals. This table only shows combinations of biomes that are inhabited by five (= 0.99%) or more genera. This accounts for 75% of the studied mammal genera, the other 25% of genera occupy less common biome combinations.

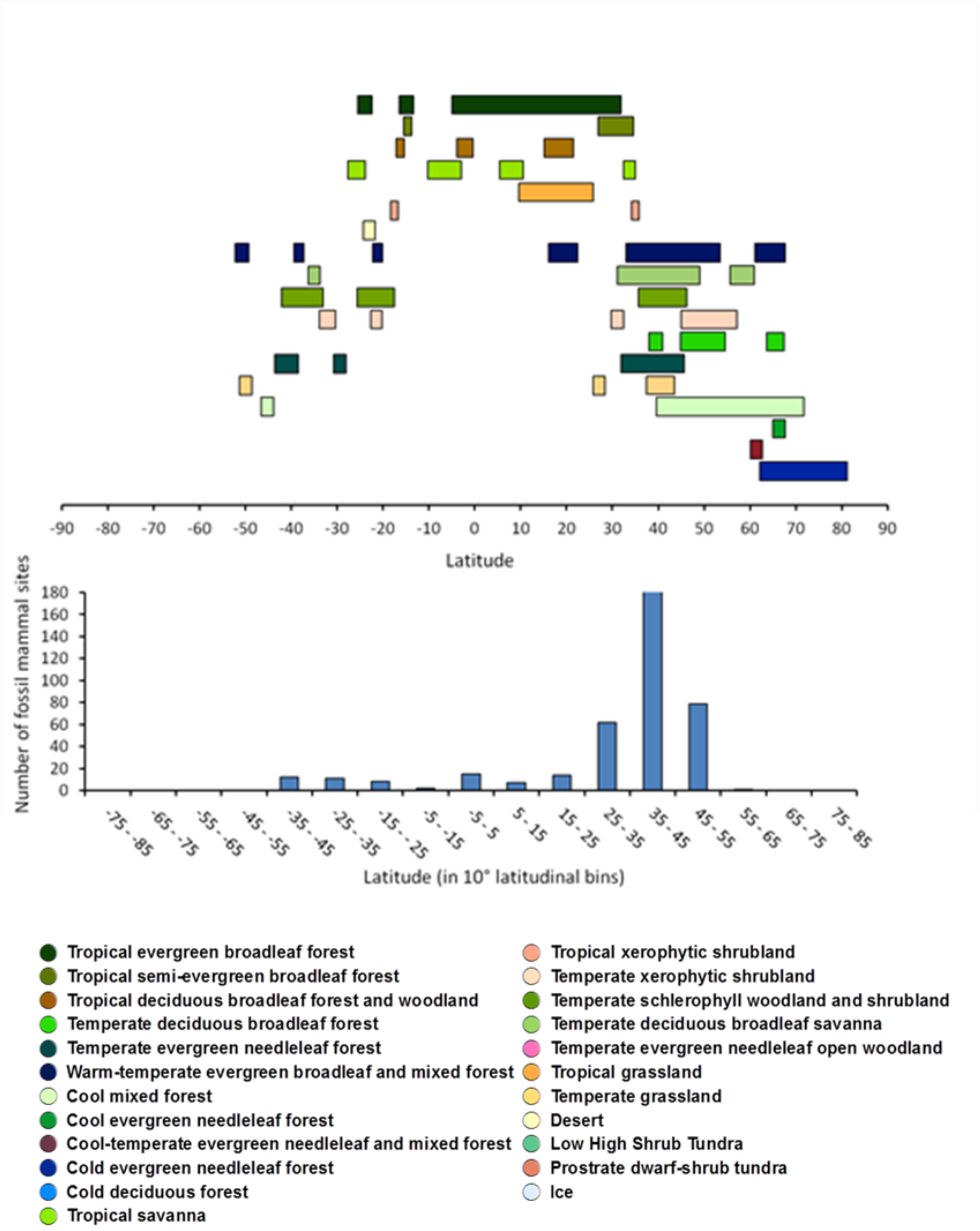


Figure 6.6. The Late Miocene latitudinal distribution of global biomes (Top) plotted from data presented in Chapter 3 compared to the latitudinal distribution of the 407 mammal fossil sites in the MAD (bottom). The distribution of mammal fossil sites is plotted in 10° latitude bins. This figure shows that although the majority of fossil mammal assemblages are concentrated between 25°N and 55°N, this is also an area of considerable biome diversity. However, it should also be noted that the low number of mammal sites in the tropics may limit the potential for identifying tropical stenobiomic taxa. The vertical scale for the biome distributions is semi-quantitative with warmest at the top to coldest at the bottom.

6.5. Conclusions

This chapter aimed to investigate whether Late Miocene mammal distributions were controlled by vegetation. Through the combination of 407 mammal localities and the vegetation data presented in Chapter 3, it has been shown that most Late Miocene mammals were controlled by vegetation. In total 69.7% of Late Miocene mammals inhabited only one or two biomes. This is a good indication that Late Miocene mammals can be used as a new means to reconstruct biomes. Increasing the available data with which model output can be evaluated and improving data – model hybrid vegetation maps.

In the following chapter a methodology will be developed to use the data presented here for the purpose of reconstructing biomes. The following chapter will also investigate if the proportion of stenobiomic taxa within each biome would have changed in response to climate.

Chapter 7
The use of Late Miocene mammals to reconstruct biomes

Tenrecs are unique to Madagascar, and striped tenrecs are only found in the eastern rainforests – David Attenborough

7.1. Introduction

In the previous chapter Late Miocene mammals were investigated to understand their palaeoecology and biome preferences. This showed that the majority (69.7%) of Late Miocene mammals were stenobiomic; inhabiting only one or two biomes. This high proportion of specialised mammals indicates that these fossils could be a valuable proxy for biomes. Chapter 3 showed that the palaeobotanical record for the Late Miocene contains significant geographical gaps. Despite this the data for the Tortonian was combined with output from HadAM3 – BIOME4 in Chapter 4, to produce a hybrid global vegetation map. Substantial areas of this map relied on model output. This could have introduced areas of model bias, which can result from inadequate boundary conditions. Within this chapter I present a novel technique to use fossil mammal assemblages to fill in geographical gaps in the palaeobotanical record. This will provide additional information of global vegetation distribution and from this a better understanding of Late Miocene climate.

Understanding the ecology of fossil mammals has come from understanding their diet and the environment within which they lived. This has often meant providing some information, for terrestrial mammals at least, on the local vegetation (e.g. Lambert, 1994; Lambert, 1997). Previously, techniques that have been used to reconstruct vegetation from mammals include: comparison to modern faunas (Guerin and Eisenmann, 1993; Solounias et al., 2010), isotopic studies (Cerling et al., 1997; Fox and Fisher, 2004; MacFadden, 1998), tooth wear analysis (Hayek et al., 1992; Merceron et al., 2010; Solounias et al., 2010; Townsend and Croft, 2008) and morphological relationships (Kaiser et al., 2003). Comparisons to modern examples range from single taxa e.g. Tapirs as forest dwellers (Guerin and Eisenmann, 1993) to facets of a fauna e.g. comparison of ungulate diversity to modern faunas (Solounias et al., 2010) to whole faunas e.g. the now obsolete view of the Pikermian fauna representing a savanna (Solounias and Dawson-Saunders, 1986 and references within). Isotopic studies have typically focused on carbon to estimate the amount of C_4 graze consumed by a mammal and how much grass was present in the local environment (Cerling et al., 1997; Fox and Fisher, 2004). Both macro- and meso- tooth wear analysis have been successfully employed to understand fossil mammal feeding habits and from this the vegetation that must have formed the habitat (Merceron et al., 2010; Solounias et al., 2010; Townsend and Croft, 2008). The morphological relationship between herbivorous mammal tooth height (hypsodonty) and the aridity of the local environment has been successfully employed in palaeoclimate studies (Fortelius et al., 2002; Tang et al., 2011). This technique does not provide information on vegetation but is a palaeoprecipitation proxy (Fortelius et al., 2002). It was believed that hypsodont dentition (high crowns) was related to the consumption of abrasive vegetation, whilst brachyodont dentitions (low crowns) was indicative of a browsing herbivore (Janis et al., 2004; Janis and Fortelius, 1988; Van Valen, 1960). However, recent work suggests that the degree of hypsodonty may relate to the amount of dust and grit consumed unintentionally, along with the food, which would still make this a palaeoprecipitation indicator (Hummel et al., 2010).

The new technique presented within this chapter uses the biome preferences of Late Miocene mammals (Chapter 6). By comparing the biome preference of each taxon within a fauna a biome, or combination of biomes, can be predicted for each mammal assemblage. This new technique provides biome information in regions were palaeobotanical data is lacking or absent.

7.2. The co-occurrence approach

Through the combination of TEVIS (Chapter 3) and MAD (Chapter 6) the biome preferences of 969 Late Miocene mammal genera has been determined (Chapter 6). Each Late Miocene mammal genus has a preference for a particular biome combination (Chapter 6). The majority (69.7%) of Late Miocene mammals were stenobiomic; inhabiting only one or two biomes (Chapter 6). These specialist genera are the most useful in reconstructing a mammal assemblage's biome habitat, as they have the most restrictive preferences. By comparing the biome preferences of all stenobiomic mammal genera (BSI of 1-4) in an assemblage a biome combination that all taxa can co – occur in can be derived (Fig. 7.1). This will be the smallest possible number of biomes, typically reflecting the most stenobiomic taxa preserved in an assemblage (Appendix E). For sites with only eurybiomic taxa, the biome preferences of these have been presented to suggest which biomes might have inhabited that area. This co – occurrence technique provides a method that is independent of morphology and nearest living relative.

Within this chapter the co – occurrence technique is applied to 233 Late Miocene localities that occur in regions lacking palaeobotanical data. These sites are divided into three, roughly equal, time slabs representing the early Tortonian (11.6 -9 Ma), late Tortonian (9 – 7.35 Ma) and the Messinian (7.35 – 5.33 Ma). Each site has had a biome combination reconstructed using the co – occurrence technique, these are plotted as either single biomes (where possible), or as multiple and/or biome combinations, where the co – occurrence of mammals reconstructs multiple biomes (Fig. 7.2). The biome classification scheme, used in this study, comes from the BIOME4 vegetation model (Kaplan, 2001). Using the BIOME4 27 biome classification scheme allows the data generated from mammals to be used in future palaeoclimate model evaluation studies of the same age.

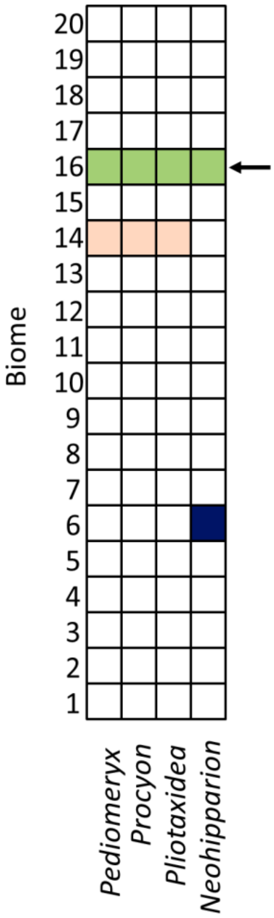


Figure 7.1. The co-occurrence technique of Turlock Lake, California (MAD Location ID 28; Wagner, 1976). The biome preferences for each stenobiomic mammal genus are shown and an arrow indicates the biome within which they could all co-occur.

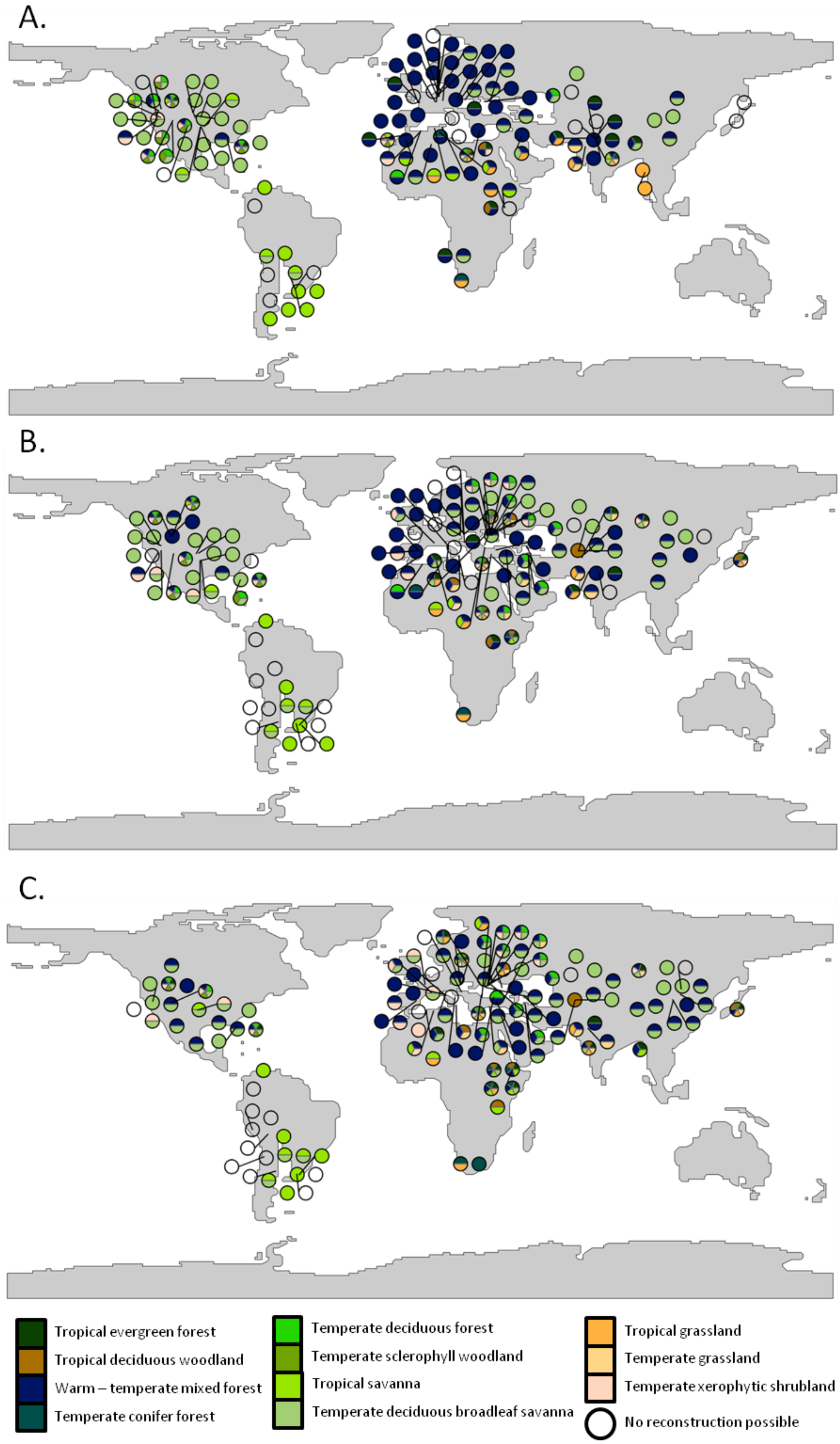


Figure 7.2. The mammal based biome reconstructions. A. The early Tortonian (11.6 – 9 Ma), B. The late Tortonian (9 – 7.35), C. The Messinian (7.35 – 5.33 Ma). The biomes are presented in the BIOME4 classification scheme (Kaplan, 2001).

7.3. Results

7.3.1. Testing the ability of mammals to be a proxy for vegetation

Of the 233 mammal assemblages subjected to the co-occurrence technique 76% reconstructed only one or two biomes (Fig. 7.3). This shows that by combining palaeobotanical data and fossil mammal data, mammals can be a proxy for vegetation. A further 15% reconstructed three or four biomes and the final 9% reconstructed between five and nine biomes (Fig. 7.3). There is little correlation between the number of mammalian taxa in a locality and the number of biomes reconstructed from them (Fig. 7.4). Although for mammal localities with fewer than five reported taxa the range of reconstructed biomes ranges from nought to nine, whereas when more than five taxa are reported the range drops to a maximum of six possible biomes (Fig. 7.4). Logically the number of reconstructed biomes shouldn't be related to the number of reported taxa. For example if three stenobiomic mammals are found at one locality then it will have a more accurate biome reconstruction than a locality with 50 eurybiomic taxa. However, as Chapter 6 showed there are considerably more stenobiomic Late Miocene mammals than eurybiomic ones. Of course the higher the number of reported taxa from a locality then the more complete a fauna should be. Both in terms of eurybiomic and stenobiomic taxa and this is reflected in the present results; only 16% of faunas with over 30 reported mammal genera reconstruct more than two biomes (Fig. 7.4).

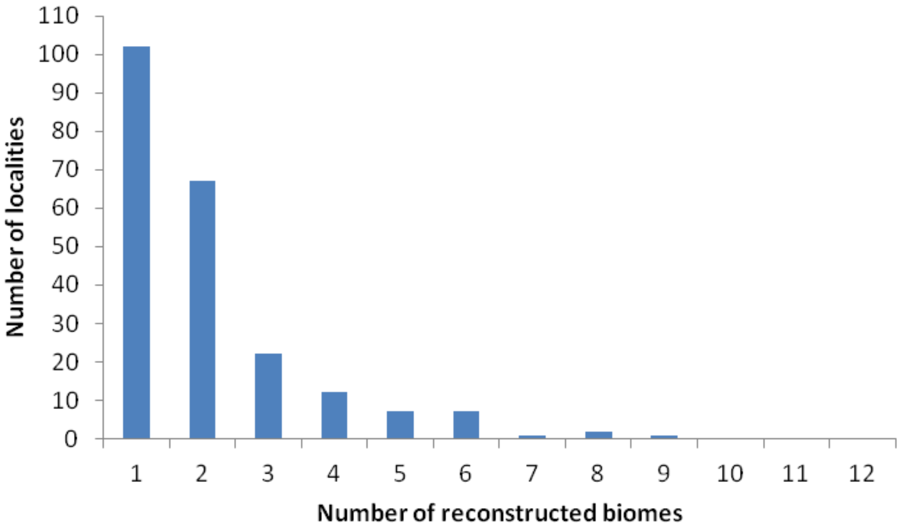


Figure 7.3. A graph to show the number of localities that reconstruct one or multiple biomes.

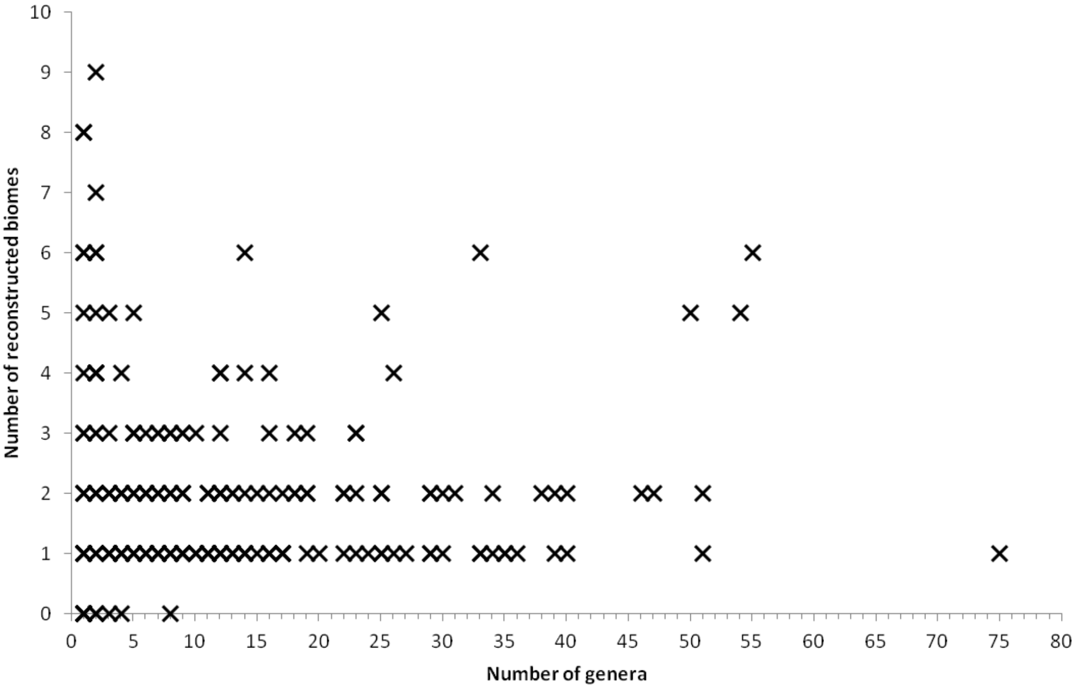


Figure 7.4. A graph to show the number of biomes reconstructed compared to the number of mammal genera in each assemblage.

In this chapter the 233 mammal localities reconstructed 13 biomes out of the BIOME4 27 biome classification scheme (Kaplan, 2001). Although this is only half the biomes in the BIOME4 classification scheme, the distribution of Late Miocene mammal fossil localities excludes the six cold biome types (e.g. cold evergreen needleleaf forest). Five tundra biomes are also excluded due to the limited distribution of tundra during the Late Miocene (Chapters 3 and 4). The three remaining biomes not reconstructed by the co-occurence approach are cool mixed forest, temperate evergreen needleleaf woodland and desert. The first of these, cool mixed forest, mainly inhabited higher latitudes during the Late Miocene, whilst the other two do not occur commonly in the Late Miocene (Chapter 3).

The most commonly reconstructed biomes, using the co-occurrence of mammals, are the warm – temperate mixed forest, temperate broadleaf savanna and tropical savanna (Fig. 7.2). These three biomes are commonly reconstructed as the only possible biome a mammal fauna could co-occur in (Fig. 7.2). To these three biomes, the temperate deciduous broadleaf forest, temperate evergreen needleaf forest, temperate sclerophyll woodland, temperate xerophytic shrubland, temperate grassland, tropical evergreen broadleaf forest, tropical deciduous broadleaf woodland and tropical grassland are added to the reconstruction at fossil mammal localities where the fauna could co-occur in either or both of two biomes (Fig. 7.2). Finally, tropical semi-evergreen broadleaf forests and tropical xerophytic shrubland are only reconstructed at mammal localities where co-occurrence could have been in more than two biomes.

7.3.2. Late Miocene mammal distributions and derived global vegetation patterns

This section will present the vegetation patterns reconstructed using the co-occurrence of Late Miocene mammals (Fig. 7.2). Each mammal assemblage contains a co-occurrence of biome specialists and generalists (Chapter 6). The reconstructed vegetation represents the minimum number of biomes where all taxa at a locality could have co-occurred.

7.3.2.1. North America

During the early Tortonian in North America, the co-occurrence of mammals has reconstructed mainly the temperate broadleaf savanna biome (Fig. 7.2A). On the west side of North America (west of 108°W) the biomes reconstructed from mammals are more diverse, north of 42°N the reconstructed biomes are a combination of temperate deciduous forest, temperate xerophytic shrubland, temperate sclerophyll woodland and temperate broadleaf savanna (Fig. 7.2A). Between 38° - 42°N the reconstructed biomes are a combination of warm – temperate mixed forest, temperate broadleaf savanna and temperate xerophytic shrubland (Fig. 7.2A). South of 38°N the biomes return to a combination of temperate deciduous forest, temperate broadleaf savanna, temperate sclerophyll and temperate xerophytic shrubland (Fig. 7.2A). By the late Tortonian the biomes reconstructed using mammalian faunas show a strong signal towards the temperate broadleaf savanna biome (Fig. 7.2B). North of 45°N, and between 108 - 112°W, the mammal based reconstructions show the presence of warm – temperate mixed forest and temperate deciduous savanna (Fig. 7.2B). South of 45°N and west of 112°W the co-occurrence of mammalian genera indicates the presence of temperate deciduous savanna and minor amounts of warm – temperate mixed forest and temperate xerophytic shrubland (Fig. 7.2B). During the Messinian the vegetation reconstructed from the co-occurrence of mammals shows that west of 114°W temperate deciduous savanna was dominant to 39°N with areas of temperate xerophytic shrubland further south (Fig. 7.2C). East of 114°W to 104°W, the reconstructed biomes are a combination of warm – temperate mixed forests and temperate deciduous savanna (Fig. 7.2C).

In central North America between 103°W and 93°W the vegetation reconstructed from mammals shows that temperate deciduous broadleaf savanna was the dominant vegetation type, for all three studied time slabs (Fig. 7.2). There is also evidence for a drier area of temperate xerophytic shrubland south of 36°N from 9 Ma (Fig. 7.2B). The temperate deciduous savanna biome was also present in the south-east region of North America (Fig. 7.2). The vegetation reconstruction, based on the mammal co-occurrence technique, also shows the presence of warm – temperate mixed forests south of 30°N (Fig. 7.2) and possibly more diverse biomes on the Late Miocene Florida Peninsula (Fig. 7.2B).

7.3.2.2. South America

Reconstructions of vegetation, using the co-occurrence technique, are concentrated in southern South America, except for one site in the north (Fig. 7.2). All mammal based vegetation reconstructions in South America show either tropical savanna or temperate deciduous broadleaf savanna (Fig. 7.2).

7.3.2.3. Eurasia, west of the Paratethys Sea

During the early Tortonian in western Eurasia, mammal based vegetation reconstructions are dominated by the warm – temperate mixed forest biome from 10°W to 33°E (Fig. 7.2A). Other biome combinations reconstructed by the mammal co-occurrence technique show the possible presence of temperate deciduous broadleaf savanna east of 33°E (Fig. 7.2A). The mammal reconstructed combination of tropical evergreen broadleaf forest and/or warm – temperate mixed forest reflects mammal genera that require dense, warm and wet forests, rather than suggesting the presence of tropical evergreen broadleaf forest in Europe during the early Tortonian (Fig. 7.2A).

The mammal based vegetation reconstructions for the late Tortonian show more diverse biome combinations than during the preceding time slab (Fig. 7.2B). The Iberian Peninsula now contained temperate xerophytic shrubland as well as the warm – temperate mixed forest, the shrubland biome is also present in southern France during the late Tortonian (Fig. 7.2B). East of 9°E temperate deciduous broadleaf forest and savanna are also reconstructed from the co-occurrence of mammals (Fig. 7.2B).

By the Messinian the reconstructed biome combinations are showing further change from the warm – temperate mixed forests that dominated during the early Tortonian (Fig. 7.2C). The main differences from the late Tortonian are the presence of temperate xerophytic shrubland and/or temperate deciduous broadleaf savanna in central France and central Italy (Fig. 7.2C). In the region of Turkey, Iraq and Iran mammal faunas consistently reconstruct a combination of warm – temperate mixed forest, temperate deciduous broadleaf forest, temperate deciduous broadleaf savanna and/ or temperate grassland (Fig. 7.2C).

7.3.2.4. North Africa

The majority of data for North Africa comes from coastal Morocco, Algeria and Tunisia (Fig. 7.2). During the early Tortonian the vegetation reconstructed from mammal assemblages shows a diverse combination of biomes including tropical savanna, tropical grassland, temperate deciduous broadleaf forest and temperate evergreen conifer forest (Fig. 7.2A). Despite this wide ranging combination of climate and vegetation types there is one consistent biome between all the mammal based reconstructions; the warm – temperate mixed forest biome is always reconstructed (Fig. 7.2A). A similar pattern can be seen during the late Tortonian (Fig. 7.2B). However, by the Messinian the mammal based vegetation reconstructions show the presence of more xerophytic shrubland (Fig. 7.2C).

Other sites in North Africa, during the oldest time slab studied, show evidence for warm – temperate mixed forest and/or temperate deciduous broadleaf savanna at 28°N, an area that is desert today (Fig. 7.2A). At 26°N, in Egypt a microvertebrate mammal assemblage reconstructs tropical evergreen broadleaf forest, tropical deciduous broadleaf woodland, warm – temperate mixed forest and/or temperate xerophytic shrubland (Fig. 7.2A). A mammal assemblage from 14°N shows the presence of tropical savanna and/or tropical grassland during the Late Miocene (Fig. 7.2).

7.3.2.5. Central and southern Africa

There are very few mammal sites in central and southern Africa (Fig. 7.2). During the early Tortonian the results from the co-occurrence technique shows evidence for tropical evergreen broadleaf forest, tropical deciduous broadleaf forest and tropical savanna around the equator (Fig. 7.2A). Further south in Namibia two microvertebrate assemblages show evidence for the presence of tropical or warm – temperate forests and/or temperate deciduous broadleaf savanna (Fig. 7.2A). In South Africa a mammal assemblage has provided evidence for temperate evergreen conifer forest and/or tropical grassland (Fig. 7.2A).

The late Tortonian and the Messinian both have only two mammal assemblages each. The older of the two has one mammal assemblage near the equator that reconstructs tropical evergreen broadleaf forest and/or tropical deciduous broadleaf woodland and a second in South Africa that shows the presence of temperate evergreen conifer forest and tropical grassland (Fig. 7.2B). The younger has one site at 4°S that reconstructs tropical deciduous broadleaf woodland or tropical savanna and another in South Africa evidence for temperate evergreen conifer forest and tropical grassland (Fig. 7.2C).

7.3.2.6. Eurasia, east of the Paratethys Sea

During the 11 – 9 Ma time slab there is mammal based evidence between 57 - 68°E and east of 104°E (Fig. 7.2A). The vegetation, reconstructed from mammal assemblages, between 57 - 68°E shows the presence of warm – temperate mixed forest, temperate deciduous broadleaf forest and temperate deciduous broadleaf savanna (Fig. 7.2A). East of 104°E the mammal based vegetation reconstructions show the presence of warm – temperate mixed forests and temperate deciduous broadleaf savanna (Fig. 7.2A).

The data for the late Tortonian covers a slightly larger geographic area than the preceding time slab, and there is only a gap between 74°E and 102°E (Fig. 7.2B). All the mammal assemblages reconstruct warm – temperate mixed forest, temperate deciduous broadleaf forest and temperate deciduous broadleaf savanna across the eastern portion of Eurasia (Fig. 7.2B). This is the same for the Messinian except that there is evidence for warm – temperate mixed forests and temperate deciduous broadleaf savanna at 84°E (Fig. 7.2C).

7.3.2.7. The Indian subcontinent and South-east Asia

During the early Tortonian vegetation reconstructions from mammal assemblages show the presence of tropical evergreen broadleaf forest, warm – temperate mixed forest, temperate deciduous broadleaf savanna and tropical grassland north of 28°N (Fig. 7.2A). South of 28°N there was tropical grassland in south - east Asia and warm – temperate mixed forest and/ or grassland on the Indian subcontinent (Fig. 7.2A). This pattern is largely the same for the late Tortonian except there is no evidence in south-east Asia south of 26°N, where a mammal assemblage reconstructs warm – temperate mixed forest and temperate deciduous broadleaf savanna (Fig. 7.2B). During the Messinian the pattern on the Indian subcontinent is again the same, this is most likely due to low resolution dating of the assemblages used in the reconstruction technique. In south – east Asia a mammal assemblage reconstructs tropical evergreen broadleaf forest, warm – temperate mixed forest and/or tropical savanna (Fig. 7.2C).

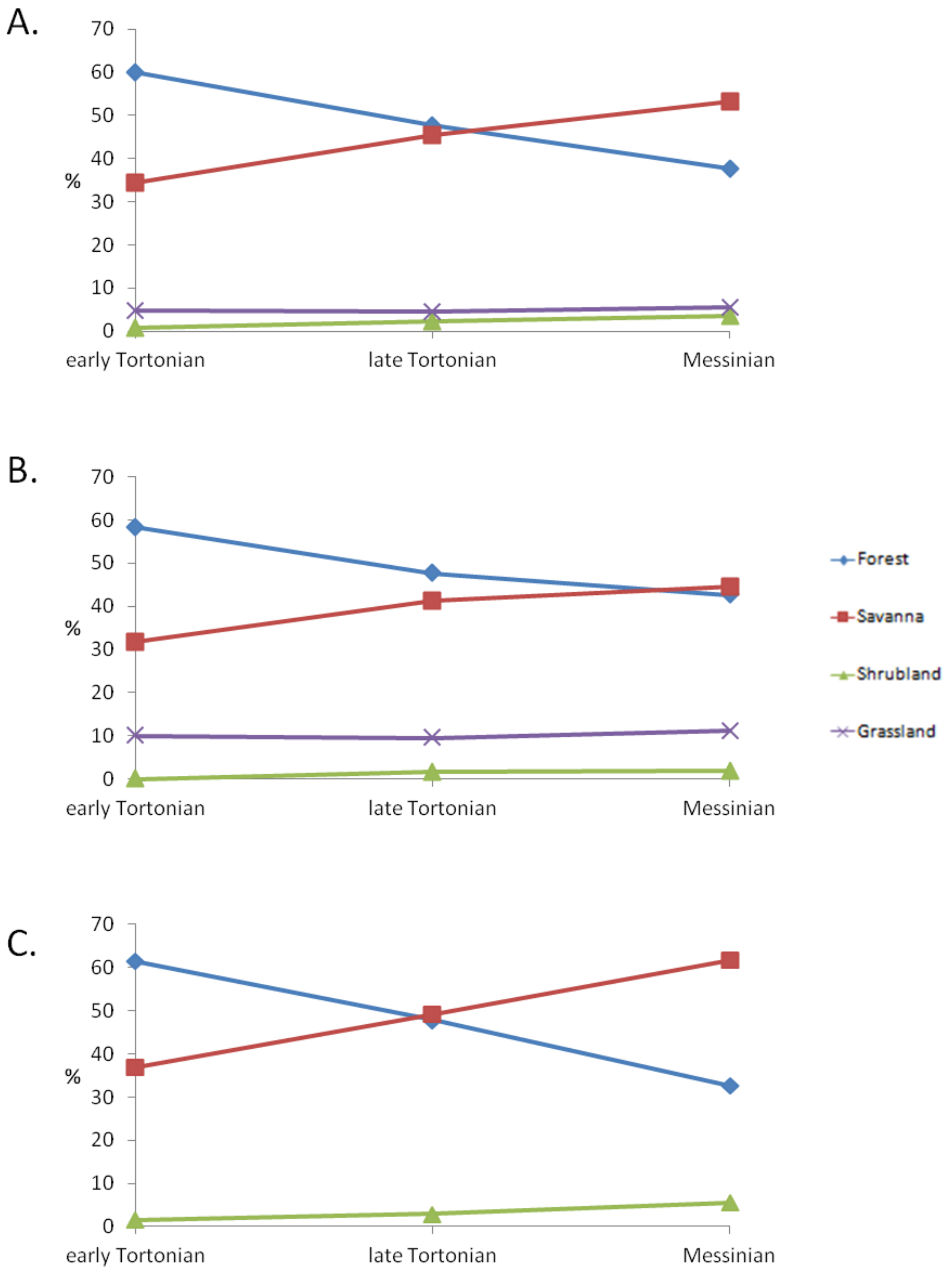


Figure 7.5. The global change in the percentage of stenobiomic mammal genera within four biome types. A. All non – carnivore genera, B. Macrovertebrate genera (Orders: Artiodactyla + Lagomorpha + Perissodactyla + Proboscidea) and C. Microvertebrate genera (Orders: Lipotyphla + Rodentia).

7.3.3. Changes in biome preferences of mammal genera during the Late Miocene

Through the three time slabs of the Late Miocene, used in this study, there are changes in the proportion of stenobiomic genera in each biome (Fig. 7.5). Looking at all stenobiomic mammal genera, excluding the Carnivora and Chiroptera orders, there is a decrease in forest adapted genera and an increase in savanna specialists (Fig. 7.5A). There is also a very small increase in the number of shrubland specialists (Fig. 7.5A). The Carnivora have been excluded from this analysis as, not only do they contain a very high proportion of eurybiomic genera, but the Mustelidae and Viverridae families are underrepresented in the fossil record (Pasitschniak-Arts and Larivière, 1995; Chapter 6). The Chiroptera were also excluded because they to have a poor fossil record (Eiting and Gunnell, 2009).

During the early Tortonian time slab around 60% of stenobiomic mammal genera were specialised for forests (Fig. 7.5A). By the late Tortonian the proportion of stenobiomic mammals specialised for forests had reduced, whilst the amount of mammals adapted for savanna biomes had increased to a comparable level to forest specialists (Fig. 7.5A). This trend continued through the Messinian. However, there were now 53% of stenobiomic genera adapted for savanna biomes and only 37% of genera specialised for forest biomes. If the stenobiomic genera are divided into macromammals (Artiodactyla, Lagomorpha, Perissodactyla and Proboscidea) and micromammals (Lipotyphla and Rodentia) then the overall trend remains the same but the timing of the change differs (Fig. 7.5B,C). The macromammals show a slower change from being predominantly forest biome specialists to being savanna biome specialists (Fig. 7.5B). Whereas, the micromammals show this change from the forest biome stenobiomic genera to savanna biome specialists during the late Tortonian (Fig. 7.5C).

This change from more mammal genera being specialised for forest biomes did not occur uniformly across the world (Fig. 7.6). In Western Europe the stenobiomic mammal genera remain predominantly forest specialists throughout the Late Miocene (Fig. 7.6). However, there is a reduction in the number of forest biome specialist mammal genera from 92% to 74%, whilst there is an increase in the amount of stenobiomic mammal genera adapted for savanna, shrubland and grassland biomes (Fig. 7.6). In the region of Greece, Turkey and the Middle East the amount of stenobiomic genera, adapted for forest biomes, drops from 65% in the early Tortonian to 47% in the Messinian. Whilst the amount of savanna biome specialists increases from 21% in the early Tortonian to 41% in the Messinian (Fig. 7.6). The East Asia region shows that in the early Tortonian the proportion of stenobiomic genera in forest and savanna biomes was almost even (Fig. 7.6). By the late Tortonian the savanna biomes contained more stenobiomic genera than the forest biomes. This increased to 55% of stenobiomic mammals inhabiting savanna biomes in East Asia, whilst only 35% were specialised for forest biomes, during the Messinian (Fig. 7.6). On the Indian subcontinent there continued to be more stenobiomic mammals inhabiting forest biomes, than savanna or grassland, throughout the Late Miocene (Fig. 7.6). However, there appears to be a gradual decrease in the proportion of forest specialists and an increase in specialists of the other biome types (Fig. 7.6). Africa shows a similar pattern to many other regions in the world; in that during the early Tortonian forest biome specialists are more numerous. By the late Tortonian the proportion of forest and savanna stenobiomic mammals is almost equal and, although there is a slight increase in forest specialists during the Messinian, this trend continues through to the end of the Miocene (Fig. 7.6). The one region that shows a dramatically different trend, when compared to the rest of the studied regions, is North America (Fig. 7.6). In North America, savanna biome specialists are the dominant stenobiomic mammals (92 – 93%) throughout the Late Miocene (Fig. 7.6).

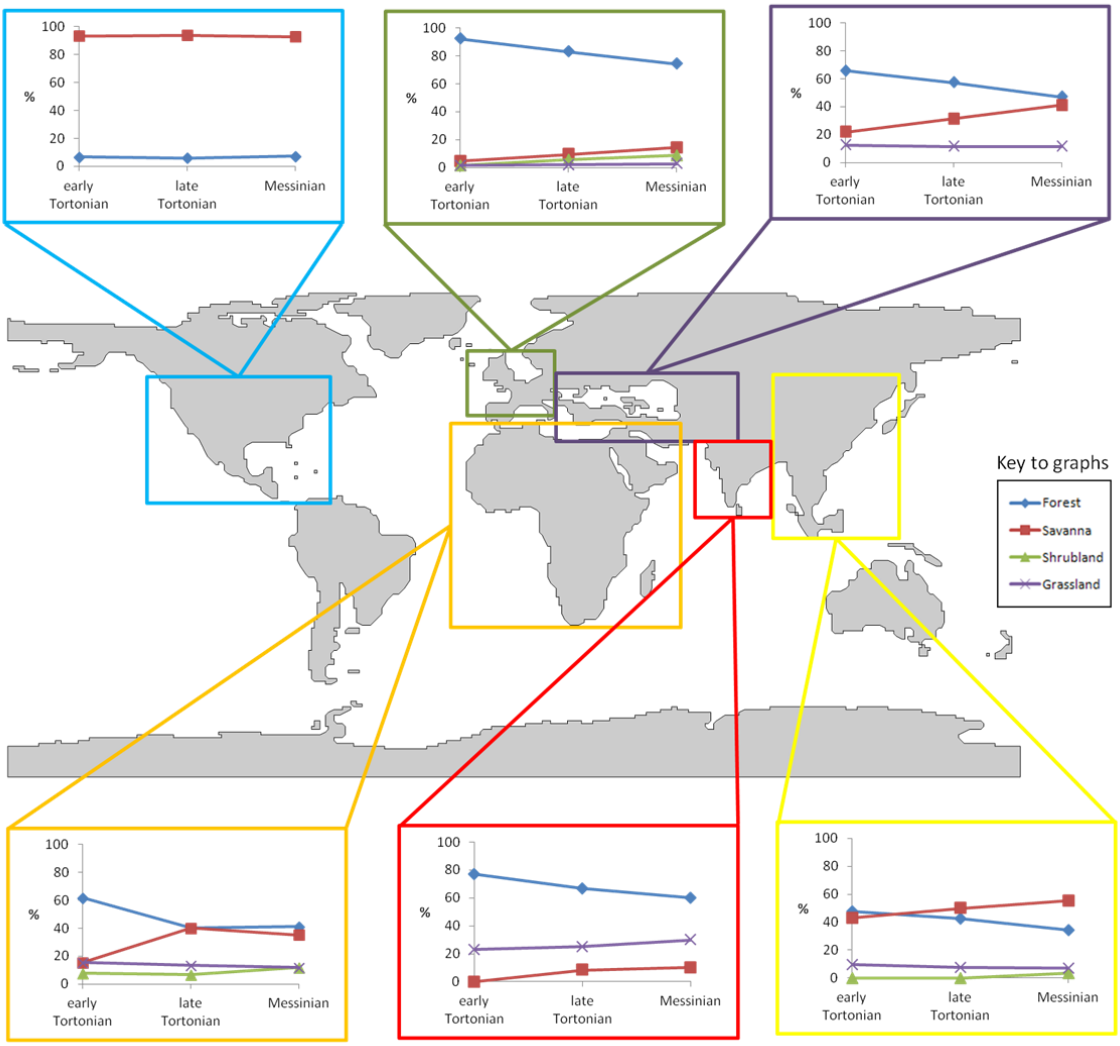


Figure 7.6. The regional changes in the percentage of all non - carnivore stenobiomic mammal genera within four biome types. Blue: North America, Green: Europe, Purple: Greece – Turkey – Middle East, Yellow: East Eurasia, Red: Indian subcontinent and Orange: Africa.

7.4. Discussion of mammal based biome reconstructions and comparison with global vegetation patterns

From the co-occurrence of mammalian genera within an assemblage from 233 localities Late Miocene vegetation has been reconstructed. The vegetation reconstructed from mammalian assemblages shows change from the early Tortonian to the Messinian. Both in terms of the reconstructed biomes (Fig. 7.2) and the proportion of stenobiomic genera specialised for particular biome types (Fig. 7.6). The co-occurrence biome reconstructions are based on the distribution of mammal genera and the distribution of palaeobotanical data (Chapters 3 and 6). The 233 localities used in this study did not overlap with palaeobotanical data and thus have provided information on the gaps in this important climate proxy record. Since the mammal based biome reconstructions have been done in the BIOME4 classification scheme (Kaplan, 2001) it is easy to compare them to and incorporate them into future data – model hybrid vegetation reconstructions (Micheels, 2003; Salzmann et al., 2008; Chapter 4).

Overall the pattern of Late Miocene vegetation is one that is warmer and wetter than the pre – industrial and modern potential natural (Micheels et al., 2007). During the Late Miocene there is a cooling and drying of the global vegetation with reduction in forests, particularly the warm – temperate mixed forest, and an expansion of savanna, grasslands, shrublands and desert (Potter and Szatmari, 2009; Sun et al., 2009; Chapter 3). These global patterns of vegetation, from palaeobotanical data and modelling studies, are also seen in the mammal based vegetation reconstructions (Fig. 7.2) and in the proportion of specialist mammals adapted to different biome types (Fig. 7.6).

At a regional scale the mammal based vegetation reconstructions compare well to reconstructions from palaeobotanical data and to modelling studies. In west North America mammal based reconstructions show the presence of diverse biomes ranging from warm – temperate mixed forests to temperate xerophytic shrublands (Fig. 7.2). This diverse patchwork biome pattern in western North America is also seen in the palaeobotanical data (Chapter 3). Furthermore, this mosaic environment shows a reduction in forest biomes and an increase in drier and/or cooler biomes from the Tortonian through the Messinian (Chapter 3). This is also seen in the mammal based reconstructions; the early Tortonian contains more reconstructed forest biomes than the late Tortonian and the Messinian (Fig. 7.2). In central and eastern North America, the palaeobotanical data shows the presence of a large region of temperate savanna, with temperate forests towards the Rocky Mountains and warm – temperate mixed forest along the south and east coasts (Chapter 3). In contrast, vegetation modelling studies tend to reconstruct a greater degree of forests in this region (François et al., 2006; Micheels et al., 2007; Chapter 4). The mammal based vegetation reconstructions show a similar pattern to the palaeobotanical data; a large region of temperate deciduous broadleaf savanna, possibly with temperate xerophytic shrublands south of 35°N, with forest type biomes towards the south and east coasts (Fig. 7.2) (Gabel et al., 1998; McCartan et al., 1990; Schiebout et al., 1996; Chapter 3). In South America, mammal assemblages reconstruct temperate and tropical savanna biomes (Fig. 7.2). This is in agreement with the palaeobotanical data (Barreda et al., 2007; Chapter 3). However, model based reconstructions either have too much forest type biomes (François et al., 2006; Micheels et al., 2007) or too great an expanse of xerophytic shrublands (Chapter 4).

In Western Europe, during the early Tortonian, the mammal based vegetation reconstructions show a predominance of warm – temperate mixed forests (Fig. 7.2A). From the late Tortonian drier and more open biomes become more commonly reconstructed (Fig. 7.2B). Though based on the stenobiomic mammals, Western Europe remains predominantly forest throughout the Late Miocene, as the proportion of forest specialist mammals remains greater than other biome types (Fig. 7.6). This is consistent with palaeobotanical data from the younger Piacenzian Age, which shows the warm – temperate mixed forest still present in Western Europe between 3.6 – 2.6 Ma (Salzmann et al., 2008). The change in biomes reconstructed from mammals is consistent with hypothesised vegetation change based on herbivore tooth wear analysis; the study showed a slight increase in overall diet abrasiveness and a significant increase in microwear from the early to the late Tortonian (Merceron et al., 2010).

Comparing the mammal based biome reconstructions with the regional palaeobotanical data shows a good agreement. The palaeobotanical data in Western Europe during the Late Miocene was predominantly warm – temperate mixed forests (Chapters 3) and vegetation modelling studies agree with this (François et al., 2006; Micheels et al., 2007). The pollen assemblages of these warm – temperate mixed forests often contain a significant herbaceous and grass component, these are believed to be from the forest understory, small open areas or disturbed ground (Harzhauser et al. 2008; von der Brelie and Wolf 1981; Chapter 2). Although the mammals do reconstruct warm – temperate mixed forests in Western Europe they also reconstruct more open biomes such as temperate savanna, temperate grassland and temperate xerophytic shrubland (Fig. 7.2). This would seem to contradict the palaeobotanical data however, it may well be a question of scale; do mammals reconstruct regional vegetation, as pollen does (Moore et al., 1992), or do they reconstruct more local environments? It is beyond the scope of this study to answer this question, but a combined study of mammals, palaeobotany, palynology and sedimentology, at the basin to regional scale, might provide some insights into this uncertainty.

In the region of Greece, Turkey and the Middle East, mammal based vegetation reconstructions show the presence of a mosaic environment, composed of warm – temperate mixed forest, temperate deciduous broadleaf forest, temperate evergreen conifer forest, temperate deciduous broadleaf savanna and temperate grassland (Fig. 7.2). This region also shows dramatic change in the proportion of stenobiomic genera specialised for particular biome types; in the early Tortonian the majority of stenobiomic taxa are adapted for forests, by the Messinian it is an even split between forest and savanna biome specialists (Fig. 7.6). Palaeobotanical data shows a mosaic of warm – temperate mixed forests and temperate deciduous savanna, with minor amounts of temperate deciduous broadleaf forest (Solounias and Dawson-Saunders, 1986; Chapter 3). There is a reasonable agreement from modelling studies which also reconstruct a mosaic of biomes in this region (François et al., 2006; Micheels et al., 2007).

The North African region has a sparse palaeobotanical record for the Late Miocene (Chapter 3). The mammal based vegetation records thus provide a valuable source of biome information for this region. The limited palaeobotanical information available for the Late Miocene of North Africa shows the presence of tropical savanna, tropical xerophytic shrubland and temperate sclerophyll woodland (Favre et al., 2007; Chapter 3). Despite the limited palaeobotanical information for North Africa the sedimentology of the region was predominantly fluvial during the Late Miocene (Swezey, 2009), suggesting more active hydrology in the region. Model based studies of the Late Miocene reflect this by reconstructing limited, or no, regions of desert (François et al., 2006; Micheels et al., 2007). The mammal based reconstructions are mostly around the coast of this region and show a mixture of forest, woodland, savanna and shrubland biome types (Fig. 7.2). The co-occurrence of mammals sometimes reconstructs multiple possible biomes in North Africa (Fig. 7.2). Despite this source of uncertainty, most likely from the small number of taxa preserved at each locality, there is drying trend from the early Tortonian to the Messinian with drier more open biomes being reconstructed towards the Messinian (Fig. 7.2). This is also confirmed by the proportion of stenobiomic taxa in this region that are adapted to savanna and shrubland biomes; 40% in the early Tortonian, increasing to >80% from the late Tortonian.

Central and southern Africa have limited palaeobotanical information for the Late Miocene and the co – occurrence of mammals could provide useful biome reconstructions (Jacobs et al., 2010; Chapter 3). In Central Africa the mammal based biome reconstructions show the presence of tropical evergreen broadleaf forests, tropical savanna and tropical grassland (Fig. 7.2). The reconstruction of warm – temperate mixed forest could be erroneous, and maybe related to a mammal that inhabits warm and humid forests. Palaeobotanical evidence for

Central Africa shows the presence of tropical forest biomes, tropical savanna and tropical grassland (Jacobs et al., 2010; Chapter 3). This is in good agreement with the biomes that have been reconstructed from the co - occurrence of mammals (Fig. 7.2). Mammal sites from Southern Africa reconstruct tropical evergreen broadleaf forest, warm – temperate mixed forest and temperate deciduous broadleaf savanna in Namibia (Fig. 7.2). In South Africa temperate evergreen conifer forest and tropical grassland has been reconstructed from the co – occurrence of Late Miocene mammals (Fig. 7.2). The reconstructions in Namibia are not in agreement with the palaeobotanical information gained from DSDP Leg 75, which showed the presence of xerophytic shrubland in Namibia during the Late Miocene (van Zinderen Bakker Sr., 1980) This would also contradict the history of the Namib desert, which is considered to have been arid from Ca. 16 Ma (Senut et al., 2009). However, the fossil mammals used in the co – occurrence approach are from the Otavi Mountains, Namibia (Mein et al., 2000; Rasmussen et al., 1996). Today this region is one of the wettest places in Namibia (Cramer and Leemans, 2001) and so the reconstruction from the mammal fauna may represent a local vegetation signal, whereas that recovered from DSDP Leg 75 may be a more regional signal. In South Africa palaeobotanical information shows the presence of temperate evergreen conifer forest biome, which is in good agreement with the mammal based reconstructions (Chapter 3).

On the Indian sub continent the co – occurrence of Late Miocene mammals reconstructs tropical evergreen broadleaf forest, warm – temperate mixed forest, tropical grassland and temperate grassland biomes (Fig. 7.2). The reconstructed forests are from the foothills of the Himalayas and are in good agreement with palaeobotanical data (Banerjee, 1968; Chapter 3; Prasad and Pradhan, 1998). The fossil mammal sites located further south, which reconstruct the presence of grassland, come from a region with poor palaeobotanical data (Chapter 3). However, the presence of some areas of grassland has been suggested from stable carbon isotope analysis, showing the spread of C_4 grasses during the late Tortonian through Pliocene (Cerling et al., 1997; Sanyal et al., 2010). Modelling studies have shown the Indian subcontinent as, a mixture of warm grassland, tropical seasonal forest and tropical evergreen forest (Micheels et al., 2007), or as predominantly tropical seasonal forest (François et al., 2006). The former would appear to be more compatible with both the palaeobotanical data and the co – occurrence of mammal results.

Mammal based reconstructions for eastern Eurasia show the presence of warm – temperate mixed forests and temperate deciduous broadleaf savanna north of 28°N, with tropical evergreen forest, warm – temperate mixed forest, tropical savanna and tropical grassland further south (Fig. 7.2). Palaeobotanical information is very good for this region and shows a biome distribution and change through the Late Miocene that is mirrored by the mammal based reconstructions (Wang, 1992; Chapter 3). In this region the change in Late Miocene biomes shows the expansion of drier, more open vegetation at the expense of forests (Wang, 1992; Chapter 3). Not only is this reflected in the mammal based co – occurrence reconstructions, but the proportion of stenobiomic taxa in each biome type changes from forest to savanna dominated (Fig. 7.6). Model based vegetation reconstructions show this region as being mainly forested, which is not in agreement with palaeobotanical information, nor the mammal based reconstructions (François et al., 2006; Micheels et al., 2007).

7.5. Summary and conclusions

The co – occurrence of mammals, at a fossil site, can be used to reconstruct vegetation. From the biome preferences of each mammal genus the vegetation under which all the assemblage could co - habit has been calculated (Fig. 7.2). This technique when applied to 233 Late Miocene localities, in areas without palaeobotanical information, reconstructed one or two biomes for 76% of the mammal assemblages (Fig. 7.3). The technique does not require a large number of taxa to be found, though for assemblages with fewer than five genera the number of reconstructed biomes can be large (Fig. 7.4). In this study the biome reconstructions from the co – occurrence of mammal genera has provided valuable information on vegetation from regions that have poor palaeobotanical information (Fig. 7.2). In regions that do have palaeobotanical information the biome reconstructions from the co – occurrence of mammals is complimentary. However, at some localities the mammal based reconstructions may provide a more local rather than regional biome signal. In this study examples of this local rather than regional scale are rare, but future work should investigate this anomaly at the basin to inter – basin level. Not only do the biome reconstructions from the co – occurrence of mammals compare well to regional palaeobotanical data, when possible. But the change in the proportion of stenobiomic taxa adapted for a particular biome type changes through time, reflecting the global changes in vegetation (Fig. 7.6).

This technique provides another tool to reconstruct fossil mammal palaeoenvironments, to provide more information for global vegetation studies and more data to evaluate palaeoclimate modelling studies. This novel technique is complimentary to previous techniques that relied on morphology (Fortelius et al., 2002; Tang et al., 2011), isotopes (Cerling et al., 1997; Fox and Fisher, 2004) and tooth wear (Merceron et al., 2010; Solounias et al., 2010). It should however be of more use to compare fossil mammals with palaeobotanical information, than to compare fossil mammal assemblages with modern equivalents because not only is the majority of the modern world anthropogenically altered (Ellis, 2011) but millions of years of the evolution created a modern world with a biosphere as unique as any in the geological past. Though inferences of diet and habitat can be made on nearest living relatives it should be used with caution. For example the modern world contains a strong bias towards ruminant grazers, this does not necessarily mean that every member of these clades has been a grazer in the geological past (Janis, 2008).

The co – occurrence of fossil mammal genera in an assemblage can be used to reconstruct the biome that they inhabited. Applying this technique to global faunas from the Late Miocene provides new information on global vegetation and biome change through time. This information is of particular importance in regions with limited palaeobotanical information, such as North Africa. The mammal based biome reconstructions show a progressive cooling and drying from the early Tortonian to the Messinian. This is accompanied by faunal turnover; changing the proportion of stenobiomic genera in many regions, from mainly forest adapted animals to those more suited to open biome types. This novel technique provides a new method to reconstruct vegetation and palaeoenvironments that can be used to further our understanding of the terrestrial biosphere.

Chapter 8
Final discussion, conclusions and outlook

Everything is transformed by nature and forced into new paths. One thing dwindles....another waxes strong - Titus Lucretius Carus 58 B.C.

8.1. Introduction

At the outset of this thesis it was introduced that the Miocene was a time interval both warmer and wetter than the present day (Chapter 1). Through the study of the terrestrial biosphere, at a global level, this thesis has shown this statement to be true and has demonstrated how much warmer and wetter the Miocene was, through the use of climate modelling (Chapters 4 and 5), which suggests the Tortonian global average MAT was 4.5°C warmer than pre – industrial and 131.4 mm/yr wetter. From the co-existence of plants preserved as pollen in Derbyshire (Chapter 2) showing that the UK was 8°C warmer than present day MAT. This also indicates a shallower than modern latitudinal temperature gradient (Chapter 3). The affect of this warmer and wetter climate has been shown to alter the distribution of global biomes. The distribution of biomes has come from palaeobotanical sources (Chapters 3 and 4) and from the newly developed co-occurrence technique (Chapters 6 and 7). Both these sources of information have shown a poleward shift of all the world's major biome types. As well as showing the response of vegetation to the changing climate from the Langhian to the Messinian (Chapter 3 and 7). In this discussion I will attempt to draw together the results and discussion presented in the preceding seven chapters and tie this into what is known about Miocene climates and terrestrial ecosystems.

8.2. The vegetation and climate of the UK during the Miocene

In Chapter 1 it was stated that despite the large number of regional studies undertaken, especially in Europe, very little is known about the UK during the Miocene (e.g. Bruch et al., 2006; Utescher et al., 2007). In section 2.1 the absence of the UK in regional Miocene vegetation and climate studies was shown to result from a sparse onshore rock record (Woodcock and Strachan, 2000). The scarcity of Miocene strata is not the only problem in the

UK. Dating and correlation of the rocks once they are identified is also problematic. Several deposits have been reported in the literature as “Miocene”, “Neogene” or “Tertiary” (e.g. Allen, 1981; Herbert-Smith, 1971; Walsh et al., 1987; 1996), the accurate dating of UK Neogene has been hindered by the lack of datable palaeontological remains and the sparse, often karstic nature of the deposits (Walsh, 2001). In Chapter 2, the Kenslow Member of the Brassington Formation was more accurately dated to the late Tortonian. The Kenslow Member had previously been assigned to the Late Miocene – Early Pliocene (Boulter, 1971a), leading to liberal interpretations of the deposits age in the literature (e.g. Westaway, 2009). The revised age was based on a re-study of the original flora (Boulter, 1971a), extraction of fresh material from Kenslow Top Pit and the comparison of these to the Neogene floras of continental Europe. With the Kenslow Member flora more chronologically constrained it has been possible to involve it in regional and global patterns of vegetation (Chapter 3). The pollen preserved in the Kenslow Member shows that during the late Tortonian a warm – temperate mixed forest inhabited modern Derbyshire. Using the co-existence approach (Mosbrugger and Utescher, 1997; Utescher and Mosbrugger, 2010) a MAT of ca. 16°C has been reconstructed showing that the climate of Derbyshire was 8°C warmer than it is today. The vegetation and climate reconstructed from the palynology of Kenslow Top Pit is in good agreement with continental Europe. During the Late Miocene Europe had a shallow east – west temperature gradient, MATs in Turkey were around 18°C (Akgün et al., 2007), whilst in Northwest Europe MATs were 14 - 17°C (Bruch et al., 2007; Larsson et al., 2011). As the data presented in Chapter 3 shows, Europe during the Late Miocene was dominated by the warm – temperate evergreen broadleaf and mixed forest. The pollen recovered from Kenslow Top Pit shows many taxonomic similarities to other European Palynomorph bearing sites and represents the same swathe of warm – temperate forest that dominated Europe.

As well as providing the first accurately dated biome and climate reconstruction, the re-dating of Kenslow Top Pit has implications for understanding the development of the Pennines and the possibility of bringing this portion of the British stratum out of what S.W. Wooldridge referred to as “ a neglected ‘Dark Age’ in the geological history of Britain” (Walsh, 2001). The myth that the UK lacks Miocene deposits really only exists because the rocks do not form easily visited outcrops and as such have received limited attention. A brief literature survey reveals a wealth of understudied “possible Miocene”, “Neogene” or “Tertiary” onshore deposits (Allen, 1981; Herbert-Smith, 1979; Walsh, 2001; Walsh and Brown, 1971), as well as the extensive fluvio-lacustrine basins of Cardigan Bay, the Irish Sea and the Bristol Channel (Holford et al., 2008; Tappin et al., 1994). As was mentioned in Chapter 2, Kenslow Top Pit is only one of around 60 karstic hollows containing the Brassington Formation (Ford and King, 1968). Although many of these are now overgrown (J.B. Riding Personal Communication, 2011) there has previously been reports of the Kenslow Member flora occurring in at least seven pits (Walsh et al., 1980). Further work on the Brassington Formation could provide additional evidence on the vegetation and climate of the UK during the Late Miocene. The possibility also exists that the stratigraphically lower Kirkham Member may yield palynomorphs (Walsh et al., 1980), which could provide further control on the age of these important deposits and test the hypothesis that the whole Brassinton Formation is Tortonian in age.

The revision of the Brassington Formation's age to a stage specific level opens up the possibility of refining the ages of other UK late Cenozoic deposits. An important starting point to this would be the Mochras Farm Borehole, Wales. The Mochras Farm Borehole cut through ca. 500m of "Tertiary" sediments and an initial report on the palynology failed to apply an age more secure than "late Tertiary" (Herbert-Smith, 1971). However, it was noted that the floras bared resemblance to those reported from the Brassington Formation and the Neogene of Germany, whilst the early Tertiary was excluded due to the absence of strongly tropical pollen (Herbert-Smith, 1979). This ambiguity in dating has led to a situation similar to that of the Brassington Formation, whereby the diagnosed age has been refined in more recent works with little or no evidence to support this. For example in several works the "late Tertiary" sediments of Herbert-Smith (1979) have been quoted as being Middle Oligocene to Early Miocene (Tappin et al., 1994) and Early Miocene (Holford et al., 2008).Walsh (2001) reports that the sediments of the Mochras Borehole are Chattian. This age assignment was based on the work of Wilkinson (1979), Wilkinson and Boulter (1980) and Wilkinson et al. (1980) who attempted to correlate a series of deposits in south west England, Wales and Northern Ireland. Using the presence of *Mediopollenites* (Santaceae) it was deemed that at 408m depth the Mochras Borehole correlated with the Upper Bovey Formation, giving it an age in the region of middle to Late Oligocene (Wilkinson and Boulter, 1980; Wilkinson et al., 1980). The Bovey Formation, Bovey basin, Devon was dated based on comparison to the Lough Neagh Clays, Northern Ireland (Wilkinson et al., 1980). The Lough Neagh Clays have been dated based on their palynology (Wilkinson et al., 1980). Principally the presence of *Boehlensipollis* (Elaeagnaceae*?*), which was considered a form genus restricted to the Oligocene (Wilkinson et al., 1980). More recently *Boehlensipollis* has been reported from the Maastrichtian (Nichols and Johnson, 2002) and the Miocene (Teodoridis, 2003). Examination of the Mochras core shows sediments remarkably similar to those preserved in the karstic hollows of Derbyshire (Personnel Observation, 2012). The list of taxa reported from Mochras shows similarity to those of the Kenslow Member flora, as was originally suggested by Herbert-Smith (1979). The presence of *Symplocos* spp. in the Mochras borehole indicates an age of at least Late Miocene and the presence of pollen grains attributable to Palmae at a depth of 408m suggests an age of at least Middle Miocene for this depth (Herbert-Smith, 1979; Wilkinson and Boulter, 1980). However, the published taxa list is short and it is not possible to refine the age any further without processing new material (Herbert-Smith, 1979). Initial processing begun by myself has already built on the original study by finding palynomorphs below 525m; the maximum depth the original study found pollen (Herbert-Smith, 1979).

As has been alluded to in the previous paragraph the sediments of the Mochras Borehole do not exist in isolation. Late Cenozoic aged sediments are known onshore from Cornwall and Devon (Walsh et al., 1987; Wilkinson and Boulter, 1980; Wilkinson et al., 1980), southern Wales (Allen, 1981; Tappin et al., 1994), north-east Wales (Walsh and Brown, 1971) and Northern Ireland (Wilkinson et al., 1980). Offshore, geophysics and boreholes in the Bristol Channel and Irish Sea have revealed extensive sedimentary basins with Cenozoic strata of more than 1.5km thickness (Boulter and Craig, 1979; Tappin et al., 1994). The age of these sediments, both onshore and offshore, could prove key to understanding the geomorphological development and palaeogeography of the UK (M. Rowberry Personnel Communication, 2012; Walsh, 2001). As the age of these deposits is of such importance, further work should be undertaken to refine the date of each core, outlier and subsidence fill. Allowing each to be placed in stratigraphic order and finally revealing the poorly understood late Cenozoic geological history of the British Isles.

8.3. The evolution and nature of Miocene climate

In chapter 1 the Miocene was introduced as a time period warmer and wetter than the pre-industrial and today, this idea was based on many sources of evidence from individual fossil localities (e.g. Blanc et al., 1974), regional studies (e.g. Utescher et al., 2011a) and from isotopic global signals (e.g. Zachos et al., 2008). From marine proxies, it is widely accepted that MMCO was the warmest time interval of the whole Neogene, followed by a reduction in global MAT during the MMCT leading into the Late Miocene (Shevenell et al., 2004; Zachos et al., 2008). Both these hypotheses are supported by the findings of this thesis. Further to this the work presented within this thesis has shown what the terrestrial world looked like and how it responded to the changing climate. Despite there being good agreement in the literature on the general trend of Miocene climate through time, the mechanisms controlling this trend are not. The complex evolution of the Earth System through the Miocene (Fig. 1.1) and the apparent decoupling of climate from CO_2 (Pagani et al., 2005) has led to many alternative suggestions to the driving force of Miocene climate evolution. These suggestions include mountain uplift (Raymo and Ruddiman, 1992), the expansion of grasslands (Retallack, 2001), the Colombia River basalts (Kender et al., 2009), changes in ocean circulation (Shevenhell et al., 2004; Smith and Pickering, 2003), superplume activity (Potter and Szatmari, 2009) and galactic cosmic ray flux (Shaviv and Veizer, 2003). Ultimately all of these factors may have had an impact on the global climate and it is easy to relate many of these ideas into a larger view of climate evolution over the MMCO, MMCT and the Late Miocene. For example the idea that elevated CO_2, partly caused by the Colombia River Basalts (Kender et al., 2009), along with significantly lower than modern mountain heights created the warmth of the MMCO allowing a poleward expanse of global biomes (Chapter 3) and a reduced Antarctic ice sheet (Lewis et al., 2008) causing a positive feedback in terms of surface albedo. In an AOGCM study of the MMCO it was found that surface albedo was a primary cause for warming of the northern hemisphere and one of many for the southern hemisphere (Herold et al., 2011).

Following the warmth of the MMCO, bottom water oxygen isotopes show a period of relatively rapid global cooling and/or ice accumulation (Zachos et al., 2008). The MMCT could originate from increased mountain uplift (Potter and Szatmari, 2009), accelerating the chemical weathering of silicate rocks and lowering atmospheric CO_2 levels (Raymo and Ruddiman, 1992). As global mountain uplift has not ceased since around 15 Ma then a feedback must have kicked in to prevent complete atmospheric CO_2 drawdown. This could be due to an expansion of grasslands during the MMCT, inhibiting the biospheres contribution to global chemical weathering (Beerling et al., 2012; Pagani et al., 2009) and preventing atmospheric CO_2 from falling any lower than 100 ppmv. However, the palaeobotanical data presented in Chapter 3 shows there is no major expansion of savannas and grassland during the Seravallian (Fig. 3.1B). Rather both palaeobotanical (Fig. 3.2) and mammalian evidence (Fig. 7.5) shows that grass dominated biomes only begin to expand in the Late Miocene. This is further supported by studies into the expansion of C_4 grasses from carbon isotopes. These studies show that the isotopic signal for the C_4 photosynthetic pathway appears globally between 8-6 Ma but only comes to dominate during the Pliocene (Cerling et al., 1997; Fox and Koch, 2004; Latorre et al., 1997; Yang et al., 1999). However, before the lack of grassland in the reconstructions presented in Chapter 3 is taken as evidence of absence, it would be prudent to investigate the global distribution of paleosols during the Miocene. As paleosols may reconstruct more arid biomes than palaeobotanical data would alone (G. Retallack Personnel Communication, 2011).

8.3.1. Tortonian vegetation, climate and CO_2 levels: A case study for the Miocene

Of the four geological ages studied in this thesis the Tortonian is the best understood. The Brassington Formation yielded a palynoflora showing the presene of warm – temperate mixed forests in the UK during the Tortonian (Chapter 2). The Tortonian has the most numerous palaeobotanical sites with which to understand the global distribution of biomes (Chapter 3). The biomes reconstructed from palaeobotanical data have been used to assess GCM simulations and develop a data-model hybrid vegetation map (Chapter 4). Modelling experiments have investigated the impacts of vegetation on the Tortonian climate (Chapter 5). The biome preferences of Tortonian mammals have been reported (Chapter 6) and these have been used to expand the distributions biomes (Chapter 7). As the terrestrial biosphere and climate have been intensively investigated in this thesis, this subsection will use it as a case study to discuss in more depth the ideas about climate and CO_2 during the Miocene. All the evidence presented in this thesis, concerning the Tortonian, suggests that it was a globally warmer world than at present. This global warming requires a forcing agent that can operate at all latitudes, an increase in CO_2 or other greenhouse gases relative to the pre-industrial would be the most likely cause. This is not the only study that has shown these changes in the vegetation during the Tortonian relate to a warmer world (François et al., 2006; Micheels et al., 2007). However estimates of CO_2 levels for the Tortonian are between the Last Glacial Maximum and mid 20th Century concentrations (Kürschner et al., 1996, 2008; Berner and Kothavala, 2001; Pearson and Palmer, 2004; Pagani et al., 2005; Tripati et al., 2009). This has led to the suggestion that Tortonian climate was decoupled from CO_2 (Shevenell et al., 2004; Pagani et al., 2005; Mosbrugger et al., 2005). However recent work by Tripati et al. (2009) has shown that climate is highly sensitive to ρCO_2 and for the last 20 Ma major climatic changes were synchronous with changes in ρCO_2. Ruddiman (2010) recently suggested that one of the possibilities for apparent low CO_2 levels over the past 22 Ma, whilst climate has fluctuated considerably, could be the incorrect calculation of CO_2 from proxies. Recently CO_2 estimates for the Pliocene have been recalculated using the alkenone proxy, which placed atmospheric CO_2 levels for 4.5 Ma at between 370-420 ppmv (Pagani et al., 2010). Previous alkenone estimates for the latest Miocene (5.37 Ma) range from 247-340 ppmv (Pagani et al., 2005). Taking the upper estimates for both alkenone records requires an increase in atmospheric CO_2 of 80 ppmv across the Miocene-Pliocene boundary. Whilst using the lower estimates requires an increase of 123 ppmv over a period of 0.87 Ma, this is not compatible with other estimates of CO_2 levels (Kürschner et al., 1996; Pearson and Palmer, 2000). Nor would it be compatible with the bottom water $\delta^{18}O$ records, which show continued climatic cooling and/or ice sheet growth across the Miocene – Pliocene boundary. If we assume a connection between global climate and greenhouse gases, falling temperatures and/or ice sheet growth would suggest falling atmospheric CO_2 levels (Zachos et al., 2008).

It has been shown that vegetation has a positive feedback on global temperatures through altering surface albedo (Notaro et al., 2006). Could this then mean that the more poleward distribution of Tortonian biomes, as shown in Chapters 2, 3, 4 and 7 is a cause of the global MAT increase on modern, rather than being just a consequence? This has been proposed following an AOGCM experiment to explore whether Tortonian global warmth can be generated with low atmospheric CO_2 levels. The study found that with a CO_2 concentration of 278 ppmv the strongest forcing agent on the warming was vegetation (Knorr et al., 2011). Globally their experiment was +3°C warmer than the pre-industrial and appears to show that it is possible to have a warm Tortonian with low CO_2 levels (Knorr et al., 2011). However, this experiment may have been destined to achieve this result from the outset because the utilized global biome reconstruction relied heavily on the climate of a world with an atmospheric CO_2 concentration of 353 ppmv (Knorr et al., 2011; Micheels, 2003). This means that the fixed vegetation boundary condition was not in equilibrium with the 278 ppmv CO_2 climate and could not respond to it either. Comparison of the global vegetation reconstruction used in the previously mentioned study and the palaeobotanical data presented in Chapter 3 shows some differences and these have been discussed in Chapter 4.The results of Chapters 4 and 5 show that higher CO_2 concentrations (395 ppmv) are required to generate a modelled climate comparable to that reconstructed from palaeobotanical data (Chapter 3). However, it is worth noting here that a primary driver of temperature in an AGCM, such as the one used in these chapters, is the prescribed SSTs. This could mean that, until we have an accurate SST profile, varying the CO_2 concentrations in these model experiments might have little impact on the climate and hence the comparison with palaeobotanical reconstructions. Recent work using the AOGCM HadCM3L has also shown that at high CO_2 levels the data model comparison is more accurate than at low CO_2 levels (Bradshaw et al., 2010; 2012). Although current estimates of CO_2 for the Tortonian do not match the warming relative to pre-industrial seen in the palaeobotanical data, it would appear to be the most likely driving force for a global increase in MAT. It may seem an obvious statement to suggest that the uncertainties surrounding the reconstruction of CO_2 might be the issue in the “low CO_2 warm Miocene” paradox (Ruddiman, 2010). However, the CO_2 proxies are often taken as definite values (e.g. Knorr et al., 2011; LaRiviere et al., 2012) and stronger communication of potential uncertainties in these proxies is required from this research community to the wider palaeoclimate one.

8.3.2. Modelling the Miocene: State of the art and future progress

As part of this thesis has been dedicated to using a climate model to understand the impact of Tortonian vegetation on the climate (Chapter 5), it seems important to discuss the results of this chapter further and suggest some directions for future research. The experiments built on those presented in Lunt et al. (2008) who used an AGCM to explore the meridional SST and its influence on Tortonian climate. One of the Lunt et al. (2008) experiments was chosen to develop a data – model hybrid global vegetation reconstruction (Chapter 4). In Chapter 5 this Tortonian hybrid vegetation was used in one of the experiments to determine the impact of Tortonian vegetation on climate. The other experiments in Chapter 5 presented the impacts on climate of global forests (the opposite to the commonly used global shrublands, see Chapter 5 for further discussion) and the influence of different land surface schemes (MOSES1 vs. MOSES2). The main results were that the experiment using the realistic Tortonian vegetation reconstruction compared most accurately to MAT estimates from palaeobotanical data (Fig. 5.11). This experiment also showed that the vegetation contributed to a further 0.12°C warming on the pre-industrial (Table 5.2). Although this appears relatively insignificant, it is important to remember that the primary driving force of temperature in an AGCM is the prescribed SSTs. A future experiment should repeat experiment Tort3 (Table 5.1) but using an AOGCM. The experiment Tort4 showed that it was possible to achieve an additional warming on the pre-industrial just by changing to the MOSES2 land surface scheme (Table 5.2). However, it showed the least robust comparison to palaeobotanical based MAP reconstructions (Fig. 5.12d). It would be beneficial to repeat Tort4 but substituting the global vegetation hybrid for the global shrublands used in Tort4. This would allow a statement to be made about whether it is best to the use of either MOSES1 or MOSES2 for modelling the Tortonian climate with HadAM3.

Despite the inclusion of a realistic vegetation reconstruction in Tort3 the data - model comparison of MAT and especially MAP was still not perfect (Figs. 5.11; 5.12). Although this may relate to the SST profile used in the AGCM, data-model inconsistencies are still present in Tortonian climate model studies that use fully coupled AOGCMs (e.g. Bradshaw et al., 2012; Micheels et al., 2011). Before these data – model inconsistencies can be assigned to problems in the models it is important to explore the accuracy of boundary conditions. These are important components of the model initialisation and if incorrectly prescribed could misguide the model to generate a climate less comparable to that shown by the palaeontological record. There are many boundary conditions used in modelling studies that could be inaccurately represented such as bathymetry (e.g. Dowsett et al., 2011) or completely absent from modelling studies such as lakes (e.g. Haywood et al., 2010). Lakes may be an important boundary condition for improving the comparison of model simulated precipitation and the records reconstructed from the palaeobotanical record. So called mega – lakes (due to their substantial size!) have been shown to increase local to regional precipitation in Quaternary and Holocene modelling experiments (Burrough et al., 2009; Sepulchre et al., 2008). There is a considerable amount of literature for Miocene mega – lakes. In Africa for example there may have been lakes with surface areas of two million km^2 in the regions of Lake Chad (Griffin, 2006) and in the Congo Basin (Peters and O'Brien, 2001). In Australia as well, there is evidence for large lakes in the Tarkarooloo Basin and Billa Kalina Basin, both in South Australia (Ambrose and Flint, 1980; Callen, 1977) and the Lake Eyre Basin, which covers large parts of Queensland, the Northern Territory and South Australia (Alley, 1998). Inclusion of these mega – lakes into a GCM experiment may increase the amount of precipitation in continental interiors and arid regions – potentially improving the data – model comparison. Sloan (1994) found that when simulating the Early Eocene of North America, the addition of a lake had as much impact on the climate of the continental interior as the 1680 ppmv CO_2 in the models atmosphere. The addition of the lake (a modest one, compared to true mega – lakes, with a surface area of 15000 km^2) deflected the winter freezing line north and improved data – model winter temperature comparisons (Sloan, 1994).

8.4. Mammals an important component of the terrestrial biosphere

There are many components of the biosphere from single celled bacteria to colossal animals. Each operates between and within the other spheres of the Earth system, making the biosphere a record of all the changes that have occurred on this dynamic planet. As the continents have moved and climates changed, organisms have recorded these events (e.g. Deng et al., 2011; Webb, 2006). This “ability” of the biosphere to record changes in the other Earth system components is one of the key pieces of palaeoclimatological data. Whether this is recording a change in oceanic chemistry (e.g. Shevenhall et al., 2004), atmospheric composition (e.g. Kurschner et al., 2008) or changes in habitable ecospace (e.g. Chapter 3) the information recorded by the biosphere is invaluable in understanding the past. As well as responding to the other spheres of the Earth system there is growing evidence and ideas for the biosphere influencing other components (Chapter 5; Hayden, 1998; Wilkinson et al., 2012). Vegetation is the most obvious component of the biosphere that influences both the lithosphere (e.g. Pagani et al., 2009) and the atmosphere (e.g. Notaro and Liu, 2008). But what of the other organisms of the biosphere? There is a growing body of literature on modern animals as ecosystem engineers (Jones et al., 1994; Wright and Jones, 2006). This is the concept that life does not simply inhabit space, but willingly or inadvertently modifies the environment. Humans being the ultimate in ecosystem engineer (Ellis, 2011; Jones et al., 1994). In the following two subsections I will firstly recap the results and discussion from Chapters 6 and 7, integrating them with other work that uses mammals as a proxy. Following that I will discuss mammals as ecosystem engineers and their possible impacts on the Earth system that may influence climates.

8.4.1. Mammals as a proxy in palaeoclimates

This thesis has been the first to attempt to use the palaeoecology and biome preferences of mammals as a global proxy in Miocene palaeoclimate studies (Chapters 6 and 7). Through the use of the Biome Specialisation Index (BSI) it has been shown that Late Miocene mammals had a similar proportion of stenobiomic and eurybiomic taxa as extant modern mammals (Chapter 6). During the Late Miocene the majority of mammal genera were specialised to only one or two biomes (Fig. 6.3). As most Late Miocene mammal genera were stenobiomic, rather than eurybiomic, they are able to be used to reconstruct biomes in regions where palaeobotanical data is absent (Chapter 7). These mammal based biome reconstructions are in good agreement with the regional and global biome distributions from Chapters 3 and 4. Previous attempts to reconstruct vegetation from Miocene mammals relied on comparisons to nearest living relative habitat preferences (Guerin and Eisenmann, 1993), inferences of diet from morphology (Fortelius et al., 2002), isotopic studies to estimate the proportion of C_3 to C_4 plants (Cerling et al., 1997) and tooth wear analysis to understand actual food consumption (Merceron et al., 2010). Each of these previous techniques has value in understanding fossil mammal ecology, but is limited for inferring large scale biome distributions. Comparing a fossil mammal with its extant descendant, though based on uniformitarianism, is probably the least reliable in reconstructing vegetation. A key issue with using a mammal’s nearest living relative to infer a fossil mammal’s habitat is that it relies on no adaptive evolution having occurred. For example if we look at modern species of the Bovidae most are adapted to be grazers (Janis, 2008). Therefore when we look back at Late Miocene Bovidae species, we would be inclined to infer each of these was a grazer. Reconstructing savanna and grasslands where ever bovid specis are preserved (de Bonis et al., 1990; 1998), even when palaeobotanical data shows the presence of forest (Ivanov, 2002; Velitzelos and Gregor, 1990). This is a major problem in the understanding of Miocene palaeoenvironments and has led to the “savanna myth” (Solounias et al., 1999). This can be best highlighted by the Late Miocene deposits of Greece and Turkey; most fossil mammals of this region are relatives of modern species only found on the African savanna (Solounias et al., 1999). Although nearest living relative comparisons can provide some information on a mammal’s ecology and the regional vegetation, these inferences should be used cautiously. Otherwise, we ignore the idea of adaptation and evolution in response to environmental changes (Benton, 2009; Bozinovic et al., 2011). This thesis has provided evidence that Late Miocene mammals were evolving in response to changing vegetation (Fig. 7.4; 7.5) and this should be fully explored in the future. Further caution should come from the idea we know the true distribution of modern mammals. The degree to which the planet has been modified through agriculture, civilisation, domestication and recent extinctions means we may have a limited idea about what a truly natural world should look like today (Ellis, 2011; Newmark, 1995; Turvey et al., 2007).

Tooth functional morphology is a cornerstone of understanding fossil mammal diets (Ungar and Williamson, 2000). From the modern families to the earliest morganucodontans tooth form in mammals is intimately related to diet (Gill et al., 2009; Janis and Fortelius, 1988; Pough et al., 2009; Clemens, 2011). This well established fact has been utilised in the hypsodonty of herbivorous mammals (Fortelius et al., 2002). As introduced in Chapter 1, hypsodonty is the relative height to width ratio of mammalian molars and is an evolutionary adaptation to abrasive food (Fortelius et al., 2002; Janis and Fortelius, 1988). A hypsodont mammal is one which has a molar tooth higher than it is wide and are typically considered grazers, whereas a brachyodont mammal has a molar that is wider than it is high and are browsers (Fortelius et al., 2002). Of course not all modern hypsodont mammals are grazers and not all extant grazers have a hypsodont dentition (Cerling et al. 2003; Fortelius et al., 2002; Sponheimer et al. 2003). In palaeoclimate studies the hypsodonty index has commonly been used as a quasi-quantitative aridity indicator; more hypsodont mammals indicates greater aridity (Fortelius et al., 2002). A combination of the hypsodonty index and the co-occurrence technique could provide some interesting information for understanding palaeoprecipitation and biomes. For example studies on European faunas has shown that there is a major expansion of hypsodont mammals at the start of the Late Miocene, whereas Europe is dominated by brachyodont mammals before 11 Ma (Fortelius et al., 2002). The vegetation data shows a dominance of the warm-temperate evergreen broadleaf and mixed forest in Europe throughout the Middle to Late Miocene, with some more open areas in the Iberian Peninsula (Fig. 3.4; 3.5). Reconstructed MAP data indicates that there is a reduction in precipitation from the Langhian to the Messinian (Tables 3.2-3.5). Ranges of MAP change from 823-2500 mm/yr in the Langhian to 700-1759 mm/yr in the Messinian. These upper values are still able to maintain evergreen rainforest, but these values provide no indication of seasonality. A combination of the co-occurrence technique (which does indicate more seasonal biomes in Europe during the Messinian), palaeobotanical data and the hypsodonty index could be used to refine our knowledge of precipitation and seasonality - evolution during the Miocene.

Isotopic study of mammal teeth studies have been used to infer vegetation based on the inferred proportion of C_3 to C_4 plants. These studies assume that any indication of the C_4 photosynthetic pathway shows the presence of grasses (Macfadden and Cerling, 1996). Overall 61% of all C_4 plants are from the family Poaceae, this means that not all C_4 plants are grasses. In fact, 550 species of the Chenopodiaceae and 250 species of the Amaranthaceae use the C_4 photosynthetic pathway (Kadereit et al., 2003). As well as these two families of predominantly shrubs, examples of C_4 pathway using plants are also found in 14 other dicot families (Kadereit et al., 2003; Sage and Monson, 1999). Although the majority of C_4 plants are grasses (61%) there is still a large proportion of non-grass C_4 plants. This may mean that carbon isotope studies from mammal teeth, which reconstruct amounts of grass in the ecosystem (e.g. Macfadden and Cerling, 1996), may not actually reflect the proportion of Poaceae in the environment. Though this argument maybe more valid in the Pliocene as many of the C_4 dicots are thought to be younger than 5 Ma (Sage, 2004).

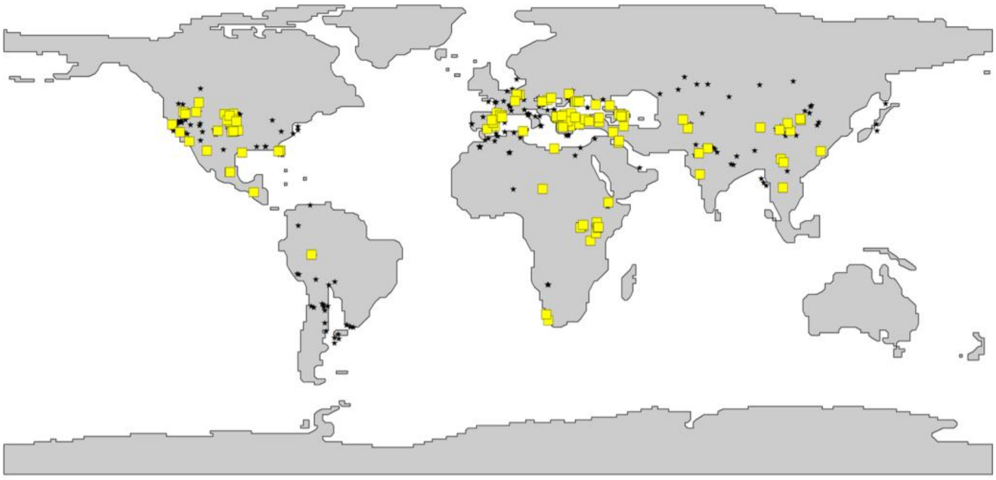
Tooth wear analysis reconstructs an animal’s diet based on the damage left on teeth through feeding (Merceron et al., 2010; Townsend and Croft, 2008). From the understanding of an animal’s diet it is possible to infer a habitat. Using microwear analysis Townsend and Croft (2008) demonstrated that Early Miocene hypsodont mammals from South America were actually browsers. They concluded that hypsodont herbivores do not always necessarily mean an open and arid environment. Microwear analysis on the Molayan locality, Afghanistan suggested the presence of an open arid environment with C_3 grass, evergreen shrubs and trees (Merceron et al., 2004). This is in good agreement with the reconstructions from the co-occurrence approach, which although it reconstructed a possible four biomes, two of these were dry and open and the other two were evergreen (Fig. 7.1). Ultimately our best understanding of the Miocene terrestrial world, using mammals to support the palaeobotanical record, will come from an integrated proxy approach. Using the co-occurrence technique to predict a biome and testing this with hypsodonty analysis, isotopic studies and tooth wear analysis.

8.4.2. Ecosystem engineers: Mammals as a component of the earth system

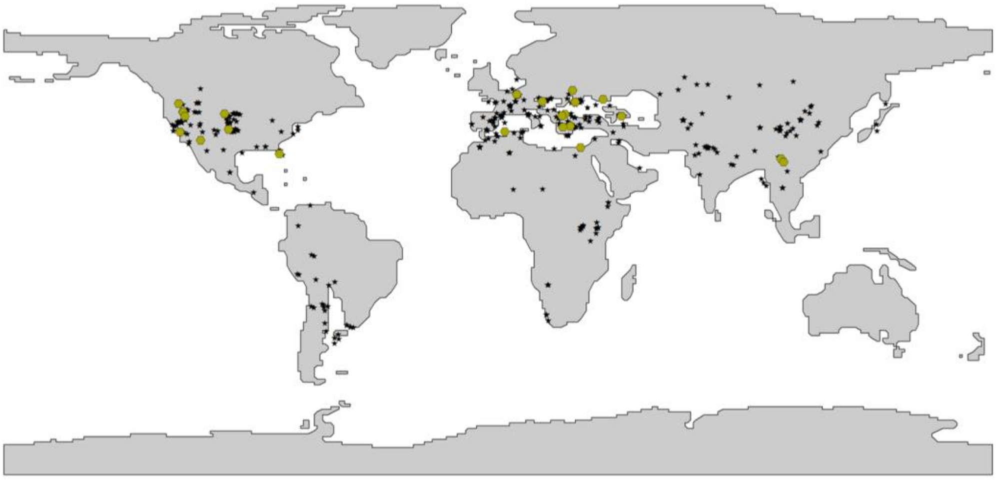
An ecosystem engineer is an organism that directly or indirectly modulates the availability of resources (other than themselves) to other species (Jones et al., 1994; Wright and Jones, 2006). Direct provision of resource such as food web transfers and decomposition are not forms of ecosystem engineering (Jones et al., 1994; Wright and Jones, 2006). Some organisms, such as plants, are autogenic ecosystem engineers. Autogenic ecosystem engineers change the environment with their own physical structure (Jones et al., 1994). The impact of plants, the archetypal autogenic ecosystem engineer, on the climate is well documented and has been discussed extensively throughout this thesis. The other type of ecosystem engineering is an allogenic organism; these modify their environment by transforming living or non-living materials from one physical state to another (Jones et al., 1994). This type of ecosystem engineer will be discussed in this section using the examples of the habitat modifying elephant and the habitat creating beaver (Jones et al., 1994). Not only are the beaver and elephant two of the most important modern ecosystem engineers, but both have greater diversity and geographic distribution during the Miocene (Chapter 6). Therefore if these mammals were ecosystem engineers during the Miocene, their impacts on the environment would have been much greater than their modern relatives. This subsection will introduce the elephant and the beaver as allogenic ecosystem engineers and explore the possibility of their impacts on the Miocene world.

African Bush Elephants (*Loxodonta africana*) are one of the largest living land mammals and are an important element in maintaining woodland – savannah – grassland dynamics (Haynes, 2012; Laws, 1970; Naiman, 1988). Studies on forest elephants (*Loxodonta cyclotis)* as ecosystem engineers are limited, but they are assumed to contribute to forest complexity by spreading seed and maintaining open areas (Short, 1981). These allogenic ecosystem engineers modify vegetation structure through physical disturbance and destruction of trees (Jones et al., 1994; Naiman, 1988). This has influences on the local fire regime, food supply to other animals, populations of other animals and the physical structure of the regional environment (Baxter and Getz, 2005; Jones et al., 1994; Laws, 1970; Naiman, 1988; Pringle, 2008). Due to the vulnerable nature of the species and the human – elephant conflict for space, elephants are often geographically restricted through fencing (Riddle et al., 2009). This unnatural range restriction has been suggested to lead to the high degrees of woody plant destruction and ecosystem engineering suggested by some authors (Guldemond and van Aarde, 2007; Laws, 1970; Mosugelo et al., 2002; Wiseman et al., 2004). This however would be difficult to prove, as the interactions between a natural elephant population and unaltered vegetation is an impossible observation in the modern world.

A. Gomphotheriidae



B. Mammutidae



C. Elephantidae

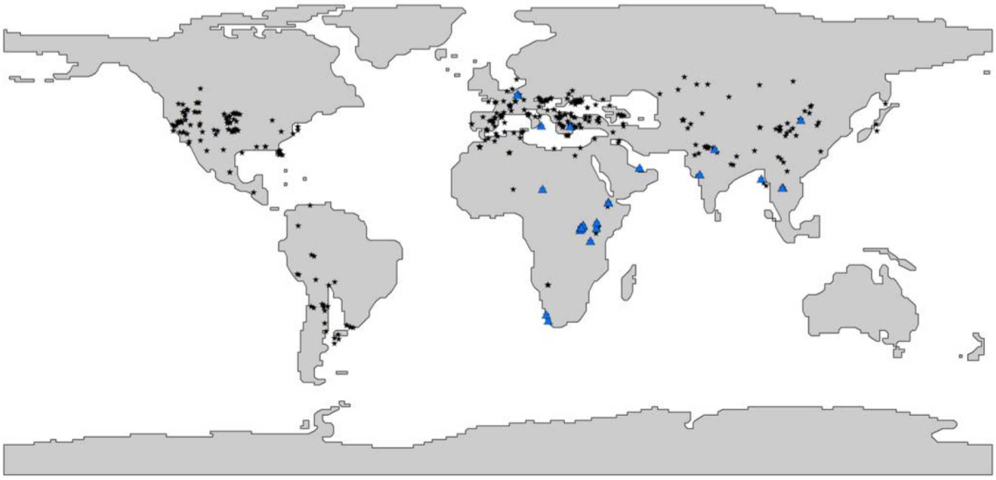
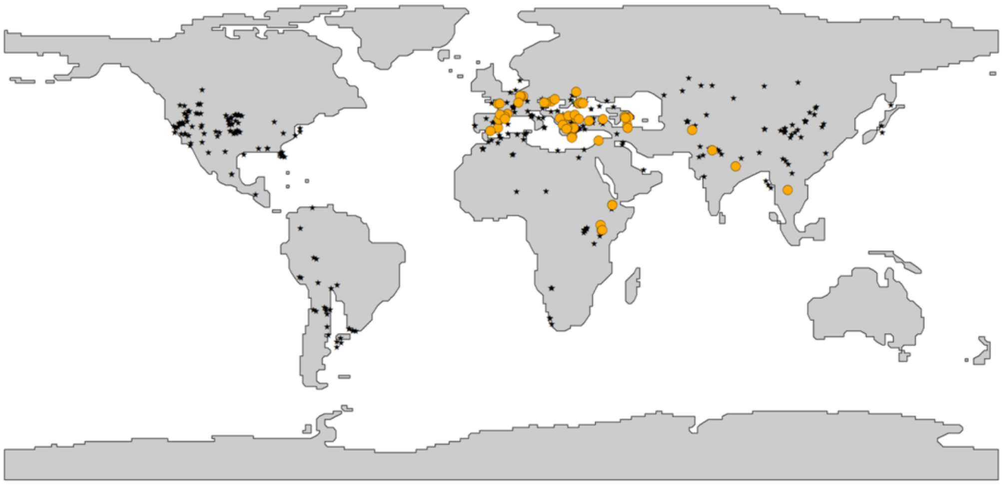
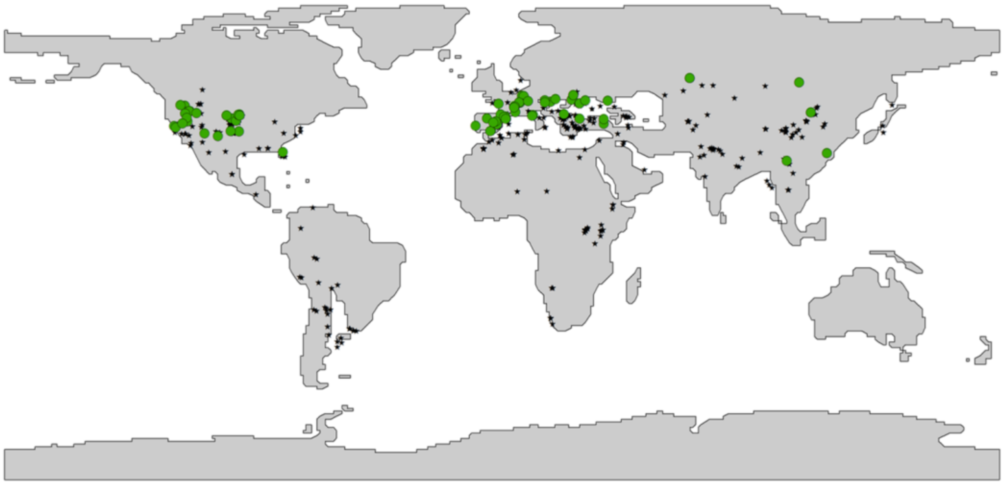


Figure 8.1. Geographic distribution of potential Late Miocene ecosystem engineer families. Coloured shapes represent an occurrence of a family, whilst the black stars show the position of all the mammal localities recorded in MAD.



D. Deinotheriidae



E. Castoridae

Figure 8.1. *Cont.* Geographic distribution of potential Late Miocene ecosystem engineer families. Coloured shapes represent an occurrence of a family, whilst the black stars show the position of all the mammal localities recorded in MAD.

The ecosystem engineering that has been observed in elephants may have implications to biome reconstructions during the Miocene. The opening up of an area of Kruger National Park, South Africa permitted elephants into woodland they had been excluded from for 32 years (Hiscocks, 1999). A transect survey five years after the removal of the fence showed that over 700 trees had been damaged and a further 300 were dead, opening up the woodland (Hiscocks, 1999). Other research in Kruger National Park has shown that a combination of elephants and fire can modify tall woodland to short woodland (Trollope et al., 1998). Observations showed that this degree of change did not happen with fire operating alone (Trollope et al., 1998). During the Late Miocene the Proboscidea were considerably more diverse both taxonomically (30 species in 16 genera compared to 2 species in 2 genera today) and geographically (all continents except Antarctica and Australia during the Late Miocene). In terms of their biome specialism, Late Miocene Proboscidea were more specialist than the modern genus *Loxodonta,* but as an order they show a similar biome flexibility; inhabiting biomes as diverse as tropical forests to temperate xerophytic shrublands (Chapter 6; Hernández Fernández and Vrba, 2005). With considerably more elephantine herbivores, could more of the biomes reconstructed as forests actually be structurally more like woodlands and woodlands more like savannas? Ultimately, the geographical range and density of Late Miocene elephants would determine their impacts on vegetation. MAD contains 282 individual records of Proboscideans, distributed in all regions that fossil mammals are reported from (Fig. 8.1). The Gomphotheriidae family were the most widespread (Fig. 8.1a). Gomphothere elephants were found in the tropical to temperate realm of North America, Eurasia and Africa. Gomphotheres even reached South America before the final closure of the CAS (Cozzuol, 2006). The mammutidae were distributed across the temperate and tropical realms of Eurasia and North America (Fig. 8.1b). The Deinotheriidae and Elephantidae were both distributed throughout Africa and Eurasia (Fig. 8.1c,d). This wide distribution of Proboscidean families is much greater than modern elephants and shows that any ecosystem engineer effects would be geographically large. Estimating population density of fossil mammals is complex. For a given community; species with greater body mass have lower population densities, due to each individual requiring a greater share of the habitats available resources (Damuth, 1981; 1982). Based on this it should be expected that Late Miocene Proboscidean population densities should not exceed modern, unless habitats were more productive. Modern population densities in the seasonal areas of South Africa are around 3 km^{-2}, though this estimate maybe slightly high due to the ongoing recovery of South Africa's elephant population and is estimated to fall to around 2.4 km^{-2} (Hall-Martin, 1992). Based on these modern population densities, a 2.5° x 3.75° grid cell could conceivably contain 240000 – 300000 individuals – a considerable number of destructive herbivores.

The modern Beavers (*Castor canadensis* and *C. fibre*) are the archetypal allogenic ecosystem engineers. Beavers are notable for their water management and landscaping activities, which impact on many aspects of the local habitat (Naiman et al., 1988). These modifications alter the river discharge regime, decreasing current velocity, giving the channel a stepped profile, expanding the area of flooded soils and increasing the retention of soil and organic matter (Naiman et al., 1988). Beavers typically dam first to fourth order streams as larger water courses typically destroy dams through freshets. Beavers dam rivers to create beaver ponds, these provide protection from predators, a means to transport food and, in regions where winter temperatures fall below freezing point, a means to store food (Jenkins and Busher, 1979; Naiman et al., 1988). As well as creating a wetland typically in the region of 1 km^2, though the largest known beaver pond covers >51 km^2 (Haynes, 2012), a colony of beavers (four to eight individuals) will fell about a metric ton of wood from around the pond (McGinley and Witham, 1985; Naiman et al., 1988). Regionally, this creates a mosaic environment that is structurally more complex and has a greater diversity of species than would exist without beavers (Naiman et al., 1988).

During the Late Miocene there were 29 species of beaver in 12 genera (Chapter 6). But did any of them, including the Miocene species of *Castor*, build dams and produce beaver ponds? Evidence exists from the Early Miocene of France for a fossilised beaver lodge (Hugueney and Escuillie, 1996). The locality of Montaigu-le-Blin contains the remains of ten *Steneofiber* within a distinct pocket of sediment, which based on size and tooth development can be divided into two mature adults, three juveniles and five kits – almost the exact demographic structure of the modern *Castor* colony (Hugueney and Escuillie, 1996). Further evidence to support an early origin for modern beaver life strategy comes from the morphology of *Steneofiber* which possessed “combing claws” these are used in extant beavers to groom the fur to maintain waterproofing (Hugueney and Escuillie, 1996). *Steneofiber* was effectively a modern beaver. The fossil evidence from Montaigu-le-Blin shows it followed a similar k-selection life strategy as *Castor* based on the family unit, all it lacked was the paddle like tail (Hugueney and Escuillie, 1996). Xu (1994) considered Steneofiber the direct ancestor of the modern genus *Castor*. Whereas Korth (2001) placed them in the same clade (Castorinae) but made no comment on the evolutionary relationships. Within the Castorinae there are three genera present in the Late Miocene: *Castor*, *Chalicomys* (= *Palaeomys*) and *Steneofiber* (Korth, 2001). Based on the evidence from Montaigu-le-Blin we can assume that, as *Steneofiber* is the oldest genus in the subfamily (present in the Early Miocene), all genera in the Castorinae had a life strategy focussed around the lodge and the beaver pond. Another branch of Castoridae evolution has also left fossil evidence of dam building activity. From the, aptly named, Pliocene Beaver Pond locality, Canada evidence exists for “beaver-cut” sticks (Hutchison and Harington, 2002; Tedford and Harrington, 2003). The beaver present at this site was *Dipoides* cf. *intermedius* (= *Procastoroides intermedius*) from the Castoroidinae subfamily (Korth, 2001; Tedford and Harrington, 2003; Zakrzewski, 1969). As a distinctly different clade than the one containing *Castor* was also tree felling to engineer the environment this means that it may be an ancestral trait, as suggested by Hugueney and Escuillie (1996). This would mean that all the Late Miocene members of the Castoridae were building dams and lodges. The MAD database records 102 occurrences of the Castoridae family during the Late Miocene in the warm –

temperate and temperate realm (Chapter 6; Fig. 8.1e). Modern beaver population densities are between 0.1 – 2 colonies km^{-2} (Anderson et al., 2009; Naiman et al., 1988). Each colony producing a beaver pond typically 1 km^{2} in surface area, that would be occupied for a few centuries before being allowed to slowly regenerate to the natural vegetation, whilst another beaver pond is created. So as well as the Proboscideans creating heterogeneic habitats through their destructive remodelling of wooded biomes, the Late Miocene Castoridae were also generating mosaic environments and increasing surface water.

Beaver ponds are also significant carbon sinks, typically holding three times as much carbon than the unaltered environment would and as they are wetlands, a source of methane (Blodau, 2002; Naiman et al., 1988; 1991; Yavitt et al., 1990). Estimates from the literature for the amount of methane released from beaver ponds ranges from <1 – 511 g m^{-2} yr^{-1} (Naiman et al., 1991; Yavitt et al., 1990). The large range in the amount of methane released from beaver ponds is partly related to the limited number of measurements and also a function of the net ecosystem productivity of a region. Net ecosystem productivity has been shown to have a positive correlation with the amount of methane released to the atmosphere (Whiting and Chanton, 1993). Methane released from beaver ponds and other wetlands is rarely in “bubbling events” but a constant diffusion into the atmosphere (Blondau, 2002; Yavitt et al., 1990). Methane is a significant greenhouse gas, which leaves little or no trace in the geological record (Beerling et al., 2009a; Kuechler et al., 2012). Using a two dimensional model Beerling et al. (2009a) estimated that Miocene methane atmospheric concentrations would have been relatively modest and contributed less than a degree centigrade to global MATs. They did however stress that their estimates were first order and likely to be built upon in future studies (Beerling et al., 2009a). This model was based on estimates of coal deposition in wetlands (Beerling et al., 2009a). However, not all wetlands produce peat and coal (Greb et al., 2006). This may mean that the estimates of CH_4 from coal deposition rates may be underestimates. As a significant creator of wetlands Late Miocene beavers may have contributed to atmospheric CH_4. The population recovery of Castor canadensis in North America since 1945 has been linked to 1% of methane emissions across the continent (Naiman et al., 1991). If North American beavers were to return to all their potential boreal habitats it is estimated that the annual methane flux would be 2.18 Tg of carbon, not bad for a rodent (Naiman et al., 1991). As there is a positive correlation between methane flux and ecosystem productivity (Whiting and Chanton, 1993), then the Miocene methane fluxes from beaver ponds are likely to be greater than modern estimates. The greater warmth and humidity of the Miocene, shown by the biome distributions presented in Chapter 3, and the amounts of lignite and coal deposited (Bartley et al., 2010; Durska, 2008; Föllmi et al., 2005;

Holdgate et al., 2007; Lücke et al., 1999) suggests the Miocene had a considerable global primary productivity. The Miocene is also a crucial period for the evolution of *Sphagnum* (Shaw et al., 2010). Today *Sphagnum* dominated peatlands account for 5-10% of methane emissions (Blodau, 2002). There exists the possibility that a combination of beaver created habitats, “normal” wetlands and *Sphagnum* bogs could contribute considerable amounts of CH_4 to the Miocene atmosphere and this warrants future investigation.

8.5. Summary conclusions

This thesis investigated Middle to Late Miocene terrestrial biota and climate, primarily from vegetation but also using mammals. The thesis has investigated life on land and climate at the site level (Chapter 2) and the global level (Chapters 3 – 7). The terrestrial biota and climate of the Middle to Late Miocene has been investigated using palynogy (Chapter 2), biome distributions (Chapters 3 & 4), GCMs (Chapters 4 & 5) and the global distribution and ecology of mammals (Chapters 6 & 7).

- The Middle to Late Miocene was a time period that was globally warmer and wetter than the pre-industrial or modern worlds. This is shown by the biome distributions presented in Chapters 3, 4 and 7. The distribution of biomes shows that the Langhian was the warmest interval during the studied time period. Following this the biome distribution shows a global cooling and drying trend. The southern hemisphere appears to have cooled quicker than the northern hemisphere; this may be related to the growth of the Antarctic ice sheet following the end of the MMCO.
- During the Late Miocene the UK had vegetation similar to mainland Europe. This warm – temperate evergreen broadleaf and mixed forest grew under an ambient MAT of around 16°C. The evidence presented in Chapter 2 is the first accurately dated onshore Miocene deposit in the UK and the only information on the terrestrial environment during this time period.
- The evidence presented in Chapters 4 and 5 shows that the level and nature of Tortonian warming (Δ+4.44°C compared to pre-industrial) reconstructed through the combination of palaeobotanical data and modelling study requires a climatic forcing mechanism operating on a global scale (i.e. CO_2). However, published Tortonian atmospheric CO_2 levels from a variety of proxies range between the Last Glacial Maximum, pre-industrial and mid-20th Century levels. Before Miocene climate is assumed to be decoupled from atmospheric CO_2, it is first necessary to reconcile this

miss-match between terrestrial proxy and climate model evidence with available techniques used to reconstruct palaeo-atmospheric CO_2.

- The use of a Tortonian global vegetation hybrid reconstruction (Chapter 4) in an AGCM experiment, improves data – model comparison. It also contributes to a small degree of the global warmth. MAP is marginally improved in an AGCM experiment with an accurate palaeo-vegetation but there is still very little similarity between data derived MAP reconstructions and model generated MAP estimates.
- Using the biome distributions reconstructed in Chapter 3 the biome specialism of Late Miocene mammals was investigated (Chapter 6). Using the BSI it has been shown that mammals were as specialised to individual biomes during the Late Miocene as they are today despite 5.33 million years of evolution, extinction and migrations.
- As the majority of Late Miocene mammals were biome specialists it has been possible to develop the co-occurrence approach. This is a technique which allows an assemblage of mammals to be translated into a biome type. The biome types reconstructed in Chapter 7, using Late Miocene mammals, show the same regional scale biome patterns as palaeobotanical data. This now means that mammals can be used to expand our knowledge of terrestrial ecosystems. This will enable more accurate biome reconstructions for palaeoclimate modelling studies and provide more data with which to compare model output.

8.6. Outlook

This thesis has provided the most up-to-date and complete view of Middle to Late Miocene terrestrial biotas and the climates they existed in. However, this should only be viewed as a beginning. The Miocene represents an interesting epoch for palaeoclimate research, it will never provide a geological analog to future anthropogenic climate change, but it can be used as a unique challenge for GCMs and an opportunity to look at how life responds to a spectacular re-design of the Earth system. As was introduced in Chapter 1 the Miocene represents the making of the modern world; mountains uplifted, seaways opened and closed, glaciers advanced and retreated and the terrestrial biosphere continued to evolve. It is likely that the Miocene climate, recorded in the fossil record, is a factor of all of these changes, other events such as the Colombia River Basalt eruptions and greenhouse gases. I will now outline a few points I feel would significantly improve our understanding of palaeoclimates in the Miocene and other parts of the Cenozoic.

- The data presented in this thesis provides what the author hopes will be the beginning of a much larger dataset. One that will incorporate all aspects of the Earth system and allow a far more complete understanding of the Earth system during the Miocene. This would not only aid the data community but could form a set of boundary conditions with which modelling of the Miocene could be improved.
- The Brassington Formation is now the most accurately dated onshore Miocene in the UK. The success at redating these challenging deposits should allow many more of the UK's "Tertiary" deposits to be re-explored. This would not only benefit the understanding of the changes that have occurred in this small part of northwest Europe but provide valuable insight into other aspects of Cenozoic climate evolution. For example, today the climate of the UK is partly controlled by the North Atlantic Current. A clear stratigraphy and related sequence of palaeontological events in the UK could provide direct evidence for the development of this important part of the modern Earth system.
- The next stage of modelling experiments on the Tortonian should use AOGCMs with the global hybrid vegetation reconstruction so that global MATs are not directly related to prescribed SSTs. The use of a dynamic vegetation model could provide interesting results; would the vegetation predicted by the model compare to the input vegetation? If not which regions would the model alter? If it were to modify regions well constrained by palaeobotanical data then we could conceivably say that there was some error in the model set up (most likely another boundary condition). If it modified one of the poorly constrained regions this would have implications for the data-model hybrid vegetation reconstruction and any model experiment using it. Experiments such as these could lead to a version two of the global vegetation hybrid vegetation.
- Miocene CO_2 reconstructions should be fully explored before this epoch is truely considered de-coupled from this important greenhouse gas. It could also be an interesting avenue of research to explore CH_4 during the Miocene and its contribution to Miocene warmth.
- Linking in with the exploration of CH_4 during the Miocene is the concept of animals as ecosystem engineers. The two most prolific ecosystem engineers of the modern world were a lot more diverse and widely distributed during the Miocene. Although it is unlikely to be one of the main controllers of global climate the role of animals in environmental modifications should no longer be excluded from palaeoclimate research. We are likely to be mislead by the modern world: current animal

distributions have been, and still are, significantly hampered by civilisation. Unfortunately modern observations will only take us so far in the understanding of the ancient biosphere.

Fin..... for now!

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List of Abbreviations

ACC – Antarctic Circumpolar Current

AGCM – Atmosphere only Global Climate Model

AOGCM – Atmosphere and Ocean Global Climate Model

BSI – Biomic Specialisation Index

CAM-CLM – Community Atmosphere Model – Community Land Model

CAS – Central American Seaway

CCSM3 – Community Climate System Model 3

CRFB – Colombia River Flood Basalt

DGVM – Dynamic Global Vegetation Model

DSDP – Deep Sea Drilling Project

ECHAM4 – European Centre atmosphere model Hamburg version 4

ECHAM5 – European Centre atmospheric model Hamburg version 5

EMIC – Earth systems Model of Intermediate Complexity

GCM – Global Climate Model / General Circulation Model

HadAM3 – Hadley Centre Atmosphere Model version 3

HadCM3L – Hadley Centre Coupled atmosphere – ocean Model version 3 Low resolution ocean

IRD – Ice Rafted Debris

LAI – Leaf Area Index

MAD – Miocene Animal Database

MAP – Mean Annual Precipitation

MAT – Mean Annual Temperature

MMCO – Middle Miocene Climatic Optimum

MMCT – Middle Miocene Climate Transition

MOSES – Met Office Surface Exchange Scheme

MPIOM – Max Planck Institute Ocean Model

NLR – Nearest Living Relative

NPP – Net Primary Productivity

PFT – Plant Functional Type

ODP – Ocean Drilling Project

OGCM – Ocean only Global Circulation Model

SAT – Surface Air Temperature (in modelling terms this is measured at 2m above surface level)

SST – Sea Surface Temperature

TEVIS – Tertiary Environments and Vegetation Information Systems

TRIFFID - Top-down Representation of Interactive Foliage and Flora Including Dynamics

Appendix A

Reference and biome code to the palaeobotanical sites presented in Chapter 3

The following four tables contain the data from TEVIS that has been presented in Chapter 3. Each age has its own table. The biome and megabiome numbers are presented in Table 3.1 and the full references to the literature are in Appendix B. The latitude and longitude are for the modern location of the site; the presented age range presents the maximum when all published uncertainty is taken into account. The Quality (Q) measure is a subjective measure of the robustness of the data. This mainly reflects the age uncertainty as this is the greatest source of error when producing large syntheses. A score of 1 reflects excellent age control, whereas a score of 5 suggests limited or no apparent age control.

Langhian (15.97 – 13.65 Ma)

Location number	Literature	latitude	longitude	Biome number	Megabiome number	Oldest age	Youngest age	Q
1	Williams et al., 2008	74.3	-123.033	7	6	16	14	3
2	Norris, 1997	69.5	-135.75	7	6	15.97	10.4	4
3	White and Ager, 1994	67.333	-141.333	7	6	15.3	15.1	1
4	Liu and Leopold, 1994	63.9	-148.941	7	6	17	14	3
5	Leopold and Liu, 1994; Grimaldi and Triplehorn, 2008	63.85	-148.376	7	6	16	13	3
6	White et al., 1997	63.9	-148.9	7	6	15.5	15	2
7	Piel, 1977	53.921	-122.778	4	2	16	11.61	3
8	Mathews and Rouse, 1984	51.505	-122.232	4	2	17	13.5	3
9	Read, 2000	51.193	-120.936	4	2	15.97	11.61	3
10	Manchester et al., 1991	49.622	-115.636	4	2	16.5	14.5	2
11	Manchester et al., 1991	48.166	-119.087	4	2	16.5	14.5	2
12	Manchester et al., 1991	47.732	-117.348	4	2	16.5	14.5	2
13	Manchester et al., 1991	47.188	-116.222	4	2	16.5	14.5	2
14	Manchester et al., 1991	47.023	-115.771	4	2	16.5	14.5	2

15	Manchester et al., 1991	46.726	-115.925	4	2	16.5	14.5	2
16	Manchester et al., 1991	46.437	-116.563	4	2	16.5	14.5	2
17	Manchester et al., 1991	46.309	-115.582	4	2	16.5	14.5	2
18	Manchester et al., 1991	45.803	-115.663	4	2	16.5	14.5	2
19	Oliver, 1936	44.414	-119.086	4	2	16.3	15.79	4
20	Chaney, 1925	44.435	-119.294	4	2	16	14.7	3
21	Axelrod and Schorn, 1994	40.66	-118.306	4	2	15.9	14.9	2
22	Axelrod, 1992	39.883	-119.574	5	6	15.6	14.8	1
23	Axelrod, 1995	39.593	-119.373	4	2	14.8	12.4	1
23	Bartley et al., 2010	39.781	-123.235	4	2	15.97	11.61	3
24	Axelrod, 1939	35.214	-118.336	14	3	15.5	11.8	4
25	Stott and Aitken, 1993; Holman, 1971	49.086	-107.798	20	4	16.3	13.6	3
26	Frederiksen, 1984; Axelrod, 2000	41.323	-70.813	4	2	16	11	4
27	Berry, 1909; Godfrey and Barnes, 2008	37.533	-77.467	4	2	19	14	4
28	Jarzen et al., 2010	30.469	-84.986	4	2	18	15	3
29	Lenhardt et al., 2006	18.996	-99.101	5	6	22	14.5	3
30	Martínez-Hernández, E., 1992	16.803	-92.906	1	1	15.97	5.33	4
31	Retallack and Kirby, 2007	9.083	-79.625	2	1	17.5	14.5	3
32	Wijninga, 1996	4.667	-74.333	1	1	15.97	11.61	3
33	Hoorn, 1994	-3.387	-71.825	1	1	14.8	12.6	3
34	Hoorn, 1994	-3.692	-73.221	1	1	14.8	12.6	3
35	Goillot et al., 2007	-4.023	-73.16	1	1	15.97	13.75	3
36	Goillot et al., 2007	-4.225	-73.364	1	1	15.97	13.75	3
37	Regali et al., 1974; Jaramillo et al., 2010	1.361	-49.339	1	1	15.97	5.33	5
38	Behling and Costa, 2004	-1.264	-48.446	1	1	15.97	5.33	5
39	Regali et al., 1974; Jaramillo et al., 2010	-16.129	-38.616	1	1	15.97	5.33	5
40	Regali et al., 1974; Jaramillo et al., 2010	-24.492	-45.51	1	1	15.97	5.33	5
41	Alpers and Brimhall, 1988	-24.297	-69.068	26	5	15	13	3
42	Quattrocchio et al., 2003	-24.862	-65.409	14	3	16	13	4
43	Barreda et al., 2006	-28.917	-67.516	15	3	14	11.61	4

44	Barreda et al., 2003	-29.539	-68.929	14	3	17.1	14	5
45	Ottone et al., 1998	-32.044	-69.793	14	3	23.03	11.61	5
46	Barreda et al., 2008	-38.67	-61.266	4	2	15.97	11.61	3
47	Quattrocchio and Guerstein, 1989	-39.286	-60.895	20	4	15.97	11.61	3
48	Quattrocchio and Guerstein, 1989	-38.912	-62.145	20	4	15.97	11.61	3
49	Barreda et al., 2008	-39.36	-62.672	4	2	15.97	11.61	3
50	Guerstein et al., 1995	-40.346	-62.91	20	4	15.97	11.61	3
51	Barreda et al., 2008	-40.723	-64.4	4	2	15.97	11.61	3
52	Macphail and Cantrill, 2006	-51.353	-60.692	4	2	15.97	5.33	5
53	Zamaloa, 2000; Zamaloa and Romero, 2005	-52.724	-68.606	4	2	18	14	4
54	Mohr, 2001	-60.896	-42.615	5	6	15.8	14.2	4
55	Anderson et al., 2011	-63.26	-53.04	24	8	16	12.8	3
56	Warny et al., 2009	-77.75	-165.283	22	8	15.7	15.5	3
57	Grimsson and Denk, 2007; Grimsson et al., 2007	65.773	-24.083	4	2	15	15	1
58	Bratseva, 1980	65.755	-24.021	4	2	16	13	3
59	Alcalá et al., 1996	42.144	-7.761	4	2	14	11.61	4
60	Gardère and Pais, 2007	43.928	-0.181	4	2	15.97	12	3
61	Jiménez-Moreno and Suc, 2007	41.174	1.102	16	3	15.97	13.65	4
62	Alvarez Ramis and Fernandez Marron, 1994	40.187	-0.664	4	2	15.97	11.61	3
63	Jiménez-Moreno and Suc, 2007	37.369	-2.969	14	3	15.97	13.65	4
64	Favre et al., 2007; Jiménez-Moreno and Suc, 2007	36.663	-2.614	14	3	14	10.2	4
65	Favre et al., 2007; Jiménez-Moreno and Suc, 2007	36.519	-4.105	14	3	14.2	11.61	4
66	Jiménez-Moreno and Suc, 2007	36.38	-4.519	14	3	14	11.61	4
67	Larsson et al., 2011	55.83	8.42	4	2	15.97	14.9	3
68	Larsson et al., 2011	55.83	8.42	4	2	14.9	13.6	3
69	Ferguson et al., 1998	50.758	6.447	4	2	15.97	11.61	4
70	Sittler, 1958	47.07	5	4	2	16	14	
71	Meon-Vilain, 1968	46.947	7.444	4	2	17	15	5
72	Châteauneuf et al., 2006	44.011	6.216	4	2	16.57	15.8	3
73	Bialkowski et al., 2006	44.028	6.234	4	2	15.97	13.75	3

74	Jiménez-Moreno and Suc, 2007	44.03	5.976	4	2	16.8	13.2	4
75	Bessedik, 1984	43.67	5.529	4	2	14	12	3
76	Jiménez-Moreno and Suc, 2007	43.536	4.928	4	2	17	15.5	4
77	Planderová, 1971	36.134	10.375	4	2	16.4	13	3
78	Gregor et al., 1989	48.848	10.857	4	2	16	13.7	3
79	Kovar-Eder et al., 1998	50.197	12.567	4	2	16.9	13.7	3
80	Kovar-Eder et al., 1998	49.311	12.173	4	2	16.9	12.75	3
81	Gregor et al., 1989	48.976	11.954	4	2	16	13.7	3
82	Böhme et al., 2007	48.55	11.9833	15	3	14.3	13.8	3
83	Böhme et al., 2007	48.55	12.05	15	3	14.3	13.8	3
84	Böhme et al., 2007	48.55	12.75	15	3	14.3	13.8	3
85	Gregor et al., 1989	48.577	13.423	4	2	16	13.7	3
86	Kovar-Eder et al., 1998	49.059	14.715	4	2	16	11.1	3
87	Durska, 2008	52.362	18.471	4	2	16	14	3
88	Kováčová et al., 2009	47.988	16.23	4	2	14.7	14.2	2
89	Jiménez-Moreno et al., 2008	43.867	16.483	4	2	15.97	14	2
90	Holcová et al., 1996	48.225	19.578	4	2	16.3	15	3
91	Erdei et al., 2007	48.182	19.525	4	2	15	13.6	2
92	Jiménez-Moreno, 2006	46.533	18.717	4	2	15.97	13.65	1
93	Jiménez-Moreno, 2006	46.166	18.513	4	2	15.97	13.65	2
94	Syabryaj et al., 2007	48.08	23.03	4	2	14	12.7	3
95	Ercegovac et al., 1997	44.717	21.233	4	2	16.3	11.6	4
96	Ivanov et al., 2002	44.029	22.765	4	2	15	12.2	3
97	Ivanov et al., 2002	43.886	22.756	4	2	14.2	12.2	3
98	Ivanov et al., 2007	43.493	28.246	4	2	14.9	11.61	3
99	Akgün and Akyol, 1999; Akgün et al., 2007	37.77	27.929	4	2	15.97	13.65	3
100	Kayseri and Akgün, 2010	37.043	28.045	4	2	15.97	13.7	3
101	Yakubovskaya and Iosifova, 1968	52.664	41.43	4	2	15.97	12	3
102	Bekker-Migdisova, 1967	45.044	41.972	4	2	15.97	11.61	3
103	Dzhabarova, 1980	40.354	47.704	4	2	14.1	12.4	3

104	Whybrow and McClure, 1980	23.931	52.268	3	1	15	14	3
105	Simon et al., 1984	5.356	-3.495	1	1	15.97	11.61	4
106	Oboh, 1992	4.656	5.953	12	3	15.97	11.61	3
107	Oboh, 1995	4.78	6.254	12	3	15.97	13.65	3
108	Wheeler et al., 2007	4.573	36.396	3	1	16	14	3
109	Behrensmeyer et al., 2002	0.756	35.772	1	1	15.8	15.6	1
110	Dugas and Retallack, 1993	-0.236	35.42	12	3	15.1	12.6	2
111	Wynn and Retallack, 2001	-0.39	35.01	12	3	15.1	13	2
112	De Wit and Bamford, 1993	-30.772	20.415	2	1	15.97	11.61	3
113	Coetzee and Rogers, 1982	-32.923	18.134	12	3	16.95	11.6	4
114	Gnibidenko et al., 1999	56.057	74.79	16	3	15.97	11.61	3
115	Gnibidenko et al., 1999	55.638	73.653	16	3	15.97	11.61	3
116	Gnibidenko et al., 1999	54.93	73.362	16	3	15.97	11.61	3
117	Abusiarova, 1966	42.05	70.125	4	2	15.97	11.61	5
118	Il'inskaya, 1962	48.036	84.092	5	6	15.97	5.33	5
119	Sun and Zhang, 2008	44.1	86.333	4	2	18	15	4
120	Sun and Wang, 2005	36.567	101.733	6	6	15.97	11.61	3
121	Gu et al., 1992	36.118	102.801	20	4	20	13.7	4
122	Jiang and Ding, 2008	36.379	106.099	16	3	20.13	14.25	2
123	Jiang and Ding, 2008	36.379	106.099	17	3	14.25	11.35	2
124	Sun and Wang, 2005	43.65	111.967	16	3	16	5.33	4
125	Baranova et al., 1970; Nikitin, 2007	63.552	128.459	7	6	15.97	13.65	3
126	Kezina and Ol'kin, 2000	54.132	128.239	4	2	15.97	13.75	3
127	Zyryanov, 1992	75.89	142.43	7	6	16	14	5
128	Lavrushin and Alekseev, 2005	75.351	139.036	7	6	15.97	11.7	4
129	Laukhin and Rybakova, 1981	70.197	146.181	7	6	15.97	5.33	4
130	Verkhovskaya and Kundyshev, 1991	68.692	158.7	8	6	16	14	4
131	Nikitin, 2007	64.818	168.664	7	6	15.97	13.65	3
132	Tao, 1997	42.5	119.25	4	2	15.97	11.61	4
133	Liu and Leopold, 1994; Sun et al., 2002	36.553	118.786	4	2	17	14	3

134	Zheng et al., 1981	33.345	120.166	4	2	15.97	5.33	4
135	Yi, 1998	35.306	123.35	4	2	23.02	11.61	3
136	Kong, 2000	42.483	130.085	4	2	15.97	11.61	4
137	Kong, 2000	40.683	128.593	4	2	15.97	11.61	4
138	Kong, 2000	38.709	127.81	4	2	15.97	11.61	4
139	Klimova, 1988	45	135	4	2	15.97	11.61	4
140	Lopatina, 2001; 2004	47.491	138.609	4	2	17	15	5
141	Igarashi et al., 2000	43.211	144.126	4	2	15.97	11.61	4
142	Fuji, 1969	37.114	136.811	4	2	15.97	11.61	3
143	Yamanoi, 1984	36.585	137.358	4	2	15.9	15.5	3
144	Matsuoka, 1990	34.658	136.029	4	2	16.1	14.3	2
145	Chung and Koh, 2005	36.085	129.31	4	2	15	14.7	2
146	Hu and Sarjeant, 1992	30.421	126.437	1	1	15.97	11.61	4
147	Hu and Sarjeant, 1992	29.365	124.818	1	1	15.97	11.61	4
148	Hu and Sarjeant, 1992	27.976	125.819	1	1	15.97	11.61	4
149	Ling, 1965; Ho, 1966	25.132	121.706	4	2	15.97	11.61	3
150	Lakhanpal and Guleria, 1986	31.95	76.267	1	1	15.97	11.61	3
151	Prasad, 1993	29.5	78.733	1	1	15.97	11.61	4
152	Prasad et al., 2004	29.267	79.517	1	1	15.97	11.61	3
153	Srivastava and Awasthi, 1994	8.857	76.616	1	1	15.97	11.61	3
154	Varma et al., 1986	8.625	76.95	1	1	23.03	11.61	3
155	Antal and Prasad, 1997	26.913	88.507	1	1	15.97	11.61	3
156	Aswal, 1993	24.245	93.107	1	1	15.97	11.61	3
157	Wang, 1988	24.123	107.259	2	1	17	11.61	3
158	Lei, 1985	22.174	113.551	4	2	15.97	5.33	3
159	Dzanh, 1990	21.098	105.783	4	2	15.97	11.61	3
160	Zhao et al., 2004	21.4	97.817	4	2	23.03	11.61	5
161	Vozenin-Serra et al., 1989	19.149	100.274	1	1	15.97	11.61	3
162	Songtham et al., 2003	17.836	99.292	1	1	15.97	11.61	4
163	Nielsen et al., 2007	13.158	108.711	1	1	13.9	10	4

164	Highton et al., 1997	10.19	102.19	1	1	15.97	12	4
165	Watanasak et al., 1995	8.024	98.882	1	1	15.97	11.61	3
166	Daneshian et al., 2007	12.136	93.114	1	1	15.97	14	3
167	Konzalova, 2005	1.85	113.62	1	1	16	5.33	5
168	Morley and Morley, 2011	-0.06	118.58	1	1	15.97	13.65	3
169	Archer et al., 1991	-20.55	139.595	1	1	16	14	3
170	Beeston et al., 1994	-21.382	147.204	4	2	17	14	3
171	Beeston et al., 1994	-21.819	148.036	4	2	17	14	3
172	Martin, 1997	-30.184	145.793	4	2	16	7.3	3
173	Martin, 1993	-34.428	140.662	4	2	15.97	11.61	4
174	Martin, 1993	-34	141.744	4	2	15.97	11.61	4
175	Martin, 1993	-34.751	143.416	4	2	15.97	11.61	4
176	Martin, 1993	-34.044	144.52	4	2	15.97	11.61	4
177	Martin, 1993	-35.421	144.859	4	2	15.97	11.61	4
178	Kershaw, 1997	-38.185	146.354	4	2	16	15	3
179	Holdgate et al., 2007	-38.189	146.319	4	2	16	11.61	3
180	Moore and Wallace, 2000	-36.86	175.434	4	2	16	13	4
181	Pole, 2003	-45.314	168.996	15	3	14	12	4
182	Field et al., 2009	-45.96	167.554	4	2	15.34	14.44	3
183	Mildenhall and Pocknall, 1984	-45.873	167.696	4	2	18	13	3
184	Lewis et al., 2008	-77.5	161.25	24	8	14.12	13.82	1

Seravallian

Location number	Literature	latitude	longitude	Biome number	Megabiome number	Oldest age	Youngest age	Q
1	Norris, 1997	69.5	-135.75	7	6	15.97	10.4	4
2	Leopold and Liu, 1994; Grimaldi and Triplehorn, 2008	63.85	-148.376	7	6	16	13	3
3	Leopold and Liu, 1994; Grimaldi and Triplehorn, 2008	63.85	-148.376	7	6	13	9	3
4	White et al., 1997	63.9	-148.9	7	6	13.6	11.6	2
5	Piel, 1977	53.921	-122.778	4	2	16	11.61	3

6	Rouse and Mathews, 1979	52.974	-122.498	6	6	13	11	4
7	Mathews and Rouse, 1963	51.011	-121.358	5	6	12	8	1
8	Mathews and Rouse, 1984	51.505	-122.232	4	2	17	13.5	3
9	Read, 2000	51.193	-120.936	4	2	15.97	11.61	3
10	Sparks et al., 1972	46.929	-124.055	5	6	12	5	4
11	Baghai and Jorstad, 1995	46.45	-115.67	4	2	12	10.5	1
12	Prakash et al., 1962	45.857	-111.474	4	2	11.8	9	4
13	Dorf, 1938	44.29	-117.092	5	6	11.8	6	4
14	Smith, 1941	43.68	-115.832	15	3	12	10	4
15	Davis and Ellis, 2010	41.951	-116.914	14	3	11.92	11.86	1
16	Axelrod, 1964; Leopold and Denton, 1987	42.097	-113.889	7	6	11.8	9	4
17	Bartley et al., 2010	39.781	-123.235	4	2	15.97	11.61	3
18	Axelrod, 1995	39.593	-119.373	4	2	14.8	12.4	1
19	Scott, 1926	37.664	-121.731	5	6	11.8	8.7	3
20	Berry, 1927; Axelrod, 1940	37.783	-117.361	5	6	12.9	12.5	2
21	Axelrod, 1939	35.214	-118.336	14	3	15.5	11.8	4
22	Gray, 1960	34.605	-112.495	14	3	11.8	9	3
23	Axelrod, 2000	36.479	-121.372	4	2	12	10	3
24	Martin and Gray, 1962	33.78	-118.261	4	2	13.6	10.3	3
25	Macginitie, 1962; Gabel et al., 1998	42.817	-101.083	16	3	13	10	4
26	Macginitie, 1962; Gabel et al., 1998	43.083	-99.833	16	3	13	10	4
27	Schiebout et al., 1996	31.047	-93.206	4	2	12	10	3
28	Pazzaglia et al., 1997	39.602	-76.038	4	2	12	9	4
29	McLaughlin et al., 2008	38.548	-75.063	4	2	12	10	3
30	Godfrey and Barnes, 2008; McLaughlin et al., 2008	38.548	-75.063	4	2	13	12	3
31	Frederiksen, 1984; Axelrod, 2000	41.323	-70.813	4	2	16	11	4
32	Castañeda-Posadas et al., 2009	19.327	-98.306	1	1	13	13	4
33	Graham, 1975	19.526	-96.905	4	2	12	10	4
34	Martínez-Hernández, 1992	16.803	-92.906	1	1	15.97	5.33	4
35	Wijninga, 1996	4.667	-74.333	1	1	15.97	11.61	3

36	Kay and Madden, 1997	3.219	-74.602	1	1	13.5	11.8	2
37	Burnham and Carranco, 2004	-2.757	-78.85	3	1	12.3	8.6	4
38	Burnham and Carranco, 2004	-2.757	-78.85	3	1	13	10.2	5
39	Burnham and Carranco, 2004	-3.991	-79.19	3	1	12.3	8.6	5
40	Hoorn, 1994	-3.692	-73.221	1	1	14.8	12.6	3
41	Hoorn, 1994	-3.387	-71.825	1	1	14.8	12.6	3
42	Regali et al., 1974; Jaramillo et al., 2010	1.361	-49.339	1	1	15.97	5.33	5
43	Behling and Costa, 2004	-1.264	-48.446	1	1	15.97	5.33	5
44	Regali et al., 1974; Jaramillo et al., 2010	-16.129	-38.616	1	1	15.97	5.33	5
45	Regali et al., 1974; Jaramillo et al., 2010	-24.492	-45.51	1	1	15.97	5.33	5
46	Alpers and Brimhall, 1988	-24.297	-69.068	26	5	15	13	3
47	Quattrocchio et al., 2003	-24.862	-65.409	14	3	16	13	4
48	Barreda et al., 2006	-28.917	-67.516	15	3	14	11.61	4
49	Ottone et al., 1998	-32.044	-69.793	14	3	23.03	11.61	5
50	Barreda et al., 2008	-38.67	-61.266	4	2	15.97	11.61	3
51	Quattrocchio and Guerstein, 1989	-39.286	-60.895	20	4	15.97	11.61	3
52	Quattrocchio and Guerstein, 1989	-38.912	-62.145	20	4	15.97	11.61	3
53	Barreda et al., 2008	-39.36	-62.672	4	2	15.97	11.61	3
54	Guerstein et al., 1995	-40.346	-62.91	20	4	15.97	11.61	3
55	Barreda et al., 2008	-40.723	-64.4	4	2	15.97	11.61	3
56	Macphail and Cantrill, 2006	-51.353	-60.692	4	2	15.97	5.33	5
57	Anderson et al., 2011	-63.26	-53.04	24	8	16	12.8	3
58	Marenssi et al., 2010	-64.167	-57.75	28		12.4	10	4
59	Denk et al., 2005; Grımsson and Denk, 2007	65.792	-23.252	4	2	12	12	1
60	Bratseva, 1980	65.755	-24.021	4	2	16	13	3
61	Grimsson et al., 2007	65.499	-23.295	4	2	13.5	13.5	1
62	Alcalá et al., 1996	42.144	-7.761	4	2	14	11.61	4
63	Antunes et al., 1997	38.469	-9.175	4	2	13	11.5	3
64	Rivas-Carballo et al., 1994	41.661	-4.784	15	3	13	11.6	3
65	Gardère and Pais, 2007	43.928	-0.181	4	2	15.97	12	3

66	Gómez-Gras et al., 2001	41.411	2.07	4	2	13.75	11.61	3
67	Alvarez Ramis and Fernandez Marron, 1994	40.187	-0.664	4	2	15.97	11.61	3
68	Jiménez-Moreno and Suc, 2007	36.38	-4.519	14	3	14	11.61	4
69	Favre et al., 2007; Jiménez-Moreno and Suc, 2007	36.519	-4.105	14	3	14.2	11.61	4
70	Favre et al., 2007; Jiménez-Moreno and Suc, 2007	36.663	-2.614	14	3	14	10.2	4
71	Ermolli, 1991	50.251	4.604	4	2	13.65	11.61	3
72	Ermolli, 1991	50.296	4.782	4	2	13.65	11.61	3
73	Ermolli, 1991	50.252	4.841	4	2	12	10	3
74	Ferguson et al., 1998	50.758	6.447	4	2	15.97	11.61	4
75	Mosbrugger et al., 1994	50.911	6.502	4	2	13.65	11.61	3
76	Figueiral et al., 1999	50.911	6.501	4	2	12	10	4
77	Jiménez-Moreno and Suc, 2007	47.056	6.747	4	2	13.4	13.2	4
78	Jiménez-Moreno and Suc, 2007	45.841	5.566	4	2	12.6	12.2	4
79	Bialkowski et al., 2006	44.028	6.234	16	3	13.75	11.61	3
80	Jiménez-Moreno and Suc, 2007	44.03	5.976	4	2	16.8	13.2	4
81	Bessedik, 1984	43.67	5.529	4	2	14	12	3
82	Larsson et al., 2011	55.83	8.42	4	2	13.6	11.61	3
83	Larsson et al., 2011	55.83	8.42	4	2	14.9	13.6	3
84	Kovar-Eder et al., 1998	49.311	12.173	4	2	16.9	12.75	3
85	Gregor et al., 1989	48.456	11.524	5	6	12.75	11.6	3
86	Gregor et al., 1989	48.468	10.965	5	6	12.75	11.6	3
87	Gregor et al., 1989	48.313	9.919	5	6	12.75	11.6	3
88	Gregor et al., 1989	47.763	10.141	4	2	13.7	12.75	3
89	Uhl et al., 2003	47.699	9.293	4	2	13	11.61	3
90	Jiménez-Moreno and Suc, 2007	42.659	9.387	16	3	12.9	12.2	4
91	Planderová, 1971	36.134	10.375	4	2	16.4	13	3
92	Kovar-Eder et al., 1998	49.059	14.715	4	2	16	11.1	3
93	Sadowska, 1997	50.3	18.666	4	2	13.6	12.6	3
94	Jiménez-Moreno, 2006	46.533	18.717	4	2	13.65	11.61	1
95	Jiménez-Moreno, 2006	46.166	18.513	4	2	13.65	11.61	2

96	Erdei et al., 2007	48.238	21.231	4	2	12.7	11.6	3
97	Erdei et al., 2007	48.268	21.357	4	2	12.7	11.6	3
98	Syabryaj et al., 2007	48.25	23	4	2	12.7	11.61	3
99	Syabryaj et al., 2007	48.08	23.03	4	2	14	12.7	3
100	Pantic and Mihajlovic, 1977	44.794	20.488	4	2	12.7	11.6	3
101	Stevanovic and Pantic, 1954; Utescher et al., 2007	44.6	20.289	4	2	13	12.4	3
102	Pantic, 1956; Utescher et al., 2007	44.271	19.89	4	2	12.7	12.4	3
103	Pantic, 1956; Utescher et al., 2007	44.368	20.737	4	2	13	12.7	3
104	Pantic, 1956; Utescher et al., 2007	44.217	20.853	4	2	13	12.4	3
105	Milovanovic and Mihajlovic, 1984; Utescher et al., 2007	44.066	21.522	4	2	13.65	12.4	3
106	Pantic, 1956; Utescher et al., 2007	43.91	21.505	4	2	13.65	13.3	3
107	Ivanov et al., 2002	44.029	22.765	4	2	15	12.2	3
108	Ivanov et al., 2002	43.886	22.756	4	2	14.2	12.2	3
109	Chirilă and Tabără, 2008	47.343	26.226	4	2	13	12	3
110	Chirilă and Tabără, 2010	47.446	26.419	4	2	12.7	12	3
111	Brânzilă and Ţabără, 2005	47.6	27.15	4	2	12.6	11.6	3
112	Brânzilă and Ţabără, 2005	47.467	27.217	4	2	12.6	11.6	3
113	Brânzilă and Ţabără, 2005	47.519	27.449	4	2	12.6	11.6	3
114	Chirilă, 2010	47.028	27.127	4	2	13	11	3
115	Brânzilă and Ţabără, 2005	47.068	27.777	4	2	12.6	11.6	3
116	Iamandei and Iamandei, 2010	46.764	27.8	4	2	12.7	11.61	3
117	Horaicu, 1989; Erdei et al., 2007	46.291	26.563	4	2	12.7	11.61	3
118	Syabryaj et al., 2007	46.75	30.52	16	3	12.7	11.61	3
119	Ivanov et al., 2007	43.493	28.246	4	2	14.9	11.61	3
120	Akgün et al., 2007	39.112	27.575	4	2	13.65	12	3
121	Ioakim and Solounias, 1985	37.72	26.863	4	2	11.9	10.48	1
122	Akgün et al., 2007	38.952	28.117	4	2	13.65	12	3
123	Karayiğit et al., 1999	38.366	28.571	4	2	13	12.4	3
124	Akgün and Akyol, 1999	37.974	28.844	16	3	12	10	3
125	Akgün et al., 2007	37.323	28.321	4	2	13.65	12	3

126	Syabryaj et al., 2007	45.27	33.43	6	6	13.3	12.7	3
127	Filipova, 2002	45.124	36.685	16	3	13.6	11.61	3
128	Akgün et al., 2007	40.167	31.921	4	2	13.65	12	3
129	Akgün et al., 2007	37.626	31.922	4	2	13.65	12	3
130	Akgün et al., 2007	40.929	35.201	4	2	13.65	12	3
131	Akgün et al., 2007	38.926	34.337	4	2	13.65	12	3
132	Yakubovskaya and Iosifova, 1968	52.664	41.43	4	2	15.97	12	3
133	Bekker-Migdisova, 1967	45.044	41.972	4	2	15.97	11.61	3
134	Fataliyev, 1970	41.547	46.76	4	2	12.7	11.61	4
135	Dzhabarova, 1980	40.354	47.704	4	2	14.1	12.4	3
136	Dzhabarova, 1980	40.354	47.704	14	3	12.4	11.61	3
137	Simon et al., 1984	5.356	-3.495	1	1	15.97	11.61	4
138	Oboh, 1992	4.656	5.953	12	3	15.97	11.61	3
139	Jacobs and Kabuye, 1989; Jacobs and Deino, 1996	0.883	35.8	1	1	12.6	12.6	1
140	Dugas and Retallack, 1993	-0.236	35.42	12	3	15.1	12.6	2
141	Wynn and Retallack, 2001	-0.39	35.01	12	3	15.1	13	2
142	De Wit and Bamford, 1993	-30.772	20.415	2	1	15.97	11.61	3
143	Coetzee and Rogers, 1982	-32.923	18.134	12	3	16.95	11.6	4
144	Arkhipov et al., 2005	56.746	61.772	16	3	12	9	3
145	Gnibidenko et al., 1999	56.057	74.79	16	3	15.97	11.61	3
146	Gnibidenko et al., 1999	55.638	73.653	16	3	15.97	11.61	3
147	Gnibidenko et al., 1999	54.93	73.362	16	3	15.97	11.61	3
148	Abusiarova, 1966	42.05	70.125	4	2	15.97	11.61	5
149	Wang; 1996; Wang et al., 2010	38.219	92.683	14	3	14.5	7.2	4
150	Sun and Wang, 2005	36.567	101.733	6	6	15.97	11.61	3
151	Jiang and Ding, 2008	36.379	106.099	17	3	14.25	11.35	2
152	Sun and Wang, 2005	43.65	111.967	16	3	16	5.33	4
153	Lavrushin and Alekseev, 2005	75.351	139.036	7	6	15.97	11.7	4
154	Laukhin and Rybakova, 1981	70.197	146.181	7	6	15.97	5.33	4
155	Nikitin, 2007	59.994	142.872	7	6	13.65	11.61	3

156	Lopatina, 2001; 2004	48.588	139.724	4	2	12	5.33	5
157	Liu et al., 1996	46.593	131.333	4	2	12	7	3
158	Klimova, 1988	45	135	4	2	15.97	11.61	4
159	Igarashi et al., 2000	43.211	144.126	4	2	15.97	11.61	4
160	Tao, 1997	42.5	119.25	4	2	15.97	11.61	4
161	Kong, 2000	42.483	130.085	4	2	15.97	11.61	4
162	Kong, 2000	40.683	128.593	4	2	15.97	11.61	4
163	Kong, 2000	38.709	127.81	4	2	15.97	11.61	4
164	Fuji, 1969	37.114	136.811	4	2	15.97	11.61	3
165	Wang et al., 2001	36.93	137.029	4	2	13	9.2	1
166	Liu, 1986	36.599	118.57	4	2	12	10	4
167	Zheng et al., 1981	33.345	120.166	4	2	15.97	5.33	4
168	Hu and Sarjeant, 1992	30.421	126.437	1	1	15.97	11.61	4
169	Hu and Sarjeant, 1992	29.365	124.818	1	1	15.97	11.61	4
170	Hu and Sarjeant, 1992	27.976	125.819	1	1	15.97	11.61	4
171	Ling, 1965; Ho, 1966	25.132	121.706	4	2	15.97	11.61	3
172	Nandi, 1980	32.215	75.854	1	1	13.1	11.1	3
173	Sarkar and Singh, 1994	31.041	76.718	1	1	13.6	10	3
174	Lakhanpal and Guleria, 1986	31.95	76.267	1	1	15.97	11.61	3
175	Prasad, 1993	29.5	78.733	1	1	15.97	11.61	4
176	Prasad et al., 2004	29.267	79.517	1	1	15.97	11.61	3
177	Srivastava and Awasthi, 1994	8.857	76.616	1	1	15.97	11.61	3
178	Varma et al., 1986	8.625	76.95	1	1	23.03	11.61	3
179	Antal and Prasad, 1997	26.913	88.507	1	1	15.97	11.61	3
180	Aswal, 1993	24.245	93.107	1	1	15.97	11.61	3
181	Wang, 1988	24.123	107.259	2	1	17	11.61	3
182	Lei, 1985	22.174	113.551	4	2	15.97	5.33	3
183	Dzanh, 1990	21.098	105.783	4	2	15.97	11.61	3
184	Dzanh, 1996	21.023	105.855	4	2	13.7	11.1	4
185	Vozenin-Serra et al., 1989	19.149	100.274	1	1	15.97	11.61	3

186	Sepulchre et al., 2010	18.933	100.233	12	3	12.4	12.2	2
187	Sepulchre et al., 2010	18.317	99.683	1	1	13.3	13.1	2
188	Songtham et al., 2003	17.836	99.292	1	1	15.97	11.61	4
189	Prakash, 1973	17.04	95.221	3	1	12	4	5
190	Watanasak et al., 1995	8.024	98.882	1	1	15.97	11.61	3
191	Nielsen et al., 2007	13.158	108.711	1	1	13.9	10	4
192	Naih, 2008	7.191	115.098	1	1	13.65	11.61	4
193	Konzalova, 2005	1.85	113.62	1	1	16	5.33	5
194	Morley and Morley, 2011	-0.06	118.58	1	1	13.65	11.61	3
195	Martin, 1997	-30.184	145.793	4	2	16	7.3	3
196	Martin, 1993	-34.428	140.662	4	2	15.97	11.61	4
197	Martin, 1993	-34	141.744	4	2	15.97	11.61	4
198	Martin, 1993	-34.751	143.416	4	2	15.97	11.61	4
199	Martin, 1993	-34.044	144.52	4	2	15.97	11.61	4
200	Martin, 1993	-35.421	144.859	4	2	15.97	11.61	4
201	Holdgate et al., 2007	-38.189	146.319	4	2	16	11.61	3
202	Moore and Wallace, 2000	-36.86	175.434	4	2	16	13	4
203	Mildenhall and Pocknall, 1984; Mildenhall et al., 2003	-41.686	174.128	4	2	12	5.33	3
204	Pole, 2003	-45.314	168.996	15	3	14	12	4
205	Mildenhall and Pocknall, 1984	-45.873	167.696	4	2	18	13	3

Tortonian

Location number	Literature	latitude	longitude	Biome number	Megabiome number	Oldest age	Youngest age	Q

1	Reinink-Smith and Leopold,2005	59.667	-151.682	7	6	10	5	2
2	Wolfe, 1994	61.221	-151.196	10	7	11.3	8	2
3	Wolfe and Leopold, 1967	60.1	-149.44	10	7	11.3	8	4
4	Wahrhaftig et al., 1969; Grimaldi and Triplehorn, 2008	64.032	-148.215	8	6	8.1	6.7	2
5	Leopold and Liu, 1994; Grimaldi and Triplehorn, 2008	63.85	-148.376	8	6	9	5.4	3
6	White et al., 1997	63.9	-148.9	10	7	11.6	6	2
7	Leopold and Liu, 1994; Grimaldi and Triplehorn, 2008	63.85	-148.376	7	6	13	9	3
8	Leopold and Liu, 1994; Grimaldi and Triplehorn, 2008	63.302	-144.573	8	6	9	5.4	2
9	Martin and Rouse, 1966; White et al., 1994	54.028	-132.033	7	6	9	5.33	4
10	Rouse and Mathews, 1979	52.974	-122.498	6	6	13	11	4
11	Mathews and Rouse, 1963	51.011	-121.358	5	6	12	8	1
12	Sparks et al., 1972	46.929	-124.055	5	6	12	5	4
13	Sparks et al., 1972	47.232	-123.176	5	6	11.6	5.33	3
14	Smiley, 1963	48.026	-120.339	4	2	10.5	9.5	4
15	Berry, 1931; Smiley, 1963	47.894	-119.19	4	2	10.5	9.5	5
16	Smiley, 1963	46.602	-120.506	4	2	10.5	9.5	4
17	Roberts and Whitehead, 1984	44.314	-123.297	4	2	11.6	7.25	4
18	Retallack et al., 2002	44.5	-119.633	16	3	7.5	7.3	1
19	Baghai and Jorstad, 1995	46.45	-115.67	4	2	12	10.5	1
20	Dorf, 1938	44.29	-117.092	5	6	11.8	6	4
21	Beuchler et al., 2007	43.053	-116.468	15	3	10	8.5	1
22	Davis and Ellis, 2010	42.138	-116.914	14	3	9	7	2
23	Smith, 1941	43.68	-115.832	15	3	12	10	4
24	Davis and Ellis, 2010	42.313	-114.259	14	3	10.61	10.43	1
25	Axelrod, 1964; Leopold and Denton, 1987	42.097	-113.889	7	6	11.8	9	4
26	Prakash et al., 1962	45.857	-111.474	4	2	11.8	9	4
27	Barnosky, 1984	43.684	-110.69	6	6	9.2	8.9	1
28	Scott, 1926	37.664	-121.731	5	6	11.8	8.7	3
29	Tidwell and Nambudiri, 1989	35.368	-117.908	14	3	10	9	2
30	Axelrod, 2000	36.479	-121.372	4	2	12	10	3

31	Ballog and Malloy, 1981; Axelrod, 2000	33.85	-120.758	14	3	10	5.33	2
32	Martin and Gray, 1972	33.78	-118.261	4	2	13.6	10.3	3
33	Davis and Moutoux, 1998	34.5	-112	14	3	7.5	2.5	2
34	Gray, 1960	34.605	-112.495	14	3	11.8	9	3
35	Macginitie, 1962; Gabel et al., 1998	43.083	-99.833	16	3	13	10	4
36	Macginitie, 1962; Gabel et al., 1998	42.817	-101.083	16	3	13	10	4
37	Thomasson, 2005	41.324	-102.132	16	3	10.3	6	3
38	Thomasson, 2005	38.511	-100.935	16	3	10.3	6	3
39	Schiebout et al., 1996	31.047	-93.206	4	2	12	10	3
40	Wrenn et al., 2003	31.847	-91.656	2	1	8.65	7.88	2
41	Farlow et al., 2001; Shunk, 2009	40.5	-85.8	16	3	9.9	8.9	3
42	McCartan et al., 1990	38.685	-76.846	4	2	10	6	3
43	Pazzaglia et al., 1997	39.602	-76.038	4	2	12	9	4
44	McLaughlin et al., 2008	38.548	-75.063	4	2	10	9	3
45	McLaughlin et al., 2008	38.548	-75.063	4	2	12	10	3
46	Greller and Rachele, 1983	40.034	-74.333	4	2	11.5	10.5	4
47	Frederiksen, 1984; Axelrod, 2000	41.323	-70.813	4	2	16	11	4
48	Graham, 1975	19.526	-96.905	4	2	12	10	4
49	Graham, 1998	14.752	-89.484	4	2	11.6	5.33	5
50	Martínez-Hernández, 1992	16.803	-92.906	1	1	15.97	5.33	4
51	Berry, 1939	23.061	-81.583	1	1	11.6	5.33	4
52	Graham, 1990	19.172	-72.724	3	1	11.6	4	5
53	Berry, 1937	10.174	-61.538	1	1	11.6	5.33	5
54	Hoorn, 1994; 2006	-0.334	-70.241	1	1	9	6.5	3
55	Hoorn, 1994; 2006	-0.418	-70.299	1	1	9	6.5	3
56	Burnham and Carranco, 2004	-2.757	-78.85	3	1	12.3	8.6	4
57	Burnham and Carranco, 2004	-2.757	-78.85	3	1	13	10.2	5
58	Berry, 1929	-4.011	-79.271	1	1	11.6	5.33	4
59	Burnham and Carranco, 2004	-3.991	-79.19	3	1	12.3	8.6	5
60	Rebata-H et al., 2006	-4.5	-73.583	1	1	10	8	3

61	Hoorn, 1994; Latrubesse et al., 2007	-4.498	-71.446	12	3	9	6.5	3
62	Hoorn, 1994; Latrubesse et al., 2007	-4.4	-70.991	1	1	9	7	4
63	Leite, unpublished; Leite et al., unpublished; Pound et al., 2011	-5.25	-71.55	1	1	9.7	8.2	4
64	Regali et al., 1974; Jaramillo et al., 2010	1.361	-49.339	1	1	15.97	5.33	5
65	Behling and Costa, 2004	-1.264	-48.446	1	1	15.97	5.33	5
66	Hoorn, 1994; Latrubesse et al., 2007	-10.155	-67.817	12	3	9	6.5	3
67	Hoorn, 1994; Latrubesse et al., 2007	-10.923	-69.927	12	3	9	6.5	3
68	Regali et al., 1974; Jaramillo et al., 2010	-16.129	-38.616	1	1	15.97	5.33	5
69	Garcia et al., 2008	-23.031	-45.545	4	2	11.6	3	4
70	Regali et al., 1974; Jaramillo et al., 2010	-24.492	-45.51	1	1	15.97	5.33	5
71	Gregory-Wodzicki, 2002	-17.257	-69.441	3	1	10.5	10.5	1
72	Gregory-Wodzicki et al., 1998; Gregory-Wodzicki, 2002	-17.335	-69.135	3	1	10.72	10.6	1
73	Alonso et al., 1991; Clarke, 2006	-24.634	-66.707	26	5	8	6	2
74	Acevedo et al., 1997	-25.389	-66.093	1	1	9	5.2	3
75	Starck and Anzótegui, 2001	-25.606	-66.134	1	1	9	4	3
76	Anzótegui and Cuadrado, 1996; Barreda et al., 2007	-25.711	-66.045	12	3	11.6	5.33	3
77	Mautino and Anzótegui, 2002a; 2002b	-27.2	-66.733	12	3	11.6	5.33	3
78	Anzótegui et al., 2007; Barreda et al., 2007	-27.801	-66.937	12	3	11.6	5.33	3
79	Anzótegui et al., 2007; Barreda et al., 2007	-29.739	-68.014	14	3	11.6	5.33	3
80	Troncoso and Encinas, 2006	-33.958	-71.871	15	3	11	5.33	3
81	Barreda et al., 2008	-38.67	-61.266	15	3	11.61	5.33	3
82	Quattrocchio and Guerstein, 1989	-38.912	-62.145	4	2	11.61	8	3
83	Barreda et al., 2008	-39.36	-62.672	15	3	11.61	5.33	3
84	Guler et al., 2001	-39.937	-60.845	14	3	11.6	5.33	3
85	Guerstein et al., 1995	-40.346	-62.91	4	2	11.61	7.25	3
86	Barreda et al., 2008	-40.642	-62.799	15	3	11.61	5.33	3
87	Barreda et al., 2008	-40.723	-64.4	15	3	11.6	5.33	3
88	Barreda et al., 2007	-40.529	-65.451	14	3	11.6	5.33	3
89	Barreda et al., 2008	-42.541	-64.284	15	3	11	9	2
90	Barreda, V., Palazzesi, L., 2007; Barreda et al., 2007	-42.681	-63.907	14	3	11.6	5.33	3

91	Macphail and Cantrill, 2006	-51.353	-60.692	4	2	15.97	5.33	5
92	Marenssi et al., 2010	-64.167	-57.75	28		12.4	10	4
93	Marenssi et al., 2010	-64.167	-57.75	0		10	9	4
94	Marenssi et al., 2010	-64.167	-57.75	28		9	5.33	4
95	Head et al., 1989	59.532	-47.783	4	2	9	6.5	3
96	Denk et al., 2005	65.4	-21.777	5	6	9	8	1
97	Denk et al., 2005	65.663	-21.94	4	2	10	10	1
98	Denk et al., 2005	65.637	-15.038	5	6	9	8	1
99	Denk et al., 2005	65.059	-14.058	4	2	10	10	1
100	Koreneva et al., 1976	69.005	-7.708	7	6	10	5.5	3
101	Boulter and Manum, 1997	79.414	2.264	10	7	11	9	5
102	Koreneva et al., 1976	67.785	5.388	7	6	11.6	10.5	4
103	Boulter, 1971; Pound et al., 2012	53.15	-1.73	4	2	9	7.25	3
104	Larsson et al., 2011	55,83	8.42	4	2	11.61	7.25	3
105	Antunes and Pais, 1984	38.699	-9.083	4	2	11.1	9.7	5
106	Antunes et al., 1997	38.469	-9.175	4	2	13	11.5	3
107	Rivas-Carballo et al., 1994	40.661	-4.786	15	3	11.6	7.25	4
108	Barrón, E., 1997	42.381	-1.851	4	2	10	9	3
109	Jiménez-Moreno and Suc, 2007; Favre et al., 2007	36.663	-2.614	14	3	14	10.2	4
110	Bachiri Taoufiq and Barhoun, 2001	34.259	-3.734	4	2	8	7.5	3
111	Bachiri Taoufiq and Barhoun, 2001	34.206	-3.732	15	3	8	7.5	3
112	Bugnicourt et al., 1988	43.109	0.323	4	2	11.6	5.33	3
113	Barrón, 1999a;1999b	42.445	1.698	4	2	11.6	9	3
114	Barrón and Diéguez, 2005	42.331	1.768	4	2	11.6	9	3
115	Agustí et al., 2003	41.561	2.011	4	2	9.2	9	2
116	Porta et al., 1977	41.184	1.471	4	2	9	7.5	3
117	Ermolli, 1991	50.252	4.841	4	2	12	10	3
118	van Der Burgh, 1987	50.817	6.271	4	2	11.6	5.33	5
119	Figueiral et al., 1999	50.911	6.501	4	2	12	10	4
120	Kvacek et al., 2002; Bruch et al., 2006	50.917	6.417	4	2	9	7.25	4

121	van der Burgh, 1994	50.499	7.233	4	2	11.6	5.33	5
122	Sittler, 1958	47.24	6.03	4	2	11.6	5.33	3
123	Mai, 1995	45.771	3.119	4	2	8.7	6	3
124	Jan du Chene, 1974	46.358	4.908	4	2	11.6	7.2	3
125	Jan du Chene, 1974	46.475	5.158	4	2	11.6	7.2	3
126	Jan du Chene, 1974	46.308	5.044	4	2	11.6	7.2	3
127	Jan du Chene, 1974	46.247	5.222	4	2	11.6	7.2	3
128	Jan du Chene, 1974	46.494	5.392	4	2	11.6	7.2	3
129	Blanc et al., 1974	46.05	5.313	4	2	10	9	3
130	Combémorel et al., 1970	46.006	5.288	4	2	11.6	9	3
131	Gregor et al., 1989	48.17	11.618	7	6	9.7	7.7	3
132	Gregor et al., 1989	48.466	12.362	7	6	11.6	7.7	3
133	Gregor et al., 1989	48.239	12.859	7	6	11.6	7.7	3
134	Harrison and Harrison, 1989	42.791	11.365	4	2	9	8.5	3
135	Bertini, 2002	43.166	11.598	4	2	11.61	6	3
136	Bertini, 1994	43.468	13.368	4	2	8.2	5.33	3
137	Bertini, 2002	38.703	16.023	4	2	11.61	6	3
138	Kovar-Eder et al., 1998	49.059	14.715	4	2	16	11.1	3
139	Gabrielová and Planderová, 1967	49.131	14.704	4	2	11.61	7.25	3
140	Mai, 1995; Bruch et al., 2006	48.12	16.339	4	2	11.7	8.7	3
141	Harzhauser et al., 2008	48.101	16.353	4	2	10	9	3
142	Erdei et al., 2007	47.234	16.51	4	2	11.6	8.9	4
143	Hofmann and Zetter, 2005	47.202	16.373	4	2	9	8.2	3
144	Worobiec et al., 2009	51.811	18.285	4	2	11.6	5.33	3
145	Worobiec and Lesiak, 1998; Worobiec and Worobiec, 2005	51.237	19.328	4	2	10	7	4
146	Kita, 1963	49.992	20.3	4	2	11.61	7.25	3
147	Oszlast, 1967	50.568	21.655	4	2	11.6	7.25	3
148	Nagy, 1967; Bruch et al., 2006	46.166	18.513	4	2	11.6	7.25	4
149	Nagy, 1984	47.322	18.962	4	2	11.6	7.25	3
150	Nagy, 1984	47.743	20.07	4	2	11.6	7.25	3

151	Erdei et al., 2009; Bruch et al., 2006	48.083	20.5	4	2	7.7	6.3	3
152	Erdei et al., 2007	47.926	21.09	4	2	11.6	8.9	3
153	Syabryaj et al., 2007	48.23	22.67	4	2	11.5	7.1	3
154	Rybakova, 1966	48.417	23.367	4	2	11.6	9	3
155	Rybakova, 1966	48.417	23.367	6	6	9	6.2	3
156	Guşă et al., 1998	47.401	26.299	4	2	11.6	9	3
157	Chirilă, 2010	47.028	27.127	4	2	13	11	3
158	Mai, 1995	46.843	29.64	4	2	9.6	8.7	3
159	Pantic, 1956; Utescher et al., 2007	44.495	20.603	4	2	8.55	7.25	3
160	Baltes, 1967	44.794	23.278	6	6	11.6	7.25	4
161	Ivanov et al., 2002	43.5	23.2	4	2	10	7.25	3
162	Ivanov and Lazarova, 2005	42.202	26.546	4	2	9.7	7.75	3
163	Ivanov et al., 2007	43.493	28.246	16	3	11.6	10	3
164	Gjani et al., 2003	41.332	19.831	4	2	11.6	7.25	3
165	Velitzelos and Gregor, 1990	40.682	21.709	4	2	11.6	5.33	4
166	Velitzelos and Gregor, 1990	40.147	22.012	4	2	11.6	5.33	4
167	Solounias and Dawson-Saunders, 1988	38.001	23.939	4	2	9	6.5	3
168	Orgetta, 1979	38.006	23.946	16	3	11.61	5.33	4
169	Zidianakis et al., 2007	35.37	24.204	4	2	7.5	6	3
170	Sachse and Mohr, 1996; Bruch et al., 2006	35.063	25.722	4	2	8	7	3
171	Ioakim et al., 1997	35.195	26.182	4	2	11.61	7.25	3
172	Sauvage, 1977	36.799	27.103	4	2	11.6	5	5
173	Ioakim and Solounias, 1985	37.72	26.863	4	2	11.9	10.48	1
174	Akgün and Akyol, 1999	37.974	28.844	16	3	12	10	3
175	Akyol and Akgün, 1990; Helvacı and Alaca, 1991	39.392	28.131	16	3	11	5.33	5
176	Filipova, 2002	45.124	36.685	4	2	10	8.5	3
177	Filipova, 2002	45.124	36.685	16	3	8.5	7	3
178	Akgün et al., 2002	40.617	37.488	16	3	8.65	7.25	3
179	Akgün et al., 2007	39.853	37.384	16	3	9.9	9.9	3
180	Akgün et al., 2007	38.675	39.223	4	2	10.6	10.6	4

181	Shatilova and Ramishvili, 1984	42.552	41.554	4	2	8	6	5
182	Dzhabarova, 1980	40.354	47.704	4	2	11.6	5.33	3
183	van Der Burgh, 1987	52.483	43.017	4	2	11.6	5.33	5
184	Alvarez Ramis et al., 2000	28.713	-17.886	4	2	11.6	4	4
185	Medus, 1975	12.618	-16.288	1	1	11.6	5.33	4
186	Medus, 1975	13.762	-13.688	1	1	11.6	5.33	4
187	Báldi-Beke et al., 1987	5.259	-3.969	1	1	10	5.33	3
188	Poumot, 1989	4	6	1	1	10	10	3
189	Morley and Richards, 1993	4.461	5.951	1	1	8.2	7.6	2
190	Morley and Richards, 1993	4.461	5.951	12	3	7.6	7.25	2
191	Médus et al., 1988	7.933	8.8	12	3	11.6	5.33	4
192	Vignaud et al., 2002	15.263	16.335	19	4	7.4	6	4
193	Poumot and Suc, 1984	31.72	31.116	12	3	11.6	7.25	3
194	Horowitz and Horowitz, 1985	33.05	35.6	13	3	10	7.1	4
195	Kingston and Hill, 1999	24.007	52.333	19	4	8	6	3
196	Yemane et al., 1985; 1987	12.583	37.1	1	1	9.8	5.33	4
197	Eisawi and Schrank, 2008	10.137	33.004	19	4	11.6	5.33	3
198	Eisawi and Schrank, 2008	8.526	33.502	19	4	11.6	5.33	3
199	Lemoigne, 1978	8.068	37	12	3	11.6	5.33	5
200	Kingston et al., 2002	0.942	35.952	1	1	7.8	6.7	1
201	Cronk, 1990	-15.958	-5.698	4	2	10.1	8.5	1
202	van Zinderen Bakker Sr, 1980	-19.188	9.386	13	3	11.25	6	5
203	Coetzee, 1978	-33.011	18.143	6	6	11.6	5.33	5
204	Coetzee, 1978	-34.061	18.701	6	6	11.6	5.33	5
205	Arkhipov et al., 2005	56.746	61.772	16	3	12	9	3
206	Volkova et al., 1986	55.35	70.151	16	3	11.5	9	4
207	Kulkova and Volkova, 1997	52.299	76.95	16	3	7.5	5.5	3
208	Abusiarova, 1966	44.143	79.142	16	3	11.6	5.33	5
209	Il'inskaya, 1962	48.036	84.092	5	6	15.97	5.33	3
210	Zyryanov et al., 1992; Fradkina et al., 2005	69.286	101.066	10	7	8.9	8.4	3

211	Chernyaeva et al., 2007	53.838	111.996	16	3	11.6	8.5	1
212	Wang, 1990	43.646	111.976	16	3	11.6	9	3
213	Sun and Wang, 2005	43.65	111.967	16	3	16	5.33	4
214	Nikitin, 2007	59.824	149.607	10	7	11.6	5.33	3
215	Nikitin, 2007	58.369	159.177	6	6	11.6	5.33	5
216	Nikitin, 2007	65.623	173.452	10	7	11.6	5.33	3
217	Lopatina, 2001; 2004	48.588	139.724	4	2	12	5.33	5
218	Liu et al., 1996	46.593	131.333	4	2	12	7	3
219	Korotky and Demidova, 1977; Korotky et al., 2005	42.708	133.073	4	2	11	10	3
220	Wang, 1996; Wang et al., 2010	38.219	92.683	14	3	14.5	7.2	4
221	Liu, 1988	37.263	94.472	16	3	11.6	5.33	3
222	Sun and Wang, 2005	39.717	98.533	4	2	11.6	8.6	5
223	Liu, 1986	39.733	98.492	16	3	11.6	5.33	3
224	Sun and Wang, 2005	39.717	98.533	20	4	8.6	8.4	5
225	Sun and Wang, 2005	39.717	98.533	16	3	8.4	6.93	5
226	Gu et al., 1992	36.045	101.978	20	4	11.1	8.7	3
227	Jiang and Ding, 2008	36.379	106.099	17	3	14.25	11.35	2
228	Jiang and Ding, 2008	36.379	106.099	14	3	11.35	8.3	2
229	Jiang and Ding, 2008	36.379	106.099	16	3	8.3	8.05	2
230	Jiang and Ding, 2008	36.379	106.099	14	3	8.05	5.5	2
231	Liu, 1988	38.481	119.211	16	3	11.6	5.33	3
232	Ma et al., 2005	35.068	107.114	16	3	8.1	6.73	2
233	Liu, 1988	34.262	108.954	16	3	11.6	5.33	3
234	Li et al., 2006	34.633	105.917	4	2	11.67	7.7	3
235	Li et al., 2006	34.633	105.917	16	3	7.7	6	3
236	Liu, 1988	30.644	104.071	16	3	11.6	5.33	3
237	Liu, 1986	36.599	118.57	4	2	12	10	4
238	Chung and Koh, 2005	36.05	129.361	5	6	10.5	9.5	3
239	Takahashi and Kim, 1979	36.006	129.383	4	2	11.6	7.25	4
240	Wang et al., 2001	36.93	137.029	4	2	13	9.2	1

241	Heusser, 1992	40.195	138.241	4	2	9	8	3
242	Fuji, 1969	37.066	136.925	4	2	11.6	5.33	3
243	Ozaki, 1991	36.69	138.772	7	6	11.6	7	4
244	Ozaki, 1991	36.346	138.879	4	2	11.6	6.4	1
245	Ozaki, 1991	36.451	138.038	5	6	10.5	7.9	2
246	Ozaki, 1991	36.139	139.34	4	2	9	7	4
247	Ozaki, 1991	35.217	137.086	4	2	9	8	3
248	Liu, 1988	34.219	120.104	16	3	11.6	5.33	3
249	Zheng et al., 1981	33.345	120.166	4	2	15.97	5.33	4
250	Li et al., 1987	32.121	118.723	4	2	11.6	9	3
251	Hu and Sarjeant, 1992	30.421	126.437	4	2	11.61	5.33	4
252	Hu and Sarjeant, 1992	29.365	124.818	4	2	11.61	5.33	4
253	Hu and Sarjeant, 1992	27.976	125.819	4	2	11.61	5.33	4
254	Canright, 1974	25.158	121.766	4	2	11.6	5.33	3
255	Gu et al., 1992	27.06	117.18	16	3	8.7	5.33	3
256	Nandi, 1980	32.215	75.854	4	2	11.1	5.33	3
257	Banerjee, 1968	31.417	76.433	6	6	10.6	6.8	5
258	Nandi, 1980	32.215	75.854	1	1	13.1	11.1	3
259	Banerjee, 1968	31.417	76.433	4	2	11	10.6	5
260	Sarkar and Singh, 1994	31.041	76.718	4	2	13.6	10	3
261	Nandi, 1980	30.047	77.891	4	2	11.1	5.33	3
262	Sarkar et al., 1994	29.973	78.157	1	1	11	4.1	4
263	Awasthi and Prasad, 1990; Mugnier et al., 1999	28.955	80.254	2	1	11.6	7	3
264	Prasad and Pradhan, 1998	28.65	81.5	1	1	11	7	4
265	Hoorn et al., 2000	27.763	82.777	20	4	8	6.5	3
266	Prasad and Pradhan, 1998	28.133	81.667	1	1	11	7	4
267	Prasad and Awasthi, 1996; Mugnier et al., 1999	27.777	82.834	1	1	11	7	3
268	Hoorn et al., 2000	27.763	82.777	4	2	11.5	8	3
269	Li and Guo, 1976	29.679	89.091	4	2	11.6	5.33	4
270	Antal et al., 1996; Mugnier et al., 1999	26.87	88.623	1	1	11	7	5

271	Awasthi and Srivastava, 1990; Guleria, 1992	12.011	75.306	1	1	11.6	4.33	4
272	Ramanujam, 1987; Guleria, 1992	9.49	76.326	1	1	11.6	4.33	4
273	Guleria, 1992; Srivastava and Awasthi, 1994	8.878	76.589	1	1	11.6	4.33	4
274	Awasthi and Ahuja, 1982; Guleria, 1992	8.727	76.71	1	1	11.6	4.33	4
275	Saxerna, 1992; Rao et al., 2009	11.517	79.455	1	1	11	5.33	4
276	Saxerna, 1992; Rao et al., 2009	11.589	79.517	1	1	11	5.33	4
277	Chandra and Kumar, 1997; Saxena et al., 1998	8.007	86.283	1	1	11	5.33	4
278	Awasthi et al., 1994	23.458	91.797	1	1	11.6	5.33	4
279	Prakash et al., 1994	24.463	92.707	1	1	10	6	5
280	Prakash et al., 1994	25.78	93.239	1	1	10	6	5
281	Banerjee et al., 1973; Uddin and Lundberg, 1999	26.983	94.63	4	2	10	6	5
282	Prakash et al., 1994	27.213	95.392	1	1	10	6	5
283	Xu et al., 2008	25.167	101.367	1	1	11.25	5.33	4
284	Xia et al., 2009	23.813	103.198	4	2	11.6	9	3
285	Dzanh, 1996	22.327	104.518	4	2	11.1	5.33	4
286	Dzanh, 1996	22.682	106.241	4	2	11.1	5.33	4
287	Dzanh, 1996	22.255	106.471	4	2	11.1	5.33	4
288	Dzanh, 1996	21.702	106.968	4	2	11.1	5.33	4
289	Dzanh, 1996	21.023	105.855	4	2	13.7	11.1	4
290	Dzanh, 1996	21.637	104.827	4	2	11.1	5.33	4
291	Dzanh, 1996	18.93	105.098	4	2	11.1	5.33	4
292	Li and Zhang, 1998	18.716	111.46	4	2	10.5	5.33	2
293	Prakash, 1973	17.04	95.221	3	1	12	4	5
294	Chaimanee et al., 2006	15.026	102.281	19	4	9	6	4
295	Dzanh, 1996	13.782	108.249	4	2	11.1	5.33	4
296	Nielson et al., 2007	13.158	108.711	1	1	13.9	10	4
297	Dzanh, 1996	11.547	107.817	4	2	11.1	5.33	4
298	Highton et al., 1997	10.19	102.09	1	1	10	5.33	4
299	Naih, 2008	7.191	115.098	1	1	11.61	5.33	4
300	Anderson and Muller, 1975	4.942	114.943	1	1	11.6	5.33	5

301	Konzalova, 2005	1.85	113.62	1	1	16	5.33	5
302	Morley and Morley, 2011	-0.06	118.58	1	1	11.61	7.25	3
303	Martin and Mcminn, 1994; Macphail, 1997	-15.291	119.241	15	3	10.5	5.2	4
304	Leopold, 1969	-11.668	162.187	2	1	11	6	4
305	Martin and McMinn, 1993	-19.124	149.399	6	6	10	6	4
306	Hekel, 1972; Martin and McMinn, 1993	-22.561	152.578	15	3	11.6	5.33	4
307	Macphail, 1997	-32.919	120.798	15	3	10.5	5.2	4
308	Stoian, 2004	-30.976	135.101	15	3	10	5.33	3
309	Stoian and Cooper, 2003; Stoian et al., 2005	-33.712	134.495	15	3	10.5	5	3
310	Martin, 1990	-30.593	139.598	15	3	10.5	5	4
311	Macphail, 1999	-34.12	144.589	16	3	8	5	4
312	Martin, 1997	-30.184	145.793	4	2	16	7.3	3
313	Martin, 1991	-33.517	148.33	15	3	10	5.5	4
314	Macphail, 1997	-37.713	147.45	15	3	10.5	5.2	5
315	Couper and McQueen, 1954; Hornibrook, 1958	-36.296	175.473	4	2	10	4.8	3
316	Moore and Wallace, 2000	-37.114	175.686	4	2	9	8	2
317	Moore and Wallace, 2000	-36.86	175.649	4	2	11	10	2
318	Mildenhall and Pocknall, 1984; Mildenhall et al., 2003	-41.749	171.482	4	2	11.6	3.5	3
319	Couper and McQueen, 1954; Hornibrook, 1958	-46.231	167.23	4	2	10	4.8	3
320	Couper and McQueen, 1954; Hornibrook, 1958	-46.587	168.368	4	2	10	4.8	3
321	Mildenhall and Pocknall, 1984; Mildenhall et al., 2003	-41.686	174.128	4	2	12	5.33	3
322	Mildenhall and Pocknall, 1984; Mildenhall et al., 2003	-45.043	169.196	7	6	10	5	3
323	Couper and McQueen, 1954; Cotton, 1958	-41.558	175.423	4	2	10	4.8	3
324	Couper and McQueen, 1954; Hornibrook, 1958	-45.855	170.51	4	2	10	4.8	3
325	Heusser, 1986	-45.899	175.607	4	2	11.6	5.33	3
326	Truswell et al., 2005	-53.021	73.303	20	4	10	5	4

Messinian

Location number	Literature	latitude	longitude	Biome number	Megabiome number	Oldest age	Youngest age	Q
1	Matthews Jr. and Ovenden, 1990; White et al., 1997	65.883	-163.117	10	7	5.9	5.5	2
2	Reinink-Smith and Leopold,2005	59.667	-151.682	7	6	10	5	2
3	Leopold and Liu, 1994; Grimaldi and Triplehorn, 2008	63.85	-148.376	8	6	9	5.4	3
4	Wahrhaftig et al., 1969; Grimaldi and Triplehorn, 2008	64.032	-148.215	8	6	8.1	6.7	2
5	White et al., 1997	63.9	-148.9	10	7	6	5	2
6	Wahrhaftig et al., 1969; Grimaldi and Triplehorn, 2008	63.302	-144.573	8	6	9	5.4	2
7	White et al., 1994	54.023	-131.794	7	6	7.25	6.5	3
8	Martin and Rouse, 1966; White et al., 1994	54.028	-132.033	7	6	9	5.33	4
9	Sparks et al., 1972	47.232	-123.176	5	6	11.6	5.33	3
10	Sparks et al., 1972	46.929	-124.055	5	6	12	5	4
11	Retallack et al., 2002	44.5	-119.633	14	3	7.2	7.1	1
12	Dorf, 1938	44.29	-117.092	5	6	11.8	6	4
13	Davis and Ellis, 2010	42.138	-116.914	14	3	9	7	2
14	Axelrod, 1980	38.508	-120.029	15	3	7	7	1
15	Davis and Moutoux, 1998	34.5	-112	14	3	7.5	2.5	2
16	Axelrod, 1950	33.855	-117.016	16	3	7	7	4
17	Ballog and Malloy, 1981; Axelrod, 2000	33.85	-120.758	14	3	10	5.33	2
18	Thomasson, 2005	41.324	-102.132	16	3	10.3	6	3
19	Thomasson et al., 1990	39.399	-100.143	16	3	7	6	3
20	Thomasson, 2005	38.511	-100.935	16	3	10.3	6	3
21	Shunk et al., 2006; DeSantis and Wallace, 2008	36.5	-82.5	5	6	7	4.5	3
22	Groot et al., 1990; Groot, 1991	37.214	-77.394	4	2	6	5	3
23	Groot et al., 1990; Groot, 1991	38.594	-76.751	4	2	6	5	3
24	McCartan et al., 1990	38.685	-76.846	4	2	10	6	3
25	Groot et al., 1990; Groot, 1991	38.48	-75.174	4	2	6	5	3
26	Berry, 1939	23.061	-81.583	1	1	11.6	5.33	4
27	Graham, 1990	19.172	-72.724	3	1	11.6	4	5

28	Martínez-Hernández, 1992	16.803	-92.906	1	1	15.97	5.33	4
29	Graham, 1998	14.752	-89.484	4	2	11.6	5.33	5
30	Berry, 1937	10.174	-61.538	1	1	11.6	5.33	5
31	Berry, 1945	6.041	-69.84	1	1	6	5	4
32	Hoorn, 1994; 2006	-0.334	-70.241	1	1	9	6.5	3
33	Hoorn, 1994; 2006	-0.418	-70.299	1	1	9	6.5	3
34	Berry, 1929	-4.011	-79.271	1	1	11.6	5.33	4
35	Hoorn, 1994; Latrubesse et al., 2007	-4.498	-71.446	12	3	9	6.5	3
36	Hoorn, 1994; Latrubesse et al., 2007	-4.4	-70.991	1	1	9	7	4
37	Regali et al., 1974; Jaramillo et al., 2010	1.361	-49.339	1	1	15.97	5.33	5
38	Behling and Costa, 2004	-1.264	-48.446	1	1	15.97	5.33	5
39	Hoorn, 1994; Latrubesse et al., 2007	-10.155	-67.817	12	3	9	6.5	3
40	Hoorn, 1994; Latrubesse et al., 2007	-10.923	-69.927	12	3	9	6.5	3
41	Graham et al., 2001	-17.183	-66.033	1	1	7	6	3
42	Regali et al., 1974; Jaramillo et al., 2010	-16.129	-38.616	1	1	15.97	5.33	5
43	Garcia et al., 2008	-23.031	-45.545	4	2	11.6	3	4
44	Regali et al., 1974; Jaramillo et al., 2010	-24.492	-45.51	1	1	15.97	5.33	5
45	Alonso et al., 1991; Clarke, 2006	-24.634	-66.707	26	5	8	6	2
46	Acevedo et al., 1997	-25.389	-66.093	1	1	9	5.2	3
47	Starck and Anzótegui, 2001	-25.606	-66.134	1	1	9	4	3
48	Anzótegui and Cuadrado, 1996; Barreda et al., 2007	-25.711	-66.045	12	3	11.6	5.33	3
49	Mautino and Anzótegui, 2002a; 2002b	-27.2	-66.733	12	3	11.6	5.33	3
50	Anzótegui et al., 2007; Barreda et al., 2007	-27.801	-66.937	12	3	11.6	5.33	3
51	Anzótegui et al., 2007; Barreda et al., 2007	-29.739	-68.014	14	3	11.6	5.33	3
52	Troncoso and Encinas, 2006	-33.958	-71.871	15	3	11	5.33	3
53	Barreda et al., 2008	-38.67	-61.266	15	3	11.61	5.33	3
54	Quattrocchio and Guerstein, 1989	-39.286	-60.895	16	3	7.25	5.33	3
55	Barreda et al., 2008	-39.36	-62.672	15	3	11.61	5.33	3
56	Guerstein et al., 1995	-40.346	-62.91	16	3	7.25	5.33	3
57	Barreda et al., 2007	-40.529	-65.451	14	3	11.6	5.33	3

58	Barreda et al., 2008	-40.723	-64.4	15	3	11.6	5.33	3
59	Barreda et al., 2008	-40.642	-62.799	15	3	11.61	5.33	3
60	Guler et al., 2001	-39.937	-60.845	14	3	11.6	5.33	3
61	Barreda, V., Palazzesi, L., 2007; Barreda et al., 2007	-42.681	-63.907	14	3	11.6	5.33	3
62	Mercer and Sutter, 1982	-46.767	-71.667	28		7.14	5.56	1
63	Macphail and Cantrill, 2006	-51.353	-60.692	4	2	15.97	5.33	5
64	Marenssi et al., 2010	-64.167	-57.75	28		9	5.33	4
65	Head et al., 1989	59.532	-47.783	7	6	6.5	5	3
66	Head et al., 1989	59.532	-47.783	4	2	9	6.5	3
67	Denk et al., 2005; Grimsson et al., 2008	64.75	-21.6	7	6	7	6	4
68	Denk et al., 2005	66.2	-15.133	7	6	7	6	1
69	Koreneva et al., 1976	69.005	-7.708	7	6	10	5.5	3
70	Boulter and Manum, 1996	79.039	-1.782	10	7	7.25	5.33	3
71	Zagwijn, 1967	50.947	6.008	4	2	7.25	5.33	3
72	van Der Burgh, 1987	50.817	6.271	4	2	11.6	5.33	5
73	van der Burgh, 1994	50.499	7.233	4	2	11.6	5.33	5
74	Sittler, 1958	47.24	6.03	4	2	11.6	5.33	3
75	Mai, 1995	45.771	3.119	4	2	8.7	6	3
76	Roiron, 1991	45.115	2.866	5	6	5.64	5.04	1
77	Bugnicourt et al., 1988	43.109	0.323	4	2	11.6	5.33	3
78	Agustí et al., 2006	42.283	1.917	4	2	7	5.3	3
79	Suc and Cravatte, 1982; Favre et al., 2007	41.167	2.024	4	2	7.25	5.96	3
80	Bessais and Cravatte, 1988; Favre et al., 2007	40.843	1.146	4	2	6.7	5.4	4
81	Planderová and Gregor, 1992	44.676	4.674	4	2	6.1	5.33	3
82	Naud and Suc, 1975	44.656	4.577	4	2	7.25	5.33	2
83	Martinetto et al., 2007	44.717	8.1	4	2	6	5.7	4
84	Bertini, 2002	44.539	8.085	4	2	6	5.33	3
85	Bertini, 2002	44.736	11.133	4	2	7.25	5.33	3
86	Bertolani Marchetti, 1984	44.436	11.406	4	2	7.25	5.33	3
87	Bertini, 1994	44.364	11.574	4	2	7.25	5.5	3

88	Bertini, 1994	43.468	13.368	4	2	8.2	5.33	3
89	Ghetti et al., 2002	43.002	11.551	4	2	7.25	5.96	3
90	Bertini, 2002	42.996	11.556	4	2	7.25	5.33	3
91	Bertini, 2002	43.166	11.598	4	2	11.61	6	3
92	Bertini, 2002	41.78	13.915	4	2	6	5.33	3
93	Bertini, 2002	38.703	16.023	4	2	11.61	6	3
94	Suc et al., 1995	37.557	14.389	14	3	7.25	6	2
95	Kohlman-Adamska et al., 2004	51.093	16.759	4	2	7.25	5.33	4
96	Worobiec et al., 2009	51.811	18.285	4	2	11.6	5.33	3
97	Worobiec and Lesiak, 1998; Worobiec and Worobiec, 2005	51.237	19.328	4	2	10	7	4
98	Oszlast and Stuchlik, 1977	49.42	20.015	4	2	7.25	5.33	3
99	Bruch et al., 2006; Erdei et al., 2009	48.083	20.5	4	2	7.7	6.3	3
100	Syabryaj et al., 2007	48.23	22.67	4	2	11.5	7.1	3
101	Syabryaj et al., 2007	48.23	22.67	6	6	7.1	5.4	3
102	Rybakova, 1966	48.417	23.367	6	6	9	6.2	3
103	Rybakova, 1966	48.417	23.367	4	2	6.2	5.33	3
104	Petrescu, 1992	44.588	22.839	4	2	6	5.6	3
105	Ivanov et al., 2002	43.5	23.2	4	2	7.25	5.2	3
106	Utescher et al., 2009	43.056	22.928	5	6	6.4	5.2	3
107	Ivanov, 2002	41.032	21.339	4	2	7	5.33	3
108	Velitzelos and Gregor, 1990	40.682	21.709	4	2	11.6	5.33	4
109	Velitzelos and Gregor, 1990	40.147	22.012	4	2	11.6	5.33	4
110	Mohr and Redenius, 1985	39.246	23.236	4	2	7.25	5.33	3
111	Solounias and Dawson-Saunders, 1988	38.001	23.939	4	2	9	6.5	3
112	Orgetta, 1979	38.006	23.946	16	3	11.61	5.33	4
113	Zidianakis et al., 2007	35.37	24.204	4	2	7.5	6	3
114	Sachse and Mohr, 1996; Bruch et al., 2006	35.063	25.722	4	2	8	7	3
115	Ioakim et al., 1997	35.195	26.182	14	3	7.25	5.33	3
116	Sauvage, 1977	36.799	27.103	4	2	11.6	5	5
117	Guernet et al., 1976	36.872	27.328	4	2	7.25	5.33	4

118	Akyol and Akgün, 1990; Helvacı and Alaca, 1991	39.392	28.131	16	3	11	5.33	5
119	Popescu, 2006	42.1	29.617	4	2	7.25	5.96	3
120	Filipova, 2002	45.124	36.685	16	3	8.5	7	3
121	Filipova, 2002	45.124	36.685	4	2	7	5.7	3
122	Filipova, 2002	45.124	36.685	16	3	5.7	5.33	3
123	van Der Burgh, 1987	52.483	43.017	4	2	11.6	5.33	5
124	Ramishvili, 1961	43.232	40.34	4	2	7	6	3
125	Shatilova and Ramishvili, 1984	42.552	41.554	4	2	8	6	5
126	Dzhabarova, 1980	40.354	47.704	4	2	11.6	5.33	3
127	Alvarez Ramis et al., 2000	28.713	-17.886	4	2	11.6	4	4
128	Bachiri Taoufiq et al., 2001	33.913	-5.875	13	3	7	6.7	3
129	Jiménez-Moreno and Suc, 2007; Favre et al., 2007	36.519	-4.105	14	3	7.25	5.96	4
130	Jiménez-Moreno and Suc, 2007; Favre et al., 2007	36.663	-2.614	14	3	7.25	5.96	4
131	Chikhi, 1992; Favre et al., 2007	35.453	-0.561	15	3	6.1	5.96	3
132	Chikhi, 1992; Fauquette et al., 2006	35.589	-0.09	15	3	6.1	5.96	3
133	Dechamps and Maes, 1987	30.169	20.096	12	3	7.25	5.33	3
134	Poumot and Suc, 1984	31.72	31.116	12	3	7.25	5.33	3
135	Horowitz and Horowitz, 1985	33.05	35.6	13	3	10	7.1	4
136	Kingston and Hill, 1999	24.007	52.333	19	4	8	6	3
137	Medus, 1975	12.618	-16.288	1	1	11.6	5.33	4
138	Medus, 1975	13.762	-13.688	1	1	11.6	5.33	4
139	Báldi-Beke et al., 1987	5.259	-3.969	1	1	10	5.33	3
140	Durugbo et al., 2010	4.55	4.267	12	3	6	5	3
141	Dunay et al., 1999	3.66	7.993	12	3	7.25	5.33	3
142	Médus et al., 1988	7.933	8.8	12	3	11.6	5.33	4
143	Vignaud et al., 2002	15.263	16.335	19	4	7.4	6	4
144	Schuster et al., 2006	16.317	18.683	26	5	7	5	4
145	Yemane et al., 1985; 1987	12.583	37.1	1	1	9.8	5.33	4
146	Eisawi and Schrank, 2008	10.137	33.004	19	4	11.6	5.33	3
147	Eisawi and Schrank, 2008	8.526	33.502	19	4	11.6	5.33	3

148	Lemoigne, 1978	8.068	37	12	3	11.6	5.33	5
149	Bonnefille, 2010	1.163	30.378	3	1	6	5.5	3
150	Jacobs and Deino, 1996	0.917	35.833	3	1	7.2	6.7	1
151	Kingston et al., 2002	0.942	35.952	1	1	7.8	6.7	1
152	van Zinderen Bakker Sr, 1980	-19.188	9.386	13	3	11.25	6	5
153	Coetzee, 1978	-33.011	18.143	6	6	11.6	5.33	5
154	Coetzee, 1978	-34.061	18.701	6	6	11.6	5.33	5
155	Belkin, 1964	67.5	64.033	7	6	7.25	5.33	3
156	Kulkova and Volkova, 1997	52.299	76.95	16	3	7.5	5.5	3
157	Il'inskaya, 1962	48.036	84.092	5	6	15.97	5.33	3
158	Abusiarova, 1966	44.143	79.142	16	3	11.6	5.33	5
159	Sun et al., 2009	38.433	81.083	26	5	7	7	3
160	Liu, 1988	37.263	94.472	16	3	11.6	5.33	3
161	Sun and Wang, 2005	39.717	98.533	16	3	8.4	6.93	5
162	Liu, 1986	39.733	98.492	16	3	11.6	5.33	3
163	Nikitin, 2007	59.824	149.607	10	7	11.6	5.33	3
164	Nikitin, 2007	68.054	162.006	10	7	7.25	5.33	4
165	Nikitin, 2007	58.369	159.177	9	6	11.6	5.33	5
166	Nikitin, 2007	65.623	173.452	10	7	11.6	5.33	3
167	Nikitin, 2007	64.758	175.046	10	7	7.25	5.33	4
168	Lopatina, 2001; 2004	48.588	139.724	4	2	12	5.33	5
169	Liu et al., 1996	46.593	131.333	4	2	12	7	3
170	Liu, 1988	38.481	119.211	16	3	11.6	5.33	3
171	Jiang and Ding, 2008	36.379	106.099	14	3	8.05	5.5	2
172	Liu, 1988	34.262	108.954	16	3	11.6	5.33	3
173	Ma et al., 2005	35.068	107.114	16	3	6.73	5.67	2
174	Ma et al., 2005	35.068	107.114	16	3	8.1	6.73	2
175	Ma et al., 2005	35.068	107.114	20	4	5.67	3.71	2
176	Li et al., 2006	34.633	105.917	16	3	7.7	6	3
177	Liu, 1988	30.644	104.071	16	3	11.6	5.33	3

178	Liu, 1988	34.219	120.104	16	3	11.6	5.33	3
179	Fuji, 1969	37.066	136.925	4	2	11.6	5.33	3
180	Ozaki, 1991	36.69	138.772	7	6	11.6	7	4
181	Ozaki, 1991	36.346	138.879	4	2	11.6	6.4	1
182	Ozaki, 1991	36.139	139.34	4	2	9	7	4
183	Ozaki, 1991	36.1	138.8	7	6	6.29	3.1	2
184	Hu and Sarjeant, 1992	30.421	126.437	4	2	11.61	5.33	4
185	Hu and Sarjeant, 1992	29.365	124.818	4	2	11.61	5.33	4
186	Hu and Sarjeant, 1992	27.976	125.819	4	2	11.61	5.33	4
187	Gu et al., 1992	27.06	117.18	16	3	8.7	5.33	3
188	Canright, 1974	25.158	121.766	4	2	11.6	5.33	3
189	Nandi, 1980	32.215	75.854	4	2	11.1	5.33	3
190	Banerjee, 1968	31.417	76.433	6	6	10.6	6.8	5
191	Nandi, 1980	30.047	77.891	4	2	11.1	5.33	3
192	Sarkar et al., 1994	29.973	78.157	1	1	11	4.1	4
193	Awasthi and Prasad, 1990; Mugnier et al., 1999	28.955	80.254	2	1	11.6	7	3
194	Prasad and Pradhan, 1998	28.65	81.5	1	1	11	7	4
195	Prasad and Awasthi, 1996; Mugnier et al., 1999	27.777	82.834	2	1	7	5.33	3
196	Hoorn et al., 2000	27.763	82.777	20	4	8	6.5	3
197	Prasad and Pradhan, 1998	28.133	81.667	1	1	11	7	4
198	Prasad and Awasthi, 1996; Mugnier et al., 1999	27.777	82.834	1	1	11	7	3
199	Lukose, 1968	26.983	84.85	1	1	6.15	5.33	3
200	Li and Guo, 1976	29.679	89.091	4	2	11.6	5.33	4
201	Antal et al., 1996; Mugnier et al., 1999	26.87	88.623	1	1	11	7	5
202	Awasthi and Srivastava, 1990; Guleria, 1992	12.011	75.306	1	1	11.6	4.33	4
203	Ramanujam, 1987; Guleria, 1992	9.49	76.326	1	1	11.6	4.33	4
204	Guleria, 1992; Srivastava and Awasthi, 1994	8.878	76.589	1	1	11.6	4.33	4
205	Awasthi and Ahuja, 1982; Guleria, 1992	8.727	76.71	1	1	11.6	4.33	4
206	Saxerna, 1992; Rao et al., 2009	11.589	79.517	1	1	11	5.33	4
207	Saxerna, 1992; Rao et al., 2009	11.517	79.455	1	1	11	5.33	4

208	Chandra and Kumar, 1997; Saxena et al., 1998	8.007	86.283	1	1	11	5.33	4
209	Handique and Dutta, 1981	27.083	95.289	4	2	6.2	5.33	3
210	Prakash et al., 1994	27.213	95.392	1	1	10	6	5
211	Banerjee et al., 1973; Uddin and Lundberg, 1999	26.983	94.63	4	2	10	6	5
212	Prakash et al., 1994	25.78	93.239	1	1	10	6	5
213	Prakash et al., 1994	24.463	92.707	1	1	10	6	5
214	Awasthi et al., 1994	23.458	91.797	1	1	11.6	5.33	4
215	Xu et al., 2008	25.167	101.367	1	1	11.25	5.33	4
216	Dzanh, 1996	22.327	104.518	4	2	11.1	5.33	4
217	Dzanh, 1996	22.682	106.241	4	2	11.1	5.33	4
218	Dzanh, 1996	22.255	106.471	4	2	11.1	5.33	4
219	Dzanh, 1996	21.702	106.968	4	2	11.1	5.33	4
220	Dzanh, 1996	21.637	104.827	4	2	11.1	5.33	4
221	Dzanh, 1996	18.93	105.098	4	2	11.1	5.33	4
222	Li and Zhang, 1998	18.716	111.46	4	2	10.5	5.33	2
223	Prakash, 1973	17.04	95.221	3	1	12	4	5
224	Chaimanee et al., 2006	15.026	102.281	19	4	9	6	4
225	Dzanh, 1996	13.782	108.249	4	2	11.1	5.33	4
226	Dzanh, 1996	11.547	107.817	4	2	11.1	5.33	4
227	Highton et al., 1997	10.19	102.09	1	1	10	5.33	3
228	Naih, 2008	7.191	115.098	1	1	11.61	5.33	4
229	Anderson and Muller, 1975	4.942	114.943	1	1	11.6	5.33	5
230	Konzalova, 2005	1.85	113.62	1	1	16	5.33	5
231	Morley and Morley, 2011	-0.06	118.58	1	1	7.25	5.33	3
232	Leopold, 1969	-11.668	162.187	2	1	11	6	4
233	Martin and Mcminn, 1994; Macphail, 1997	-15.291	119.241	15	3	10.5	5.2	4
234	Martin and McMinn, 1993	-19.124	149.399	6	6	10	6	4
235	Hekel, 1972; Martin and McMinn, 1993	-22.561	152.578	15	3	11.6	5.33	4
236	Macphail, 1997	-32.919	120.798	15	3	10.5	5.2	4
237	Stoian and Cooper, 2003; Stoian et al., 2005	-33.712	134.495	15	3	10.5	5	3

238	Stoian, 2004	-30.976	135.101	15	3	10	5.33	3
239	Martin, 1990	-30.593	139.598	15	3	10.5	5	5
240	Macphail, 1999	-34.12	144.589	16	3	8	5	3
241	Martin, 1991	-33.517	148.33	15	3	10	5.5	3
242	Macphail, 1997	-37.713	147.45	15	3	10.5	5.2	3
243	Couper and McQueen, 1954; Hornibrook, 1958	-36.296	175.473	4	2	10	4.8	3
244	Mildenhall and Pocknall, 1984; Mildenhall et al., 2003	-41.749	171.482	4	2	11.6	3.5	3
245	Couper and McQueen, 1954; Hornibrook, 1958	-46.231	167.23	4	2	10	4.8	3
246	Couper and McQueen, 1954; Hornibrook, 1958	-46.587	168.368	4	2	10	4.8	3
247	Mildenhall and Pocknall, 1984; Mildenhall et al., 2003	-41.686	174.128	4	2	12	5.33	3
248	Mildenhall and Pocknall, 1984; Mildenhall et al., 2003	-45.043	169.196	7	6	10	5	3
249	Couper and McQueen, 1954; Cotton, 1958	-41.558	175.423	4	2	10	4.8	3
250	Couper and McQueen, 1954; Hornibrook, 1958	-45.855	170.51	4	2	10	4.8	3
251	Heusser, 1986	-45.899	175.607	4	2	11.6	5.33	3
252	Truswell et al., 2005	-53.021	73.303	20	4	10	5	4

Appendix B

Bibliography for Appendix A

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Appendix C

The fossil mammal localities presented in Chapter 6

The following table presents the 407 mammal localities recorded in MAD and used in Chapters 6 and 7. The latitude and longitude represent the present day location, whilst the age range represents the maximum range when all uncertainty is taken into account. The Q rating is the same as was presented in Appendix A. The full references for the mammal localities can be found in Appendix D.

Location number	Location name	Latitude	Longitude	Oldest age	Youngest age	References	Q
1	Courtney Pit	51.50	-112.30	9	7	Burns and Young, 1988	3
2	Westend Blowout, OR	45.80	-119.30	7.4	7	Shotwell, 1958	3
3	McKay Reservoir, OR	45.50	-118.80	10	8	Shotwell, 1956	3
4	Intermediary Gulch, MT	46.21	-112.75	7.5	6.7	Carrasco *et al.*, 2005	3
5	Gravel Pit, MT	46.22	-112.84	7.5	6.7	Carrasco *et al.*, 2005	3
6	Dempsey Creek, MT	46.40	-112.80	9.4	7.9	Konizeski, 1957	3
7	Johnson Gulch, MT	46.22	-112.73	9	7.5	Carrasco *et al.*, 2005	3
8	Little Valley, OR	43.60	-117.50	9.9	9.7	Shotwell, 1970	3
9	Juniper Creek, OR	43.60	-117.50	10.9	9.1	Shotwell, 1970	3
10	Rome, OR	43.60	-117.50	11.5	11.3	Wilson, 1937	3
11	Stroud claim, ID	43.00	-114.90	11.3	11.1	Malde and Powers, 1962	3
12	Rockland Valley Quarry, ID	42.80	-112.90	7.6	7.2	Gillette, 1999	3
13	Rockland Mole, ID	42.80	-112.90	10.4	7	Tedrow, 1997	3
14	Otis Basin, OR	42.70	-118.70	10	8.8	Shotwell, 1970	3
15	Bartlett Mountain, OR	42.70	-118.70	10.4	10.3	Shotwell, 1970	3
16	Star Valley, ID	42.00	-117.00	8	7.9	Becker and McDonald, 1998	3
17	Thousand Creek, NV	41.10	-117.80	10	9	Stirton, 1940	3
18	Nightingale Road, NV	39.86	-119.00	11.7	7.5	Macdonald, 1956	3

19	Hazen, NV	39.56	-119.11	9.81	9.81	Emry *et al.*, 2005	1
20	Churchill Butte, NV	39.00	-119.20	9.7	9.4	Kelly and Lugaski, 1999	3
21	Smiths Valley, NV	39.00	-119.20	10.9	10.8	Macdonald, 1959	3
22	Smiths Valley, NV	38.80	-119.32	10.9	8	Macdonald and Macdonald, 1976	3
23	Silver Springs, NV	39.30	-118.90	6.2	6.1	Kelly, 1998	3
24	Washoe, NV	38.80	-119.50	7.4	4.6	Kelly, 1997	3
25	Bollinger Canyon	37.82	-122.06	13.6	10.3	Edwards, 1982	3
26	Black Hawk Ranch, CA	38.04	-122.18	9.7	9	Stirton, 1939; Tseng *et al.*, 2010; White, 1991	3
27	Siphon Canal, CA	37.60	-120.80	8.35	8.03	Hirschfeld, 1981	1
28	Turlock Lake, CA	37.60	-120.80	7.7	7.6	Wagner, 1976	3
29	Point Reyes Peninsula, CA	37.90	-122.72	6.8	6	Zeigler *et al.*, 1997	3
30	Warren, CA	35.30	-118.50	7.3	5.3	Reynolds *et al.*, 1991	3
31	Powerline Road Tom Quarry, CA	35.37	-117.99	9.3	9.2	Wang *et al.*, 2005; Whistler and Burbank, 1992	1
32	Kam's False Cat Locality	35.33	-118.08	10.2	8.4	Tseng *et al.*, 2010	2
33	Sycamore, CA	35.30	-118.50	10.8	9.6	Reynolds and Czaplewski, 1989	3
34	Lava Mountains, CA	34.80	-117.00	10.8	10.7	Reynolds *et al.*, 1991	3
35	Golgotha Hill, UT	38.10	-114.17	5.89	5.23	Carrasco *et al.*, 2005; Reynolds and Lindsay, 1999	0
36	42SVO66V, UT	38.62	-112.32	10.3	7	Korth and Blieux, 2010	3
37	Pinole Junction 1,CA	37.89	-112.09	9.2	9.1	Korth and Blieux, 2010; Stirton, 1939	3
38	White Cone, AZ	35.61	-110.07	6.85	5.3	Baskin, 1979; Carraway, 2010	2
39	Rio Arriba, NM	36.50	-107.00	10.1	8.9	MacFadden, 1977	3
40	Espanola Basin	36.21	-106.07	11	10.5	Fox and Fisher, 2004	3
41	Gabaldon Badlands, NM	34.80	-106.90	11.6	11.4	Lozinsky and Tedford, 1991	3
42	The Pits, NE	42.40	-103.80	10.7	10.6	Skinner *et al.*, 1977	3
43	ZXBar, NE	42.40	-103.80	10.5	10.4	Skinner *et al.*, 1977	3
44	Rock Ledge Mastodon Quarry, NE	42.52	-100.50	10.5	9.5	Fox and Fisher, 2004	3
45	Mefferdi Quarry, NE	42.70	-100.90	11.8	10.4	Mook, 1946	3

46	Rick Irwin Site, NE	42.80	-99.60	9.2	9.1	Tucker, 2003	3
47	Honey Creek, NE	42.70	-98.80	8.7	7.7	Voorhies, 1990	3
48	Santee, NE	42.80	-97.80	7.3	7.2	Voorhies, 1990	3
49	Mailbox, NE	42.40	-98.10	8.4	8.2	Voorhies, 1990	3
50	Verdigre Creek, NE	42.39	-98.12	11	10	Voorhies and Thomasson, 1979	3
51	Kepler Quarry, NE	41.92	-103.05	11.8	9	Lambert, 2007; Voorhies, 1990	3
52	Lemoyne Quarry, NE	41.29	-101.84	10.3	4.9	Bown, 1980	3
53	Uptegrove, NE	41.10	-103.00	10.6	7.4	Voorhies, 1984	3
54	Beecher Island, CO	40.10	-102.20	9.4	9.2	Frye *et al.*, 1956	3
55	Found Quarry, KS	38.90	-101.70	8.6	8.4	Bennett, 1979	3
56	Lost Quarry, KS	38.90	-101.70	8.4	7.6	Bennett, 1979	3
57	Minium Quarry Unit 5, KS	39.40	-100.14	7	6	Thomasson *et al.*, 1990	3
58	Jack Swayze Quarry, KS	39.06	-100.76	8.5	7.5	Fox and Fisher, 2004	3
59	Amebelodon fricki Quarry, NE	40.50	-100.50	11.2	11	Voorhies, 1990	3
60	Long Island Quarry, KS	39.80	-99.40	11.1	10.1	Zakrzewski, 1988	3
61	Buis Ranch, OK	36.80	-100.50	6.6	6.5	Hibbard, 1954	3
62	Optima, OK	36.70	-101.40	9	8	Hesse, 1936; Savage, 1941	3
63	Coffee Ranch, TX	35.90	-100.20	9	7	Dalquest, 1980	3
64	Cole Highway Pit, TX	36.32	-100.07	9.5	8.5	Fox and Fisher, 2004	3
65	Lipscomb Pit 1, TX	36.10	-100.10	10.3	4.9	Lim *et al.*, 2001; Schultz, 1990	3
66	Port of Entry Pit, OK	36.03	-99.96	11.2	7.5	Fox and Fisher, 2001; Schultz, 1990	3
67	Arnett, OK	36.14	-99.94	11.9	9	Kitts, 1957	3
68	Beckerdite, KS	37.20	-99.90	11.7	8.8	Liggett, 1997	3
69	Whisenhunt Quarry, OK	36.78	-100.04	12.7	10.7	Dalquest *et al.*, 1996; Smith, 2005	3
70	Higgins Quarry,TX	36.40	-98.40	9.3	9	Dalquest and Patrick, 1989; Schultz, 1990	3
71	Pipe Creek Sinkhole, IN	40.50	-85.80	9.9	8.9	Farlow *et al.*, 2001; Martin *et al.*, 2002	3
72	Gray Fossil Site, TN	36.40	-82.50	10.1	9.9	Wallace and Wang, 2004	3
73	Lee Creek Mine, NC	35.40	-76.80	6.5	6.4	Tedford and Hunter, 1984	3
74	Sunken Meadow Pond, VA	37.20	-76.90	11.6	7.2	Baum and Wheeler, 1977;	3

75	John Seyfried beach, MD	38.40	-76.41	10	9	Godfrey and Barnes, 2008 Fuller and Godfrey, 2007	3
76	Cove Point, MD	38.35	-76.40	10	9	Godfrey and Barnes, 2008	3
77	Love Bone Bed, FL	29.55	-82.52	9.9	9.5	Baskin, 1980, 1981, 1986, 2005; Hulbert-Jr., 2005; MacFadden and Cerling, 1996; Webb *et al.*, 1981	3
78	Moss Acres Racetrack, FL	29.30	-82.35	9	8.9	Hulbert Jr., 1988; Lambert, 1997	3
79	Phosphate Pit, Polk County, FL	27.90	-81.80	10.3	4.9	Olsen, 1960; Webb, 1969	3
80	Payne Creek, FL	27.90	-81.80	7.9	7.8	Berta and Morgan, 1985; Hulbert, 1987	3
81	Palmetto Washer, FL	27.76	-81.98	7.9	7.8	Webb, 1969; Wright and Webb, 1984	3
82	Tiger Bay Mine, FL	27.90	-81.80	6.5	6.4	Webb, 1981	3
83	Withlacouchee 4a, FL	29.00	-82.26	7	6	Berta and Morgan, 1985; Hulbert, 1993; Tedford et al., 1987; Webb, 1969	3
84	Mauvilla, AL	30.81	-88.19	10.3	9	Hulbert Jr. and Whitmore Jr., 1997; MacFadden and Dobie, 1998	3
85	Chicasabogue Creek, AL	30.80	-88.10	10.3	4.9	Isphording and Lamb, 1971	3
86	Tunica Hills, LA	30.60	-91.30	10	5.7	Manning and MacFadden, 1989	3
87	Lepara Creek, TX	28.60	-97.70	12	11	Prothero and Manning, 1987	3
88	Screw Bean, TX	29.29	-103.07	9	7.5	Carrasco *et al.*, 2005	3
89	Redington, AZ	32.42	-110.50	6.25	5.21	Jacobs, 1977	1
90	Mount Eden, CA	33.90	-117.00	7	6	Baskin, 1982; Frick, 1921	3
91	Lawrence Canyon, CA	33.20	-117.40	7.25	5.33	Berta and Morgan, 1985; Domning and Demere, 1984	3
92	Yepomera	28.80	-108.00	5.8	5.7	Lindsay, 1984; MacFadden, 1984	3
93	Rancho el Ocote	21.11	-100.70	10.1	6.3	Carranza-Castaneda and Ferrusquía-Villafranca, 1979; Carranza-Castaneda and Miller, 1996	2
94	Rancho el Ocote	21.11	-100.70	5.7	5.6	Carranza-Castaneda and Ferrusquía-Villafranca,	2

						1979	
95	La Rinconada	21.10	-100.80	10.1	6.3	Miller and Carranza-Castaneda, 1998	3
96	Gracias	14.64	-88.59	11.8	8	Webb and Perrigo, 1984	4
97	Tio Gregorio	11.25	-70.31	11.6	5.33	Aguilera *et al.*, 2006; Carlini *et al.*, 2006a,b,c; Domning and Aguilera, 2008; Negri and Ferigolo, 2004; Riff and Aguilera, 2008; Sanchez-Villagra et al., 2003	3
98	Huila	3.30	-75.20	11.61	5.33	Miller, 1953	3
99	Acre State	-8.18	-70.48	9	6.8	Cozzuol, 2006	3
100	Talisma	-8.20	-70.50	11.61	5.33	Cozzuol, 2006	3
101	Sud Sacaco	-15.58	-74.82	6	6	Gregory McDonald and de Muizon, 2002	4
102	Sud Sacaco	-15.58	-74.82	5	5	Gregory McDonald and de Muizon, 2002	4
103	Aguada de Lomas	-15.54	-74.73	8	7	de Muizon et al., 2003; Muizon and De Vries, 1985	3
104	Achiri	-17.21	-69.00	9	6.8	Saint-André, 1996; Villarroel and Marshall, 1983	3
105	Muyu Huasi	-19.00	-65.30	11.61	5.33	Villarroel and Marshall, 1989	3
106	Petaca	-17.80	-63.20	11.61	5.33	Marshall and Sempere, 1991	3
107	Estanques de Copec	-27.03	-70.80	8.9	6.3	Canto *et al.*, 2008	1
108	Caldera	-27.10	-70.90	11.6	5.33	Walsh and Naish, 2002	3
109	Chiquimil	-26.31	-66.78	9	6.8	Magdalena Candela, 2004	3
110	El Cajon Valley	-26.61	-66.38	9	6.8	Nasif *et al.*, 2000	3
111	Tiopunca	-26.66	-66.04	12	10.7	Herbst *et al.*, 2000; Kleinert and Strecker, 2001	3
112	Villavil	-27.19	-66.89	10.7	9.3	Herbst *et al.*, 2000; Muruaga et al., 2003	3
113	Sierra de Velasco	-28.30	-67.00	11.61	5.33	Tauber, 2005	3
114	Arroyo La Petra	-33.28	-65.94	9	6.8	Cerdeño *et al.*, 2008	3
115	Telen	-36.27	-65.51	9	6.8	Montalvo *et al.*, 2008	3

116	Bajada de los Toros	-38.61	-63.00	10	9	Deschamps *et al.*, 2007	3
117	Villarino	-40.61	-63.11	10	9	Marshall, 1976; Zárate *et al.*, 2007	3
118	Salias Grandes de Hidalgo	-37.40	-61.30	9	6.8	Vizcaíno and Fariña, 1999.	3
119	Grubein	-38.80	-62.20	11.61	5.33	Deschamps, 2005	3
120	Barrancas del rio Parana	-33.70	-59.30	11.61	7.25	Marshall, 1977	3
121	Entre Rios	-33.70	-59.30	10.7	7.14	Herbst *et al.*, 2000; Muruaga *et al.*, 2003	3
122	Entre Rios	-33.70	-59.30	12	10.7	Herbst *et al.*, 2000; Muruaga *et al.*, 2003	3
123	Kiyu Beach	-34.68	-56.80	9	6.8	Rinderknecht *et al.*, 2010	3
124	Kiyu Beach	-34.74	-56.84	9	6.8	Rinderknecht *et al.*, 2007	3
125	Bahia de Colonia	-34.50	-57.80	11.61	5.33	Verde and Perea, 1992	3
126	La Plata	-34.62	-56.92	11.6	5.33	Vizcaino *et al.*, 2003	3
127	Asseiceira	39.25	-9.08	9.5	9	Fortelius, 2011	3
128	Freiria do Rio Major	39.32	-9.07	9.5	9	Fortelius, 2011	3
129	Ampudia	41.92	-4.78	11.2	9.5	Fortelius, 2011; Rossner and Heissig, 1999	0
130	Ampudia	41.92	-4.78	9.5	9	Fortelius, 2011; Rossner and Heissig, 1999	0
131	Alfacar	37.23	-3.57	8.2	7.1	Bernor *et al.*, 1996; Markov, 2008	3
132	Arenas del Rey	36.97	-3.90	7.1	5.33	Fortelius, 2011	3
133	Salobrena	36.50	-3.50	7.25	5.33	Aguilar *et al.*, 1984	3
134	Los Mansuetos	40.30	-2.60	9	5.33	de Bruijn and Mein, 1968	3
135	Batallones-1	40.65	-1.72	8.994	8.958	Fortelius, 2011; Sanchéz *et al.*, 2009	2
136	Concud3	40.38	-1.15	9	5.3	Forsten, 1979; Fortelius, 2011	3
137	Venta del Moro	39.50	-1.30	9	5.33	Mathisen and Morales, 1981	3
138	Crevillente 2	38.29	-0.79	8.7	8	Fortelius, 2011; Freudenthal *et al.*, 1991; Montoya *et al.*, 2001; van der Made *et al.*, 1992	3
139	Santa Margarita	39.70	3.10	11.61	7.25	Colom and Bauza, 1949	3
140	San Caprasio	41.74	-0.45	11	10	Agusti *et al.*, 1994	3
141	Los Valles de Fuentiduena	41.42	-0.30	11.2	9.5	Alberdi, 1981; Alberdi *et al.*, 1981; Ginsburg *et al.*, 1981;	3

						Hoyos *et al.*, 1981; Mazo, 1981; Morales *et al.*, 1981; Morales and Soria, 1981; Sese Benito and Lopez Martinez, 1981	
142	Orignac	43.12	0.17	9.5	9	Fortelius, 2011; Rossner and Heissig, 1999	3
143	El Firal	42.37	1.45	11.2	9.5	Fortelius, 2011; Rossner and Heissig, 1999	3
144	Estevar	42.47	2.00	11.2	9.5	Rossner and Heissig, 1999	3
145	Baixas	42.50	2.50	11.61	7.25	Aguilar *et al.*, 1986	3
146	Can Ponsic 1	41.60	2.08	10.6	10.58	Agusti *et al.*, 1997; Fortelius, 2011; Hartenberger and Crusafont, 1979	3
147	Can llobateres	41.53	2.10	9.7	9.5	Agusti *et al.*, 1997; Fortelius, 2011; Golpe-Posse and Crusafont-Pairo, 1982; Moya-Sola and Kohler, 1996; Petter, 1967; Robles *et al.*, 2010	3
148	Montredon	43.33	2.89	10	9	Aguilar, 1982; Aguilar and Crochet, 1982; Crochet and Green, 1982; de Beaumont, 1988; Eisenmann, 1988; Ginsburg, 1988; Ginsburg and Thomas, 1988; Guérin, 1988; Lopez Martinez, 1988; Sen, 1988; Tobien, 1988	3
149	Bretagne	47.50	-2.50	11.61	7.25	Plusquellec and Racheboeuf, 2000	3
150	Doue-la-Fontaine	47.20	-0.30	11.2	9.5	Ginsburg *et al.*, 1979	3
151	Esveres	47.30	0.30	11.2	9.5	Fortelius, 2011; Ginsburg, 1990	3
152	La Tour	47.30	2.75	7.1	5.33	Fortelius, 2011; Rossner and Heissig, 1999	3
153	Deurne	51.20	4.50	11.61	7.25	Lambert, 2005	3
154	Groenlo	52.00	6.60	11.61	5.33	van Deinse, 1931	3
155	Esbjerg	55.47	8.45	11.6	8	Pyenson and Hoch, 2007	3
156	Amberieu 1	45.96	5.36	8.7	7.75	Farjanel and Mein, 1984;	3

						Fortelius, 2011	
157	Amberieu 2A	45.96	5.36	9.7	8.7	Farjanel and Mein, 1984; Fortelius, 2011	3
158	Amberieu 2C	45.96	5.36	9.7	8.7	Farjanel and Mein, 1984; Fortelius, 2011	3
159	Amberieu 3	45.96	5.36	8.7	7.75	Farjanel and Mein, 1984; Fortelius, 2011	3
160	La Grive-St. Albans	45.60	5.23	12.75	11.1	Freudenthal and Mein, 1989	3
161	Mollon	45.57	5.15	9	8.2	Fortelius, 2011	3
162	Priay	46.01	5.29	11.6	9	Combémorel *et al.*, 1970	3
163	Soblay	46.10	5.35	9.7	8.7	Rossner and Heissig, 1999; Viret, 1949	3
164	Cucuron	43.78	5.43	7.75	7	Ballesio *et al.*, 1979; Fortelius, 2011; Mein and Michaux, 1979;	3
165	Charmoille	47.43	7.22	11.2	9.5	Kälin, 1997; Fortelius, 2011	3
166	Nebelbergweg	47.40	7.61	11.2	9.5	Fortelius, 2011; Rossner and Heissig, 1999	3
167	Wissberg	49.85	8.01	11.6	9	Tobien, 1980	3
168	Gau-Weinheim	49.85	8.05	11.6	9	Tobien, 1980	3
169	Steinberg	49.88	8.00	11.6	9	Tobien, 1980	3
170	Dintesheim	49.71	8.14	11.6	9	Tobien, 1980	3
171	Bermersheim	49.78	8.10	11.6	9	Tobien, 1980	3
172	Westhofen	49.70	8.25	11.6	9	Tobien, 1980	3
173	Dorn-Durkheim 1	49.77	8.27	9	8.2	Kaiser *et al.*, 2003	3
174	Eppelsheim	49.72	8.98	9.7	9.5	Franzen *et al.*, 2003	3
175	Hammerschmiede	47.90	10.60	11.1	9.7	Mayr and Fahlbusch, 1975	3
176	Stirone River	44.84	9.96	11.6	7.25	Bisconti, 2010	3
177	Baccinello V1	42.80	11.40	9	5.33	Fortelius, 2011; Hurzeler, 1987; Hurzeler and Engesser, 1976	3
178	Baccinello V2	42.70	11.10	8.2	7.1	Fortelius, 2011; Hurzeler, 1987; Hurzeler and Engesser, 1976	3
179	Baccinello V3	42.70	11.10	7.1	5.33	Fortelius, 2011; Hurzeler, 1987; Hurzeler and Engesser, 1976	3
180	Baccinello-Cinigiano Basin	42.78	11.25	7.58	7.52	Delfino and Rook, 2008; Fortelius, 2011	1
181	Fosso-Cassoto	43.00	11.55	7.25	5.96	Ghetti *et al.*, 2002	3

182	Roccamorice	42.40	14.00	11.61	5.33	Koretsky, 2001	3
183	Gargano	41.80	15.40	6	5	Delfino *et al*., 2007; Fortelius, 2011	3
184	Cessaniti	38.66	16.03	9	5.33	Markov, 2008	3
185	Tropea	38.68	15.90	11.61	7.25	Bagnato *et al*., 2000	3
186	Blancone 1	45.90	15.50	11.61	5.33	Freudenthal and Martin-Suarez, 2006	3
187	Mariathal	48.60	16.10	11.2	9.5	Bernor *et al*., 1996; Fortelius, 2011	3
188	Richardhof	48.10	16.30	11.1	9.7	Ziegler, 2006	3
189	Gotzendorf	47.99	16.63	11.1	9.7	Bernor *et al*., 1993; Fortelius, 2011	3
190	Kohfidisch	47.15	16.35	8.7	7.75	Bernor *et al*., 1996; Markov, 2008	3
191	Baltavar	47.00	17.00	8.2	7.1	Bernor *et al*., 1996; Markov, 2008	3
192	Sumeg	46.98	17.28	9.7	8.7	Fortelius, 2011; Mészáros, 1998	3
193	Tardosbanya	47.66	18.45	7.75	7.1	Fortelius, 2011; Mészáros, 1998	3
194	Csakvar	47.39	18.46	8.7	7.75	Fortelius, 2011; Mészáros, 1998	3
195	Polgardi-4	47.05	18.31	7.1	5.33	Fortelius, 2011; Mészáros, 1998	3
196	Pestszentlorinez	47.50	19.04	9	5.33	Bernor *et al*., 1996; Markov, 2008	3
197	Rudabanya	48.39	20.64	11	10	Fortelius, 2011; Kordos and Begun, 1997; 2002	3
198	FT3/8	47.97	20.40	11.5	9.7	Hír and Kókay, 2010	3
199	Kreka	44.42	18.45	9	5.3	van der Made and Stefanovic, 2006	3
200	Mala Miliva	44.10	21.40	11.61	7.25	Petronijevic, 1967	3
201	Belka	50.82	28.18	8.2	7.1	Bernor *et al*., 1996; Markov, 2008	3
202	Grytsiv	49.59	27.12	11.2	9.5	van der Made *et al*., 1999	3
203	FT3/10	47.98	26.40	11.4	9.7	Hír and Kókay, 2010	3
204	Pogana	46.32	27.57	9	6.1	Codrea *et al*., 2010; Fortelius, 2011	3
205	Kishinev	47.00	28.83	12	11	Fortelius, 2011; Kazár and Grigorescu, 2005	3
206	Cimislia	46.50	28.80	8.2	7.1	Bernor *et al*., 1996; Markov, 2008	3
207	Taraklia	46.50	29.00	8.2	7.1	Bernor *et al*., 1996; Markov, 2008	3

208	Orekhovka	45.66	28.95	7.1	5.33	Nesin and Storch, 2004	3
209	Frunzovka-2	47.28	29.70	8.7	7.7	Nesin and Storch, 2004	3
210	Grebbeniki	46.88	29.82	9.5	9	Bernor *et al*., 1996; Markov, 2008	3
211	Novoclizavetovka-2	47.25	30.32	8.7	7.7	Nesin and Storch, 2004	3
212	Novodizavetovka-3	47.17	30.33	7.7	7.1	Nesin and Storch, 2004	3
213	Protopopovka-3	46.88	30.07	7.7	7.1	Nesin and Storch, 2004	3
214	Novoukrainka-1	46.84	30.15	7.1	5.33	Nesin and Storch, 2004	3
215	Novoukrainka-2	46.70	30.11	7.7	7.1	Nesin and Storch, 2004	3
216	Novaya Emetovka	46.65	30.60	9.75	9	Vangengeim and Tesakov, 2008	2
217	Novaya Emetovka	46.65	30.60	8.7	8.1	Vangengeim and Tesakov, 2008	2
218	Cherevichnoe-3	46.67	30.64	7.7	7.1	Nesin and Storch, 2004	3
219	Vinogradovka-1	46.58	30.70	7.1	5.33	Nesin and Storch, 2004	3
220	Odessa	46.47	30.73	7.1	5.33	Nesin and Storch, 2004; Fortelius, 2011	3
221	Mikhailovka	47.58	31.26	9.7	7.7	Nesin and Nadachowski, 2001; Nesin and Storch, 2004	3
222	Andreevka	46.89	31.37	7.1	5.33	Fortelius, 2011; Nesin and Storch, 2004	3
223	Dolni Disan	41.33	21.97	9	5.33	Bernor *et al*., 1996; Markov, 2008	3
224	Hrabarsko	42.80	23.06	7.25	5.33	Fortelius, 2011; Spassov and Ginsburg, 1999	3
225	Dytiko	40.86	22.53	7	5.5	Bouvrain and de Bonis, 2007; de Bonis *et al*., 1995; Koufos, 1988	3
226	Pentalaphos 1	40.74	22.85	11.9	9	de Bonis et al., 1992; 1994; Geraads and Koufos, 1990; Koufos, 2000	3
227	Ravin de la Pluie	40.85	22.96	11.6	9	de Bonis *et al*., 1992; 1998; Fortelius, 2011; Geraads, 1979; Koufos, 1984	3
228	Kalimantsi	41.42	23.33	11.6	9	Geraads *et al*., 2001; Kostopoulos *et al*., 2001	3
229	Kalimantsi	41.42	23.33	9	7	Geraads *et al*., 2001; Kostopoulos *et al*., 2001; Liu *et al*., 2004	3

230	Thermopigi	41.29	23.36	9	5.3	Fortelius, 2011; Geraads *et al.*, 2007	3
231	Maramena	41.20	23.50	9	5.33	de Bruijn, 1989	3
232	Lefkon	41.10	23.50	9.7	8.7	Armour-Brown *et al.*, 1977	3
233	Hadjidimovo	41.52	23.85	7.75	7	Fortelius, 2011; Kostopoulos *et al.*, 2001	3
234	Vathylakkos-2	41.00	23.00	7.75	7	Koufos *et al.*, 2004	3
235	Ahmatovo	42.11	25.05	9	5.33	Bernor *et al.*, 1996; Markov, 2008	3
236	Ezerovo	42.02	25.30	9	5.33	Kostopoulos *et al.*, 2001	3
237	Perivolaki	39.41	22.66	7.3	7.1	Kostopoulos, 2006; Kostopoulos and Koufos, 2006b; Koufos, 2006a,b; Koufos *et al.*, 2006; Sylvestrou and Kostopoulos, 2006; Sylvestrou and Koufos, 2006; Vlachou and Koufos, 2006	2
238	Perivolaki	39.30	22.74	7.3	7.1	Kostopoulos and Koufos, 2006a	3
239	Kerassia - 3	38.85	23.32	7.75	7	Giaourtsakis *et al.*, 2006	3
240	Halmyropotamos	38.50	24.20	8.2	7.1	Bernor *et al.*, 1996; Markov, 2008	3
241	Chomateri	38.01	23.96	7.7	7	Fortelius, 2011; Roussiakis, 2009	4
242	Pikermi	38.02	23.99	8.7	7.1	Fortelius, 2011; Roussiakis, 2009	3
243	Pikermi-Valley 1	38.01	23.95	9	7	Theodorou *et al.*, 2010	3
244	Kastellios-K1	35.05	25.25	9.6	9.2	Fortelius, 2011	3
245	Maronia	35.14	26.08	11.6	5.33	Athanassiou, 2004	3
246	Gela	35.21	26.10	9	8	Poulakakis *et al.*, 2005	3
247	Gulpinar	39.53	26.12	9.5	9	Geraads and Güleç, 1999	3
248	Gulpinar-1	39.53	26.09	9	7.1	Fortelius, 2011	3
249	Gulpinar-2	39.52	26.09	8.2	7.1	Fortelius, 2011	3
250	Esendere	38.59	26.56	9	7	Kaya *et al.*, 2005	3
251	Manisa	38.58	27.20	8.2	7.1	Geraads and Güleç, 1999	3
252	Mytilinii	37.73	26.91	7.75	7.2	Kostopoulos *et al.*, 2003; Solounias, 1981	2

253	Amasya	37.80	28.30	7	4.9	Engesser, 1980	3
254	Serefkoy	37.35	28.22	8.2	7.1	Geraads and Güleç, 1999	0
255	Bayir	37.20	27.97	8.2	7.1	Fortelius, 2011; Geraads and Güleç, 1999	3
256	Kemiklitepe	37.50	29.00	9	8.2	Geraads and Güleç, 1999	3
257	Burgas	42.50	27.47	9	5.33	Bernor *et al.*, 1996; Markov, 2008	3
258	Yulafli	41.37	27.60	8.7	7	Geraads *et al.*, 2005; Kaya and Heissig, 2001	3
259	Kucukcekmece West	40.98	28.77	11.2	9	Rossner and Heissig, 1999	3
260	Kucukcekmece	40.98	28.77	9	8.2	Sickenburg, 1975	3
261	Garkin	38.42	30.32	9	8.2	Geraads and Güleç, 1999	3
262	Kavakdere	37.22	30.80	8.2	7.1	Geraads and Güleç, 1999	3
263	Kayadibi	40.23	32.40	9	8.2	Geraads and Güleç, 1999	3
264	Cobanpinar	41.16	32.53	6.3	5.8	Fortelius, 2011; van der Made et al., 2002	3
265	Kavurca	41.00	34.00	7	4.9	Engesser, 1980	3
266	Akkasdagi	39.49	33.66	7.2	7	Antoine and Saraç, 2005; de Bonis, 2005; Kazancı *et al.*, 2005; Kostopoulos, 2005; Kostopoulos and Saraç, 2005; Koufos and Vlachou, 2005; Liu and Kostopoulos, 2005; Saraç and Sen, 2005; Tassy, 2005; Valli, 2005	3
267	Hayranli-3	39.74	36.81	9.5	8.2	Fortelius, 2011	3
268	Sivas	39.71	36.93	9	7	Bibi and Güleç, 2008	3
269	Duzyayla	40.62	37.49	8.65	7.25	Akgun *et al.*, 2000; Fortelius, 2011	3
270	Kangal	39.03	37.35	7.25	5.33	Fortelius, 2011; Kaya and Forsten, 1999	3
271	Sevastopol	44.50	33.60	11	9.88	Fortelius, 2011	3
272	Kertch	45.36	36.52	9	5.33	Bernor *et al.*, 1996; Markov, 2008	3
273	Morskaya 2	47.29	39.10	7.75	7	Rossina *et al.*, 2006; Titov *et al.*, 2006	3
274	Rustavi	45.08	41.55	9	5.33	Fortelius, 2011	3

275	Iaghludja	41.71	44.80	9.7	8.7	Vekua and Lordkipanidze, 2008	3
276	Udabno	41.50	45.40	8.7	7.8	Fortelius, 2011; Vekua and Lordkipanidze, 2008	3
277	Dzedzvtakhevi	41.68	45.75	7.75	7	Vekua and Lordkipanidze, 2008	3
278	El'dar	41.00	45.70	9.7	8.7	Beliaeva, 1962	3
279	Eldari	41.18	46.73	9.7	8.7	Vekua and Lordkipanidze, 2008	3
280	Ivand-1	38.35	46.13	8	7	Fortelius, 2011; Sen and Purabrishemi, 2010	3
281	Maragheh	37.33	46.41	9.5	7	Bernor, 1986; Fortelius, 2011	1
282	Karatchok Dagh	37.06	42.23	9	5.33	Astre, 1936	3
283	Bakhtiari	34.50	44.60	11.61	9	Thomas *et al.*, 1980	3
284	Injana	33.49	44.41	10	9	Brune and Heintz, 1983; Geraads and Güleç, 1999	3
285	Bekaa Valley	33.66	35.76	9	5.33	Malez and Forsten, 1989	3
286	Afoud 1,2,8	31.03	-6.57	7.1	5.33	Benammi, 1997; Fortelius, 2011	3
287	Afoud 5	31.03	-6.57	8.2	7.1	Benammi, 1997; Fortelius, 2011	3
288	Menacer	36.44	2.62	9	5.33	Thomas and Petter, 1986	3
289	Afoud 6	31.03	-6.57	11.2	9.5	Benammi, 1997; Fortelius, 2011	3
290	d'Amama	36.22	6.03	10	9	Jaeger, 1977	0
291	Afoud 7	31.03	-6.57	9.5	9	Benammi, 1997	3
292	d'Amama	36.22	6.03	7.8	6.6	Jaeger, 1977	0
293	Oued-Tabia	31.17	-6.50	11.2	9	Fortelius, 2011	3
294	L'oued Zra	33.71	-4.60	11.6	10	Jaeger, 1977	3
295	Khendek-el-Ouaich	34.08	-3.36	8.6	6.2	Jaeger, 1977	3
296	Oued el Atheuch	33.40	-1.10	11.61	5.33	Bernor and Jaeger, 1982	3
297	Raz el Ain	35.70	-0.60	7.25	5.33	Muizon, 1981	3
298	L'Oued el Hammam	35.18	-0.10	11.6	7.25	Arambourg, 1959; Ouda and Ameur, 1978	1
299	Sidi Salem	35.12	0.08	11.6	9	Fortelius, 2011; Jaeger, 1977	3
300	Jebel Semmene	36.93	9.44	11.8	10.5	Jaeger, 1977	3

301	Oued Mellegue	36.36	8.75	11.6	8.5	Robinson and Black, 1974	3
302	Beglia	34.35	8.34	10	10	Agrasar, 2003; Fortelius, 2011; Pickford, 2000	5
303	El Menia	29.28	4.63	11.6	9	Amard *et al*., 1992	3
304	Oued Mya 1	28.93	4.20	11.6	9	Sudre and Hartenberger, 1992	3
305	Sahabi	30.08	20.75	7.1	5.33	Boaz *et al*., 1987; Markov, 2008	3
306	Sheikh Abdallah	27.74	28.46	11	10	Mein and Pickford, 2010; Pickford *et al*., 2006	3
307	Wadi El Natrun	30.46	30.36	9	7	James and Slaughter, 1974	3
308	Shuwaihat	24.10	52.44	8	6	Barry, 1999; Bishop and Hill, 1999; de Bruijn, 1999; Eisenmann and Whybrow, 1999; Gentry, 1999a,b; Rauhe *et al*., 1999; Tassy, 1999	3
309	N885	15.53	5.72	11	5	Pickford *et al*., 2009	4
310	Toros Menalla	15.26	16.34	7.4	6	Boisserie *et al*., 2005; Brunet *et al*., 2002; de Bonis *et al*., 2005; Geraads *et al*., 2008; Hautier *et al*., 2009; 2007; 2010; Lehmann *et al*., 2006; Likius *et al*., 2007; Peigné *et al*., 2005a,b; 2008a,b; Vignaud *et al*., 2002	4
311	Adu-Asa	10.17	40.33	5.8	5.2	Haile-Selassie, 2001; Haile-Selassie *et al*., 2004; WoldeGabriel *et al*., 2001	1
312	Alaya VPL2	10.03	40.30	5.8	5.5	Haile-Selassie and WoldeGabriel, 2009; Vrba and Haile-Selassie, 2006	1
313	Oromiya (Belticha)	8.90	40.30	10.5	10	Fortelius, 2011; Suwa *et al*., 2007	1
314	Albertine 1	2.00	31.00	7.25	5.33	Fortelius, 2011; Senut *et al*., 1994	3
315	Albertine 1C	1.33	30.25	7.25	5.33	Fortelius, 2011; Senut *et al*., 1994	3
316	Albertine 14	1.00	30.08	7.25	5.33	Fortelius, 2011; Senut *et al*., 1994	3

317	Albertine 7	1.08	30.42	7.25	5.33	Fortelius, 2011; Senut *et al*., 1994	3
318	Albertine 6	1.17	30.50	11.61	7.25	Fortelius, 2011; Senut *et al*., 1994	3
319	Albertine 11	0.17	30.00	7.25	5.33	Fortelius, 2011; Senut *et al*., 1994	3
320	Sinda-Mohari	1.50	31.00	7	4.5	Aoki, 1992; Van Neer, 1994	4
321	Lothagam	2.91	36.07	7.49	6.5	Fortelius, 2011; Weston, 2000	2
322	SH22	1.31	36.58	9.79	9.25	Ishida and Pickford, 1997; Tsujikawa, 2005a,b	1
323	Nakali	1.18	36.40	10	9	Aguirre and Leakey, 1974; Fortelius, 2011; Flynn and Sabatier, 1984; Morales and Pickford, 2006	3
324	Cheboit	0.85	35.86	6.1	5.9	Fortelius, 2011; Guérin and Pickford, 2005	5
325	Site 2/49A	0.90	35.90	12	9	Maglio, 1974	2
326	Lemudong'o	-1.11	35.74	6.1	6.04	Fortelius, 2011; Howell and Garcia, 2007	1
327	Manonga Valley-1	-3.90	33.73	7.1	5.33	Harrison, 1997	3
328	Harasib 3a	-19.45	17.92	11.1	9.7	Fortelius, 2011; Mein *et al*., 2000	3
329	Berk Aukas 1-31	-19.50	18.30	11.1	9.7	Conroy *et al*., 1992; Rasmussen *et al*., 1996	3
330	Swarthintjies-2	-30.30	17.30	11.6	5.33	Pickford and Senut, 1997	3
331	Groenrivier	-30.83	17.57	7.1	5.33	Fortelius, 2011	3
332	E Quarry	-32.97	18.15	6	5	Hendey, 1981	4
333	Shetirgiz	48.80	60.00	11.2	5.33	Kordikova, 1998	3
334	Ashut	50.17	66.67	11.2	5.33	Fortelius, 2011; Kordikova, 1998	3
335	Petropavlovska	54.80	69.20	11.2	5.33	Kordikova, 1998	3
336	Selety-1A	52.41	73.12	7.1	5.33	Fortelius, 2011; Vislobokova and Lavrov, 2009	3
337	Pavlodar	52.30	77.03	7.1	5.33	Fortelius, 2011; Vislobokova and Lavrov, 2009	3
338	Pavlodar	52.30	77.03	7.75	7.1	Fortelius, 2011; Vislobokova and Lavrov, 2009	3
339	Sor	39.27	67.65	8.2	7.1	Forsten and Sharapov, 2000	3

340	Marmar	39.33	67.83	9	5.33	Forsten and Sharapov, 2000	3
341	Magian	39.20	67.89	8	7	Sotnikova *et al.*, 1997	3
342	Pedjikent	39.47	68.09	8	7	Fortelius, 2011; Sotnikova *et al.*, 1997	3
343	Molayan	36.32	69.42	8	7.5	Brunet *et al.*, 1984; Heintz *et al.*, 1981; Merceron *et al.*, 2004; Sen, 2001	3
344	Y311, Potwar Plateau	33.88	72.38	10.4	8.6	Lihoreau *et al.*, 2004; Pilbeam *et al.*, 1979; 1990	3
345	Daraispon	38.52	70.62	9	8	Sotnikova *et al.*, 1997	3
346	Ortok	42.38	74.92	8	7	Fortelius, 2011; Sotnikova *et al.*, 1997	3
347	Kalmakpay	47.63	84.46	7	6	Fortelius, 2011; Sotnikova *et al.*, 1997	3
348	Taralyk Cher	51.90	95.60	7.75	7	Vislobokova, 2009a,b	3
349	CD9805	37.22	96.75	11	9	Dong, 2007	3
350	Tsaidam	37.00	97.00	11.2	9.5	Qiu and Qiu, 1995	3
351	Olkhon Island	53.19	107.57	7.5	6.5	Vislobokova and Lavrov, 2009	3
352	Qunke	36.05	101.98	11.1	8.7	Gu et al., 1992	3
353	Songshan	36.96	103.27	7.1	5.33	Fortelius, 2011	3
354	Songshan 80007	37.10	103.50	9	5.33	Zheng, 1982	3
355	Songshan 80008	37.00	103.50	9	5.33	Zheng, 1982	3
356	Jinchanggou	35.60	103.22	11.1	4.9	Wang and Qiu, 2004	3
357	Guonigou	35.64	103.27	11.1	11.1	Deng, 2007; Fortelius, 2011	3
358	Hezheng Area	35.50	103.50	9	5.33	Liu *et al.*, 2004	3
359	Wuzhong	38.00	106.20	11.2	9.5	Qiu and Qiu, 1995	3
360	Longjiagou Valley	33.40	104.92	9	5.3	Xiang-Xu and Coombs, 1985; Xue *et al.*, 2006	3
361	Yaodian	34.63	105.92	10.54	10.3	Li *et al.*, 2006; Sahni, 1979	3
362	Taohuapo Hill	35.12	107.35	7	6	Xue *et al.*, 2006	4
363	Qingyang	36.08	108.25	7.1	5.33	Qiu and Qiu, 1995	3
364	Bahe	33.40	109.10	11.6	9	Calandra *et al.*, 2008; Qiu and Qiu, 1995	3
365	Wangdaifuliang	39.00	111.10	11.61	9	Qiu, 1990	3

366	Lamagou	39.26	110.95	8	7	Xue *et al*., 2006	4
367	Miaoliang	39.26	110.95	6	5.3	Xue *et al*., 2006	4
368	Pao-te-lok 43	39.02	111.09	7.23	5.34	Fortelius, 2011	3
369	Amuwusu	42.37	112.74	11.2	9.5	Qiu and Qiu, 1995	3
370	Harr Obo	41.91	114.07	7	5.33	Fahlbusch, 1987; 1992; Fahlbusch and Moser, 2004; Qiu, 1985; 1987; 1991; 2003; Storch, 1987; 1995; Storch and Qiu, 1983; Wu, 1985; 1991;	3
371	Ertemte	41.89	114.06	7	5.33	Fahlbusch, 1987; 1992; Fahlbusch and Moser, 2004; Qiu, 1985; 1987; 1991; 2003; Storch, 1987; 1995; Storch and Qiu, 1983; Wu, 1985; 1991;	3
372	Baogeda Ula	44.14	114.59	8	7	Tseng and Wang, 2007	3
373	Baogedawula	44.63	114.98	7.59	6.63	Fortelius, 2011; Storch and Ni, 2002	3
374	Zibo-Zhangdian	37.75	118.08	9	5.3	Fortelius, 2011	3
375	Zhangqiu	36.67	117.47	9	5.3	Fortelius, 2011	3
376	Ichibangawa River	43.40	141.62	12	10	Kohno, 2006	2
377	Zephyreduncinus	36.27	139.00	11.41	9	Kimura and Hasegawa, 2010	3
378	Nishikoiso Coast	35.96	139.30	8.6	6.6	Zin-Maung-Maung-Thein *et al*., 2009	3
379	Xiadongshan	27.06	117.18	8.7	5.33	Gu *et al*., 1992	3
380	Leilao	25.83	101.75	9	7	Dong *et al*., 2004; Pickford *et al*., 2004; Storch and Ni, 2002	3
381	Lufeng	25.17	102.67	8.2	7.1	Qiu and Qiu, 1995; Qiu and Storch, 1990; Storch and Qiu, 1991; Yuerong, 1988	3
382	Xiaolongtan	23.58	103.25	12.5	11.1	Qiu and Qiu, 1995	3
383	Hangmon	20.93	104.02	10.3	5.4	Covert *et al*., 2001	3
384	Charlem Prakieat	15.03	102.28	9	7	Chaimanee *et al*., 2004, 2006; Fortelius, 2011	3

385	Tha Sang Sand Pit 8	15.08	102.33	7.4	5.9	Fortelius, 2011; Hanta *et al.*, 2008	4
386	Tebingan Village	19.96	95.14	11.6	9	Fortelius, 2011; Thaung-Htike *et al.*, 2007	3
387	Chaungsong	21.22	94.47	11.6	9	Thaung-Htike *et al.*, 2007	3
388	Chaing Zauk	21.51	94.60	7.25	5.33	Fortelius, 2011	3
389	Bulong	31.57	93.83	9.5	9	Qiu and Qiu, 1995	3
390	Jilong	28.87	85.18	8.2	7.1	Qiu and Qiu, 1995	3
391	Tinau Khola	27.70	83.45	11.5	6.5	Hoorn *et al.*, 2000; West *et al.*, 1991	4
392	Dang Valley	27.84	82.53	11.5	6.5	Hoorn *et al.*, 2000; West *et al.*, 1991	4
393	Piram Island	21.60	72.36	7.25	5.33	Fortelius, 2011; Prasad, 1971; Sahni, 1979	3
394	Dera Bugti Sartaaf	29.03	69.15	9.5	5.33	Welcomme *et al.*, 1997	3
395	Zinda	30.07	70.07	11.2	5.33	Raza *et al.*, 2002	3
396	Minanwali	32.90	71.70	11.61	7.25	Hussain and West, 1979; Moonen *et al.*, 1978	3
397	Chinji	33.03	72.48	10.8	10.8	Pickford, 2007; Pilbeam *et al.*, 1979, 1990	3
398	Chinji	33.03	72.48	9.3	9.3	Pilbeam *et al.*, 1979, 1990	3
399	Nagri	32.80	72.50	11.61	5.33	Moonen *et al.*, 1978	3
400	Ramanagar	32.82	72.37	13.1	11.1	Basu, 2004; Pickford, 2007; Vasishat *et al.*, 1979	3
401	Potwar Plateau	33.25	72.75	12.1	10.5	Baskin, 1996; Pilbeam *et al.*, 1979	3
402	Potwar Plateau	33.25	72.75	9.75	9.1	Baskin, 1996; Pilbeam *et al.*, 1979	3
403	Potwar Plateau	33.25	72.75	7.3	7.3	Baskin, 1996; Pilbeam *et al.*, 1979	3
404	Jalalpur	32.67	73.42	11	10	Cheema *et al.*, 2000	3
405	Sangaum Village	32.74	75.09	11	10	Pickford and Gupta, 2001	3
406	Ladhyani	31.53	76.67	8	6	Pickford, 2007; Sahni and Khare, 1977	3
407	Dera Gopipur	31.88	76.21	13	10	Gupta *et al.*, 1982	3

Location number	Location name	Latitude	Longitude	Oldest age	Youngest age	References
1	Courtney Pit	51.50	-112.30	9	7	Burns & Young, 1988
2	Westend Blowout, OR	45.80	-119.30	7.4	7	Shotwell, 1958
3	McKay Reservoir, OR	45.50	-118.80	10	8	Shotwell, 1956
4	Intermediary Gulch, MT	46.21	-112.75	7.5	6.7	Carrasco *et al.*, 2005

5	Gravel Pit, MT	46.22	-112.84	7.5	6.7	Carrasco *et al.*, 2005
6	Dempsey Creek, MT	46.40	-112.80	9.4	7.9	Konizeski, 1957
7	Johnson Gulch, MT	46.22	-112.73	9	7.5	Carrasco *et al.*, 2005
8	Little Valley, OR	43.60	-117.50	9.9	9.7	Shotwell, 1970
9	Juniper Creek, OR	43.60	-117.50	10.9	9.1	Shotwell, 1970
10	Rome, OR	43.60	-117.50	11.5	11.3	Wilson, 1937
11	Stroud claim, ID	43.00	-114.90	11.3	11.1	Malde & Powers, 1962
12	Rockland Valley Quarry, ID	42.80	-112.90	7.6	7.2	Gillette, 1999
13	Rockland Mole, ID	42.80	-112.90	10.4	7	Tedrow, 1997
14	Otis Basin, OR	42.70	-118.70	10	8.8	Shotwell, 1970
15	Bartlett Mountain, OR	42.70	-118.70	10.4	10.3	Shotwell, 1970
16	Star Valley, ID	42.00	-117.00	8	7.9	Becker & McDonald, 1998
17	Thousand Creek, NV	41.10	-117.80	10	9	Stirton, 1940
18	Nightingale Road, NV	39.86	-119.00	11.7	7.5	Macdonald, 1956
19	Hazen, NV	39.56	-119.11	9.81	9.81	Emry *et al.*, 2005
20	Churchill Butte, NV	39.00	-119.20	9.7	9.4	Kelly & Lugaski, 1999
21	Smiths Valley, NV	39.00	-119.20	10.9	10.8	Macdonald, 1959
22	Smiths Valley, NV	38.80	-119.32	10.9	8	Macdonald & Macdonald, 1976
23	Silver Springs, NV	39.30	-118.90	6.2	6.1	Kelly, 1998
24	Washoe, NV	38.80	-119.50	7.4	4.6	Kelly, 1997
25	Bollinger Canyon	37.82	-122.06	13.6	10.3	Edwards, 1982
26	Black Hawk Ranch, CA	38.04	-122.18	9.7	9	Stirton, 1939; White, 1991; Tseng *et al.*, 2010
27	Siphon Canal, CA	37.60	-120.80	8.35	8.03	Hirschfeld, 1981
28	Turlock Lake, CA	37.60	-120.80	7.7	7.6	Wagner 1976
29	Point Reyes Peninsula, CA	37.90	-122.72	6.8	6	Zeigler *et al.*, 1997
30	Warren, CA	35.30	-118.50	7.3	5.3	Reynolds *et al.*, 1991
31	Powerline Road Tom Quarry, CA	35.37	-117.99	9.3	9.2	Whistler & Burbank, 1992; Wang *et al.*, 2005
32	Kam's False Cat Locality	35.33	-118.08	10.2	8.4	Tseng *et al.*, 2010
33	Sycamore, CA	35.30	-118.50	10.8	9.6	Reynolds & Czaplewski, 1989
34	Lava Mountains, CA	34.80	-117.00	10.8	10.7	Reynolds *et al.*, 1991
35	Golgotha Hill, UT	38.10	-114.17	5.89	5.23	Reynolds & Lindsay, 1999; Carrasco *et al.*, 2005
36	42SVO66V, UT	38.62	-112.32	10.3	7	Korth & Blieux, 2010
37	Pinole Junction 1,CA	37.89	-112.09	9.2	9.1	Stirton, 1939; Korth & Blieux, 2010
38	White Cone, AZ	35.61	-110.07	6.85	5.3	Baskin, 1979; Carraway, 2010
39	Rio Arriba, NM	36.50	-107.00	10.1	8.9	MacFadden,

						1977
40	Espanola Basin	36.21	-106.07	11	10.5	Fox & Fisher, 2004
41	Gabaldon Badlands, NM	34.80	-106.90	11.6	11.4	Lozinsky & Tedford, 1991
42	The Pits, NE	42.40	-103.80	10.7	10.6	Skinner *et al.*, 1977
43	ZXBar, NE	42.40	-103.80	10.5	10.4	Skinner *et al.*, 1977
44	Rock Ledge Mastodon Quarry, NE	42.52	-100.50	10.5	9.5	Fox & Fisher, 2004
45	Mefferdi Quarry, NE	42.70	-100.90	11.8	10.4	Mook, 1946
46	Rick Irwin Site, NE	42.80	-99.60	9.2	9.1	Tucker, 2003
47	Honey Creek, NE	42.70	-98.80	8.7	7.7	Voorhies, 1990
48	Santee, NE	42.80	-97.80	7.3	7.2	Voorhies, 1990
49	Mailbox, NE	42.40	-98.10	8.4	8.2	Voorhies, 1990
50	Verdigre Creek, NE	42.39	-98.12	11	10	Voorhies & Thomasson, 1979
51	Kepler Quarry, NE	41.92	-103.05	11.8	9	Voorhies, 1990; Lambert, 2007
52	Lemoyne Quarry, NE	41.29	-101.84	10.3	4.9	Bown, 1980
53	Uptegrove, NE	41.10	-103.00	10.6	7.4	Voorhies, 1984
54	Beecher Island, CO	40.10	-102.20	9.4	9.2	Frye *et al.*, 1956
55	Found Quarry, KS	38.90	-101.70	8.6	8.4	Bennett, 1979
56	Lost Quarry, KS	38.90	-101.70	8.4	7.6	Bennett, 1979
57	Minium Quarry Unit 5, KS	39.40	-100.14	7	6	Thomasson *et al.*, 1990
58	Jack Swayze Quarry, KS	39.06	-100.76	8.5	7.5	Fox & Fisher, 2004
59	Amebelodon fricki Quarry, NE	40.50	-100.50	11.2	11	Voorhies, 1990
60	Long Island Quarry, KS	39.80	-99.40	11.1	10.1	Zakrzewski, 1988
61	Buis Ranch, OK	36.80	-100.50	6.6	6.5	Hibbard, 1954
62	Optima, OK	36.70	-101.40	9	8	Hesse, 1936; Savage, 1941
63	Coffee Ranch, TX	35.90	-100.20	9	7	Dalquest, 1980
64	Cole Highway Pit, TX	36.32	-100.07	9.5	8.5	Fox & Fisher, 2004
65	Lipscomb Pit 1, TX	36.10	-100.10	10.3	4.9	Schultz, 1990; Lim *et al.*, 2001
66	Port of Entry Pit, OK	36.03	-99.96	11.2	7.5	Schultz, 1990; Fox & Fisher, 2001
67	Arnett, OK	36.14	-99.94	11.9	9	Kitts, 1957
68	Beckerdite, KS	37.20	-99.90	11.7	8.8	Liggett, 1997
69	Whisenhunt Quarry, OK	36.78	-100.04	12.7	10.7	Dalquest *et al.*, 1996; Smith, 2005
70	Higgins Quarry,TX	36.40	-98.40	9.3	9	Dalquest & Patrick, 1989; Schultz, 1990
71	Pipe Creek Sinkhole, IN	40.50	-85.80	9.9	8.9	Farlow *et al.*, 2001; Martin *et al.*, 2002
72	Gray Fossil Site, TN	36.40	-82.50	10.1	9.9	Wallace & Wang, 2004
73	Lee Creek Mine, NC	35.40	-76.80	6.5	6.4	Tedford & Hunter, 1984
74	Sunken Meadow Pond, VA	37.20	-76.90	11.6	7.2	Baum & Wheeler, 1977; Godfrey & Barnes, 2008

75	John Seyfried beach, MD	38.40	-76.41	10	9	Fuller & Godfrey, 2007
76	Cove Point, MD	38.35	-76.40	10	9	Godfrey & Barnes, 2008
77	Love Bone Bed, FL	29.55	-82.52	9.9	9.5	Baskin, 1980, 1981, 1986, 2005; Webb *et al.*, 1981; MacFadden & Cerling, 1996; Hulbert-Jr., 2005
78	Moss Acres Racetrack, FL	29.30	-82.35	9	8.9	Hulbert Jr., 1988; Lambert, 1997
79	Phosphate Pit, Polk County, FL	27.90	-81.80	10.3	4.9	Olsen, 1960; Webb, 1969
80	Payne Creek, FL	27.90	-81.80	7.9	7.8	Berta & Morgan, 1985; Hulbert, 1987
81	Palmetto Washer, FL	27.76	-81.98	7.9	7.8	Webb, 1969; Wright & Webb, 1984
82	Tiger Bay Mine, FL	27.90	-81.80	6.5	6.4	Webb, 1981
83	Withlacouchee 4a, FL	29.00	-82.26	7	6	Webb, 1969; Berta & Morgan, 1985; Tedford et al., 1987; Hulbert, 1993;
84	Mauvilla, AL	30.81	-88.19	10.3	9	Hulbert Jr. & Whitmore Jr., 1997; MacFadden & Dobie, 1998
85	Chicasabogue Creek, AL	30.80	-88.10	10.3	4.9	Isphording & Lamb, 1971
86	Tunica Hills, LA	30.60	-91.30	10	5.7	Manning & MacFadden, 1989
87	Lepara Creek, TX	28.60	-97.70	12	11	Prothero & Manning, 1987
88	Screw Bean, TX	29.29	-103.07	9	7.5	Carrasco *et al.*, 2005
89	Redington, AZ	32.42	-110.50	6.25	5.21	Jacobs, 1977
90	Mount Eden, CA	33.90	-117.00	7	6	Frick, 1921; Baskin, 1982
91	Lawrence Canyon, CA	33.20	-117.40	7.25	5.33	Domning & Demere, 1984; Berta & Morgan, 1985
92	Yepomera	28.80	-108.00	5.8	5.7	Lindsay, 1984; MacFadden, 1984
93	Rancho el Ocote	21.11	-100.70	10.1	6.3	Carranza-Castaneda & Ferrusquía-Villafranca, 1979; Carranza-Castaneda & Miller, 1996
94	Rancho el Ocote	21.11	-100.70	5.7	5.6	Carranza-Castaneda & Ferrusquía-Villafranca, 1979
95	La Rinconada	21.10	-100.80	10.1	6.3	Miller & Carranza-Castaneda, 1998
96	Gracias	14.64	-88.59	11.8	8	Webb & Perrigo, 1984

97	Tio Gregorio	11.25	-70.31	11.6	5.33	Sanchez-Villagra et al., 2003; Negri & Ferigolo, 2004; Aguilera *et al.*, 2006; Carlini *et al.*, 2006a,b,c; Domning & Aguilera, 2008; Riff & Aguilera, 2008;
98	Huila	3.30	-75.20	11.61	5.33	Miller, 1953
99	Acre State	-8.18	-70.48	9	6.8	Cozzuol, 2006
100	Talisma	-8.20	-70.50	11.61	5.33	Cozzuol, 2006
101	Sud Sacaco	-15.58	-74.82	6	6	Gregory McDonald & de Muizon, 2002
102	Sud Sacaco	-15.58	-74.82	5	5	Gregory McDonald & de Muizon, 2002
103	Aguada de Lomas	-15.54	-74.73	8	7	Muizon & De Vries, 1985; de Muizon et al., 2003
104	Achiri	-17.21	-69.00	9	6.8	Villarroel & Marshall, 1983; Saint-André, 1996
105	Muyu Huasi	-19.00	-65.30	11.61	5.33	Villarroel & Marshall, 1989
106	Petaca	-17.80	-63.20	11.61	5.33	Marshall & Sempere, 1991
107	Estanques de Copec	-27.03	-70.80	8.9	6.3	Canto *et al.*, 2008
108	Caldera	-27.10	-70.90	11.6	5.33	Walsh & Naish, 2002
109	Chiquimil	-26.31	-66.78	9	6.8	Magdalena Candela, 2004
110	El Cajon Valley	-26.61	-66.38	9	6.8	Nasif *et al.*, 2000
111	Tiopunca	-26.66	-66.04	12	10.7	Herbst *et al.*, 2000; Kleinert & Strecker, 2001
112	Villavil	-27.19	-66.89	10.7	9.3	Herbst *et al.*, 2000; Muruaga et al., 2003
113	Sierra de Velasco	-28.30	-67.00	11.61	5.33	Tauber, 2005
114	Arroyo La Petra	-33.28	-65.94	9	6.8	Cerdeño *et al.*, 2008
115	Telen	-36.27	-65.51	9	6.8	Montalvo *et al.*, 2008
116	Bajada de los Toros	-38.61	-63.00	10	9	Deschamps *et al.*, 2007
117	Villarino	-40.61	-63.11	10	9	Marshall, 1976; Zárate *et al.*, 2007
118	Salias Grandes de Hidalgo	-37.40	-61.30	9	6.8	Vizcaíno & Fariña, 1999.
119	Grubein	-38.80	-62.20	11.61	5.33	Deschamps, 2005
120	Barrancas del rio Parana	-33.70	-59.30	11.61	7.25	Marshall, 1977
121	Entre Rios	-33.70	-59.30	10.7	7.14	Herbst *et al.*, 2000; Muruaga *et al.*, 2003
122	Entre Rios	-33.70	-59.30	12	10.7	Herbst *et al.*, 2000; Muruaga *et al.*, 2003
123	Kiyu Beach	-34.68	-56.80	9	6.8	Rinderknecht *et al.*, 2010

124	Kiyu Beach	-34.74	-56.84	9	6.8	Rinderknecht *et al.*, 2007
125	Bahia de Colonia	-34.50	-57.80	11.61	5.33	Verde & Perea, 1992
126	La Plata	-34.62	-56.92	11.6	5.33	Vizcaino *et al.*, 2003
127	Asseiceira	39.25	-9.08	9.5	9	Fortelius, 2011
128	Freiria do Rio Major	39.32	-9.07	9.5	9	Fortelius, 2011
129	Ampudia	41.92	-4.78	11.2	9.5	Rossner & Heissig, 1999; Fortelius, 2011
130	Ampudia	41.92	-4.78	9.5	9	Rossner & Heissig, 1999; Fortelius, 2011
131	Alfacar	37.23	-3.57	8.2	7.1	Bernor *et al.*, 1996; Markov, 2008
132	Arenas del Rey	36.97	-3.90	7.1	5.33	Fortelius, 2011
133	Salobrena	36.50	-3.50	7.25	5.33	Aguilar *et al.*, 1984
134	Los Mansuetos	40.30	-2.60	9	5.33	de Bruijn & Mein, 1968
135	Batallones-1	40.65	-1.72	8.994	8.958	Sanchéz *et al.*, 2009; Fortelius, 2011
136	Concud3	40.38	-1.15	9	5.3	Forsten, 1979; Fortelius, 2011
137	Venta del Moro	39.50	-1.30	9	5.33	Mathisen & Morales, 1981
138	Crevillente 2	38.29	-0.79	8.7	8	Freudenthal *et al.*, 1991; van der Made *et al.*, 1992; Montoya *et al.*, 2001; Fortelius, 2011
139	Santa Margarita	39.70	3.10	11.61	7.25	Colom & Bauza, 1949
140	San Caprasio	41.74	-0.45	11	10	Agusti *et al.*, 1994
141	Los Valles de Fuentiduena	41.42	-0.30	11.2	9.5	Alberdi, 1981; Alberdi *et al.*, 1981; Ginsburg *et al.*, 1981; Hoyos *et al.*, 1981; Mazo, 1981; Morales *et al.*, 1981; Morales & Soria, 1981; Sese Benito & Lopez Martinez, 1981
142	Orignac	43.12	0.17	9.5	9	Rossner & Heissig, 1999; Fortelius, 2011
143	El Firal	42.37	1.45	11.2	9.5	Rossner & Heissig, 1999; Fortelius, 2011
144	Estevar	42.47	2.00	11.2	9.5	Rossner & Heissig, 1999
145	Baixas	42.50	2.50	11.61	7.25	Aguilar *et al.*, 1986
146	Can Ponsic 1	41.60	2.08	10.6	10.58	Hartenberger & Crusafont, 1979; Agusti *et al.*, 1997; Fortelius, 2011
147	Can llobateres	41.53	2.10	9.7	9.5	Petter, 1967; Golpe-Posse & Crusafont-Pairo, 1982; Moya-Sola &

						Kohler, 1996; Agusti *et al.*, 1997; Robles *et al.*, 2010; Fortelius, 2011
148	Montredon	43.33	2.89	10	9	Aguilar, 1982; Aguilar & Crochet, 1982; Crochet & Green, 1982; de Beaumont, 1988; Eisenmann, 1988; Ginsburg, 1988; Ginsburg & Thomas, 1988; Guérin, 1988; Lopez Martinez, 1988; Sen, 1988; Tobien, 1988
149	Bretagne	47.50	-2.50	11.61	7.25	Plusquellec & Racheboeuf, 2000
150	Doue-la-Fontaine	47.20	-0.30	11.2	9.5	Ginsburg *et al.*, 1979
151	Esveres	47.30	0.30	11.2	9.5	Ginsburg, 1990; Fortelius, 2011
152	La Tour	47.30	2.75	7.1	5.33	Rossner & Heissig, 1999; Fortelius, 2011
153	Deurne	51.20	4.50	11.61	7.25	Lambert, 2005
154	Groenlo	52.00	6.60	11.61	5.33	van Deinse, 1931
155	Esbjerg	55.47	8.45	11.6	8	Pyenson & Hoch, 2007
156	Amberieu 1	45.96	5.36	8.7	7.75	Farjanel & Mein, 1984; Fortelius, 2011
157	Amberieu 2A	45.96	5.36	9.7	8.7	Farjanel & Mein, 1984; Fortelius, 2011
158	Amberieu 2C	45.96	5.36	9.7	8.7	Farjanel & Mein, 1984; Fortelius, 2011
159	Amberieu 3	45.96	5.36	8.7	7.75	Farjanel & Mein, 1984; Fortelius, 2011
160	La Grive-St. Albans	45.60	5.23	12.75	11.1	Freudenthal & Mein, 1989
161	Mollon	45.57	5.15	9	8.2	Fortelius, 2011
162	Priay	46.01	5.29	11.6	9	Combémorel *et al.*, 1970
163	Soblay	46.10	5.35	9.7	8.7	Viret, 1949; Rossner & Heissig, 1999
164	Cucuron	43.78	5.43	7.75	7	Ballesio *et al.*, 1979; Mein & Michaux, 1979; Fortelius, 2011
165	Charmoille	47.43	7.22	11.2	9.5	Kälin, 1997; Fortelius, 2011
166	Nebelbergweg	47.40	7.61	11.2	9.5	Rossner & Heissig, 1999; Fortelius, 2011
167	Wissberg	49.85	8.01	11.6	9	Tobien, 1980
168	Gau-Weinheim	49.85	8.05	11.6	9	Tobien, 1980
169	Steinberg	49.88	8.00	11.6	9	Tobien, 1980
170	Dintesheim	49.71	8.14	11.6	9	Tobien, 1980
171	Bermersheim	49.78	8.10	11.6	9	Tobien, 1980

172	Westhofen	49.70	8.25	11.6	9	Tobien, 1980
173	Dorn-Durkheim 1	49.77	8.27	9	8.2	Kaiser *et al*., 2003
174	Eppelsheim	49.72	8.98	9.7	9.5	Franzen *et al*., 2003
175	Hammerschmiede	47.90	10.60	11.1	9.7	Mayr & Fahlbusch, 1975
176	Stirone River	44.84	9.96	11.6	7.25	Bisconti, 2010
177	Baccinello V1	42.80	11.40	9	5.33	Hurzeler & Engesser, 1976; Hurzeler, 1987; Fortelius, 2011
178	Baccinello V2	42.70	11.10	8.2	7.1	Hurzeler & Engesser, 1976; Hurzeler, 1987; Fortelius, 2011
179	Baccinello V3	42.70	11.10	7.1	5.33	Hurzeler & Engesser, 1976; Hurzeler, 1987; Fortelius, 2011
180	Baccinello-Cinigiano Basin	42.78	11.25	7.58	7.52	Delfino & Rook, 2008; Fortelius, 2011
181	Fosso-Cassoto	43.00	11.55	7.25	5.96	Ghetti *et al*., 2002
182	Roccamorice	42.40	14.00	11.61	5.33	Koretsky, 2001
183	Gargano	41.80	15.40	6	5	Delfino *et al*., 2007; Fortelius, 2011
184	Cessaniti	38.66	16.03	9	5.33	Markov, 2008
185	Tropea	38.68	15.90	11.61	7.25	Bagnato *et al*., 2000
186	Blancone 1	45.90	15.50	11.61	5.33	Freudenthal & Martin-Suarez, 2006
187	Mariathal	48.60	16.10	11.2	9.5	Bernor *et al*., 1996; Fortelius, 2011
188	Richardhof	48.10	16.30	11.1	9.7	Ziegler, 2006
189	Gotzendorf	47.99	16.63	11.1	9.7	Bernor *et al*., 1993; Fortelius, 2011
190	Kohfidisch	47.15	16.35	8.7	7.75	Bernor *et al*., 1996; Markov, 2008
191	Baltavar	47.00	17.00	8.2	7.1	Bernor *et al*., 1996; Markov, 2008
192	Sumeg	46.98	17.28	9.7	8.7	Mészáros, 1998; Fortelius, 2011
193	Tardosbanya	47.66	18.45	7.75	7.1	Mészáros, 1998; Fortelius, 2011
194	Csakvar	47.39	18.46	8.7	7.75	Mészáros, 1998; Fortelius, 2011
195	Polgardi-4	47.05	18.31	7.1	5.33	Mészáros, 1998; Fortelius, 2011
196	Pestszentlorinez	47.50	19.04	9	5.33	Bernor *et al*., 1996; Markov, 2008
197	Rudabanya	48.39	20.64	11	10	Kordos & Begun, 1997; 2002; Fortelius, 2011
198	FT3/8	47.97	20.40	11.5	9.7	Hír & Kókay, 2010

199	Kreka	44.42	18.45	9	5.3	van der Made & Stefanovic, 2006
200	Mala Miliva	44.10	21.40	11.61	7.25	Petronijevic, 1967
201	Belka	50.82	28.18	8.2	7.1	Bernor *et al.*, 1996; Markov, 2008
202	Grytsiv	49.59	27.12	11.2	9.5	van der Made *et al.*, 1999
203	FT3/10	47.98	26.40	11.4	9.7	Hír & Kókay, 2010
204	Pogana	46.32	27.57	9	6.1	Codrea *et al.*, 2010; Fortelius, 2011
205	Kishinev	47.00	28.83	12	11	Kazár & Grigorescu, 2005; Fortelius, 2011
206	Cimislia	46.50	28.80	8.2	7.1	Bernor *et al.*, 1996; Markov, 2008
207	Taraklia	46.50	29.00	8.2	7.1	Bernor *et al.*, 1996; Markov, 2008
208	Orekhovka	45.66	28.95	7.1	5.33	Nesin & Storch, 2004
209	Frunzovka-2	47.28	29.70	8.7	7.7	Nesin & Storch, 2004
210	Grebbeniki	46.88	29.82	9.5	9	Bernor *et al.*, 1996; Markov, 2008
211	Novoclizavetovka-2	47.25	30.32	8.7	7.7	Nesin & Storch, 2004
212	Novodizavetovka-3	47.17	30.33	7.7	7.1	Nesin & Storch, 2004
213	Protopopovka-3	46.88	30.07	7.7	7.1	Nesin & Storch, 2004
214	Novoukrainka-1	46.84	30.15	7.1	5.33	Nesin & Storch, 2004
215	Novoukrainka-2	46.70	30.11	7.7	7.1	Nesin & Storch, 2004
216	Novaya Emetovka	46.65	30.60	9.75	9	Vangengeim & Tesakov, 2008
217	Novaya Emetovka	46.65	30.60	8.7	8.1	Vangengeim & Tesakov, 2008
218	Cherevichnoe-3	46.67	30.64	7.7	7.1	Nesin & Storch, 2004
219	Vinogradovka-1	46.58	30.70	7.1	5.33	Nesin & Storch, 2004
220	Odessa	46.47	30.73	7.1	5.33	Nesin & Storch, 2004; Fortelius, 2011
221	Mikhailovka	47.58	31.26	9.7	7.7	Nesin & Nadachowski, 2001; Nesin & Storch, 2004
222	Andreevka	46.89	31.37	7.1	5.33	Nesin & Storch, 2004; Fortelius, 2011
223	Dolni Disan	41.33	21.97	9	5.33	Bernor *et al.*, 1996; Markov, 2008
224	Hrabarsko	42.80	23.06	7.25	5.33	Spassov & Ginsburg, 1999; Fortelius, 2011
225	Dytiko	40.86	22.53	7	5.5	Koufos, 1988; de Bonis *et al.*, 1995; Bouvrain & de Bonis, 2007
226	Pentalaphos 1	40.74	22.85	11.9	9	Geraads & Koufos, 1990; de Bonis et al.,

						1992; 1994; Koufos, 2000
227	Ravin de la Pluie	40.85	22.96	11.6	9	Geraads, 1979; Koufos, 1984; de Bonis *et al.*, 1992; 1998; Fortelius, 2011
228	Kalimantsi	41.42	23.33	11.6	9	Geraads *et al.*, 2001; Kostopoulos *et al.*, 2001
229	Kalimantsi	41.42	23.33	9	7	Geraads *et al.*, 2001; Kostopoulos *et al.*, 2001; Liu *et al.*, 2004
230	Thermopigi	41.29	23.36	9	5.3	Geraads *et al.*, 2007; Fortelius, 2011
231	Maramena	41.20	23.50	9	5.33	de Bruijn, 1989
232	Lefkon	41.10	23.50	9.7	8.7	Armour-Brown *et al.*, 1977
233	Hadjidimovo	41.52	23.85	7.75	7	Kostopoulos *et al.*, 2001; Fortelius, 2011
234	Vathylakkos-2	41.00	23.00	7.75	7	Koufos *et al.*, 2004
235	Ahmatovo	42.11	25.05	9	5.33	Bernor *et al.*, 1996; Markov, 2008
236	Ezerovo	42.02	25.30	9	5.33	Kostopoulos *et al.*, 2001
237	Perivolaki	39.41	22.66	7.3	7.1	Kostopoulos, 2006; Kostopoulos & Koufos, 2006b; Koufos, 2006a,b; Koufos *et al.*, 2006; Sylvestrou & Kostopoulos, 2006; Sylvestrou & Koufos, 2006; Vlachou & Koufos, 2006
238	Perivolaki	39.30	22.74	7.3	7.1	Kostopoulos & Koufos, 2006a
239	Kerassia - 3	38.85	23.32	7.75	7	Giaourtsakis *et al.*, 2006
240	Halmyropotamos	38.50	24.20	8.2	7.1	Bernor *et al.*, 1996; Markov, 2008
241	Chomateri	38.01	23.96	7.7	7	Roussiakis, 2009; Fortelius, 2011
242	Pikermi	38.02	23.99	8.7	7.1	Roussiakis, 2001; Fortelius, 2011
243	Pikermi-Valley 1	38.01	23.95	9	7	Theodorou *et al.*, 2010
244	Kastellios-K1	35.05	25.25	9.6	9.2	Fortelius, 2011
245	Maronia	35.14	26.08	11.6	5.33	Athanassiou, 2004
246	Gela	35.21	26.10	9	8	Poulakakis *et al.*, 2005
247	Gulpinar	39.53	26.12	9.5	9	Geraads & Güleç, 1999
248	Gulpinar-1	39.53	26.09	9	7.1	Fortelius, 2011
249	Gulpinar-2	39.52	26.09	8.2	7.1	Fortelius, 2011

250	Esendere	38.59	26.56	9	7	Kaya *et al*., 2005
251	Manisa	38.58	27.20	8.2	7.1	Geraads & Güleç, 1999
252	Mytilinii	37.73	26.91	7.75	7.2	Solounias, 1981; Kostopoulos *et al*., 2003
253	Amasya	37.80	28.30	7	4.9	Engesser, 1980
254	Serefkoy	37.35	28.22	8.2	7.1	Geraads & Güleç, 1999
255	Bayir	37.20	27.97	8.2	7.1	Geraads & Güleç, 1999; Fortelius, 2011
256	Kemiklitepe	37.50	29.00	9	8.2	Geraads & Güleç, 1999
257	Burgas	42.50	27.47	9	5.33	Bernor *et al*., 1996; Markov, 2008
258	Yulafli	41.37	27.60	8.7	7	Kaya & Heissig, 2001; Geraads *et al*., 2005
259	Kucukcekmece West	40.98	28.77	11.2	9	Rossner & Heissig, 1999
260	Kucukcekmece	40.98	28.77	9	8.2	Sickenburg, 1975
261	Garkin	38.42	30.32	9	8.2	Geraads & Güleç, 1999
262	Kavakdere	37.22	30.80	8.2	7.1	Geraads & Güleç, 1999
263	Kayadibi	40.23	32.40	9	8.2	Geraads & Güleç, 1999
264	Cobanpinar	41.16	32.53	6.3	5.8	van der Made et al., 2002; Fortelius, 2011
265	Kavurca	41.00	34.00	7	4.9	Engesser, 1980
266	Akkasdagi	39.49	33.66	7.2	7	Antoine & Saraç, 2005; de Bonis, 2005; Kazancı *et al*., 2005; Kostopoulos, 2005; Kostopoulos & Saraç, 2005; Koufos & Vlachou, 2005; Liu & Kostopoulos, 2005; Saraç & Sen, 2005; Tassy, 2005; Valli, 2005
267	Hayranli-3	39.74	36.81	9.5	8.2	Fortelius, 2011
268	Sivas	39.71	36.93	9	7	Bibi & Güleç, 2008
269	Duzyayla	40.62	37.49	8.65	7.25	Akgun *et al*., 2000; Fortelius, 2011
270	Kangal	39.03	37.35	7.25	5.33	Kaya & Forsten, 1999; Fortelius, 2011
271	Sevastopol	44.50	33.60	11	9.88	Fortelius, 2011
272	Kertch	45.36	36.52	9	5.33	Bernor *et al*., 1996; Markov, 2008
273	Morskaya 2	47.29	39.10	7.75	7	Rossina *et al*., 2006; Titov *et al*., 2006
274	Rustavi	45.08	41.55	9	5.33	Fortelius, 2011

275	Iaghludja	41.71	44.80	9.7	8.7	Vekua & Lordkipanidze, 2008
276	Udabno	41.50	45.40	8.7	7.8	Vekua & Lordkipanidze, 2008; Fortelius, 2011
277	Dzedzvtakhevi	41.68	45.75	7.75	7	Vekua & Lordkipanidze, 2008
278	El'dar	41.00	45.70	9.7	8.7	Beliaeva, 1962
279	Eldari	41.18	46.73	9.7	8.7	Vekua & Lordkipanidze, 2008
280	Ivand-1	38.35	46.13	8	7	Sen & Purabrishemi, 2010; Fortelius, 2011
281	Maragheh	37.33	46.41	9.5	7	Bernor, 1986; Fortelius, 2011
282	Karatchok Dagh	37.06	42.23	9	5.33	Astre, 1936
283	Bakhtiari	34.50	44.60	11.61	9	Thomas *et al.*, 1980
284	Injana	33.49	44.41	10	9	Brune & Heintz, 1983; Geraads & Güleç, 1999
285	Bekaa Valley	33.66	35.76	9	5.33	Malez & Forsten, 1989
286	Afoud 1,2,8	31.03	-6.57	7.1	5.33	Benammi, 1997; Fortelius, 2011
287	Afoud 5	31.03	-6.57	8.2	7.1	Benammi, 1997; Fortelius, 2011
288	Menacer	36.44	2.62	9	5.33	Thomas & Petter, 1986
289	Afoud 6	31.03	-6.57	11.2	9.5	Benammi, 1997; Fortelius, 2011
290	d'Amama	36.22	6.03	10	9	Jaeger, 1977
291	Afoud 7	31.03	-6.57	9.5	9	Benammi, 1997
292	d'Amama	36.22	6.03	7.8	6.6	Jaeger, 1977
293	Oued-Tabia	31.17	-6.50	11.2	9	Fortelius, 2011
294	L'oued Zra	33.71	-4.60	11.6	10	Jaeger, 1977
295	Khendek-el-Ouaich	34.08	-3.36	8.6	6.2	Jaeger, 1977
296	Oued el Atheuch	33.40	-1.10	11.61	5.33	Bernor & Jaeger, 1982
297	Raz el Ain	35.70	-0.60	7.25	5.33	Muizon, 1981
298	L'Oued el Hammam	35.18	-0.10	11.6	7.25	Arambourg, 1959; Ouda & Ameur, 1978
299	Sidi Salem	35.12	0.08	11.6	9	Jaeger, 1977; Fortelius, 2011
300	Jebel Semmene	36.93	9.44	11.8	10.5	Jaeger, 1977
301	Oued Mellegue	36.36	8.75	11.6	8.5	Robinson & Black, 1974
302	Beglia	34.35	8.34	10	10	Pickford, 2000; Agrasar, 2003; Fortelius, 2011
303	El Menia	29.28	4.63	11.6	9	Amard *et al.*, 1992
304	Oued Mya 1	28.93	4.20	11.6	9	Sudre & Hartenberger, 1992
305	Sahabi	30.08	20.75	7.1	5.33	Boaz *et al.*, 1987; Markov, 2008
306	Sheikh Abdallah	27.74	28.46	11	10	Pickford *et al.*,

						2006; Mein & Pickford, 2010
307	Wadi El Natrun	30.46	30.36	9	7	James & Slaughter, 1974
308	Shuwaihat	24.10	52.44	8	6	Barry, 1999; Bishop & Hill, 1999; de Bruijn, 1999; Eisenmann & Whybrow, 1999; Gentry, 1999a,b; Rauhe *et al.*, 1999; Tassy, 1999
309	N885	15.53	5.72	11	5	Pickford *et al.*, 2009
310	Toros Menalla	15.26	16.34	7.4	6	Brunet *et al.*, 2002; Vignaud *et al.*, 2002; Boisserie *et al.*, 2005; de Bonis *et al.*, 2005; 2007; 2010; Peigné *et al.*, 2005a,b; 2008a,b; Lehmann *et al.*, 2006; Likius *et al.*, 2007; Geraads *et al.*, 2008; Hautier *et al.*, 2009
311	Adu-Asa	10.17	40.33	5.8	5.2	Haile-Selassie, 2001; WoldeGabriel *et al.*, 2001; Haile-Selassie *et al.*, 2004
312	Alaya VPL2	10.03	40.30	5.8	5.5	Vrba & Haile-Selassie, 2006; Haile-Selassie & WoldeGabriel, 2009
313	Oromiya (Belticha)	8.90	40.30	10.5	10	Suwa *et al.*, 2007; Fortelius, 2011
314	Albertine 1	2.00	31.00	7.25	5.33	Senut *et al.*, 1994; Fortelius, 2011
315	Albertine 1C	1.33	30.25	7.25	5.33	Senut *et al.*, 1994; Fortelius, 2011
316	Albertine 14	1.00	30.08	7.25	5.33	Senut *et al.*, 1994; Fortelius, 2011
317	Albertine 7	1.08	30.42	7.25	5.33	Senut *et al.*, 1994; Fortelius, 2011
318	Albertine 6	1.17	30.50	11.61	7.25	Senut *et al.*, 1994; Fortelius, 2011
319	Albertine 11	0.17	30.00	7.25	5.33	Senut *et al.*, 1994; Fortelius, 2011
320	Sinda-Mohari	1.50	31.00	7	4.5	Aoki, 1992; Van Neer, 1994
321	Lothagam	2.91	36.07	7.49	6.5	Weston, 2000; Fortelius, 2011
322	SH22	1.31	36.58	9.79	9.25	Ishida & Pickford, 1997; Tsujikawa, 2005a,b
323	Nakali	1.18	36.40	10	9	Aguirre & Leakey, 1974;

						Flynn & Sabatier, 1984; Morales & Pickford, 2006; Fortelius, 2011
324	Cheboit	0.85	35.86	6.1	5.9	Guérin & Pickford, 2005; Fortelius, 2011
325	Site 2/49A	0.90	35.90	12	9	Maglio, 1974
326	Lemudong'o	-1.11	35.74	6.1	6.04	Howell & Garcia, 2007; Fortelius, 2011
327	Manonga Valley-1	-3.90	33.73	7.1	5.33	Harrison, 1997
328	Harasib 3a	-19.45	17.92	11.1	9.7	Mein *et al.*, 2000; Fortelius, 2011
329	Berk Aukas 1-31	-19.50	18.30	11.1	9.7	Conroy *et al.*, 1992; Rasmussen *et al.*, 1996
330	Swarthintjies-2	-30.30	17.30	11.6	5.33	Pickford & Senut, 1997
331	Groenrivier	-30.83	17.57	7.1	5.33	Fortelius, 2011
332	E Quarry	-32.97	18.15	6	5	Hendey, 1981
333	Shetirgiz	48.80	60.00	11.2	5.33	Kordikova, 1998
334	Ashut	50.17	66.67	11.2	5.33	Kordikova, 1998; Fortelius, 2011
335	Petropavlovska	54.80	69.20	11.2	5.33	Kordikova, 1998
336	Selety-1A	52.41	73.12	7.1	5.33	Vislobokova & Lavrov, 2009; Fortelius, 2011
337	Pavlodar	52.30	77.03	7.1	5.33	Vislobokova & Lavrov, 2009; Fortelius, 2011
338	Pavlodar	52.30	77.03	7.75	7.1	Vislobokova & Lavrov, 2009; Fortelius, 2011
339	Sor	39.27	67.65	8.2	7.1	Forsten & Sharapov, 2000
340	Marmar	39.33	67.83	9	5.33	Forsten & Sharapov, 2000
341	Magian	39.20	67.89	8	7	Sotnikova *et al.*, 1997
342	Pedjikent	39.47	68.09	8	7	Sotnikova *et al.*, 1997; Fortelius, 2011
343	Molayan	36.32	69.42	8	7.5	Heintz *et al.*, 1981; Brunet *et al.*, 1984; Sen, 2001; Merceron *et al.*, 2004
344	Y311, Potwar Plateau	33.88	72.38	10.4	8.6	Pilbeam *et al.*, 1979; 1990; Lihoreau *et al.*, 2004
345	Daraispon	38.52	70.62	9	8	Sotnikova *et al.*, 1997
346	Ortok	42.38	74.92	8	7	Sotnikova *et al.*, 1997; Fortelius, 2011
347	Kalmakpay	47.63	84.46	7	6	Sotnikova *et al.*, 1997; Fortelius, 2011
348	Taralyk Cher	51.90	95.60	7.75	7	Vislobokova, 2009a,b
349	CD9805	37.22	96.75	11	9	Dong, 2007

350	Tsaidam	37.00	97.00	11.2	9.5	Qiu & Qiu, 1995
351	Olkhon Island	53.19	107.57	7.5	6.5	Vislobokova & Lavrov, 2009
352	Qunke	36.05	101.98	11.1	8.7	Gu et al., 1992
353	Songshan	36.96	103.27	7.1	5.33	Fortelius, 2011
354	Songshan 80007	37.10	103.50	9	5.33	Zheng, 1982
355	Songshan 80008	37.00	103.50	9	5.33	Zheng, 1982
356	Jinchanggou	35.60	103.22	11.1	4.9	Wang & Qiu, 2004
357	Guonigou	35.64	103.27	11.1	11.1	Deng, 2007; Fortelius, 2011
358	Hezheng Area	35.50	103.50	9	5.33	Liu *et al*., 2004
359	Wuzhong	38.00	106.20	11.2	9.5	Qiu & Qiu, 1995
360	Longjiagou Valley	33.40	104.92	9	5.3	Xiang-Xu & Coombs, 1985; Xue *et al*., 2006
361	Yaodian	34.63	105.92	10.54	10.3	Sahni, 1979; Li *et al*., 2006
362	Taohuapo Hill	35.12	107.35	7	6	Xue *et al*., 2006
363	Qingyang	36.08	108.25	7.1	5.33	Qiu & Qiu, 1995
364	Bahe	33.40	109.10	11.6	9	Qiu & Qiu, 1995; Calandra *et al*., 2008
365	Wangdaifuliang	39.00	111.10	11.61	9	Qiu, 1990
366	Lamagou	39.26	110.95	8	7	Xue *et al*., 2006
367	Miaoliang	39.26	110.95	6	5.3	Xue *et al*., 2006
368	Pao-te-lok 43	39.02	111.09	7.23	5.34	Fortelius, 2011
369	Amuwusu	42.37	112.74	11.2	9.5	Qiu & Qiu, 1995
370	Harr Obo	41.91	114.07	7	5.33	Storch & Qiu, 1983; Qiu, 1985; 1987; 1991; 2003; Wu, 1985; 1991; Fahlbusch, 1987; 1992; Storch, 1987; 1995; Fahlbusch & Moser, 2004
371	Ertemte	41.89	114.06	7	5.33	Storch & Qiu, 1983; Qiu, 1985; 1987; 1991; 2003; Wu, 1985; 1991; Fahlbusch, 1987; 1992; Storch, 1987; 1995; Fahlbusch & Moser, 2004
372	Baogeda Ula	44.14	114.59	8	7	Tseng & Wang, 2007
373	Baogedawula	44.63	114.98	7.59	6.63	Storch & Ni, 2002; Fortelius, 2011
374	Zibo-Zhangdian	37.75	118.08	9	5.3	Fortelius, 2011
375	Zhangqiu	36.67	117.47	9	5.3	Fortelius, 2011
376	Ichibangawa River	43.40	141.62	12	10	Kohno, 2006
377	Zephyreduncinus	36.27	139.00	11.41	9	Kimura & Hasegawa, 2010
378	Nishikoiso Coast	35.96	139.30	8.6	6.6	Zin-Maung-Maung-Thein *et*

						al., 2009
379	Xiadongshan	27.06	117.18	8.7	5.33	Gu *et al.*, 1992
380	Leilao	25.83	101.75	9	7	Storch & Ni, 2002; Dong *et al.*, 2004; Pickford *et al.*, 2004
381	Lufeng	25.17	102.67	8.2	7.1	Yuerong, 1988; Qiu & Storch, 1990; Storch & Qiu, 1991; Qiu & Qiu, 1995
382	Xiaolongtan	23.58	103.25	12.5	11.1	Qiu & Qiu, 1995
383	Hangmon	20.93	104.02	10.3	5.4	Covert *et al.*, 2001
384	Charlem Prakieat	15.03	102.28	9	7	Chaimanee *et al.*, 2004, 2006; Fortelius, 2011
385	Tha Sang Sand Pit 8	15.08	102.33	7.4	5.9	Hanta *et al.*, 2008; Fortelius, 2011
386	Tebingan Village	19.96	95.14	11.6	9	Thaung-Htike *et al.*, 2007; Fortelius, 2011;
387	Chaungsong	21.22	94.47	11.6	9	Thaung-Htike *et al.*, 2007
388	Chaing Zauk	21.51	94.60	7.25	5.33	Fortelius, 2011
389	Bulong	31.57	93.83	9.5	9	Qiu & Qiu, 1995
390	Jilong	28.87	85.18	8.2	7.1	Qiu & Qiu, 1995
391	Tinau Khola	27.70	83.45	11.5	6.5	West *et al.*, 1991; Hoorn *et al.*, 2000
392	Dang Valley	27.84	82.53	11.5	6.5	West *et al.*, 1991; Hoorn *et al.*, 2000
393	Piram Island	21.60	72.36	7.25	5.33	Prasad, 1971; Sahni, 1979; Fortelius, 2011
394	Dera Bugti Sartaaf	29.03	69.15	9.5	5.33	Welcomme *et al.*, 1997
395	Zinda	30.07	70.07	11.2	5.33	Raza *et al.*, 2002
396	Minanwali	32.90	71.70	11.61	7.25	Moonen *et al.*, 1978; Hussain & West, 1979
397	Chinji	33.03	72.48	10.8	10.8	Pilbeam *et al.*, 1979, 1990; Pickford, 2007
398	Chinji	33.03	72.48	9.3	9.3	Pilbeam *et al.*, 1979, 1990
399	Nagri	32.80	72.50	11.61	5.33	Moonen *et al.*, 1978
400	Ramanagar	32.82	72.37	13.1	11.1	Vasishat *et al.*, 1979; Basu, 2004; Pickford, 2007
401	Potwar Plateau	33.25	72.75	12.1	10.5	Pilbeam *et al.*, 1979; Baskin, 1996
402	Potwar Plateau	33.25	72.75	9.75	9.1	Pilbeam *et al.*, 1979; Baskin, 1996
403	Potwar Plateau	33.25	72.75	7.3	7.3	Pilbeam *et al.*, 1979; Baskin, 1996
404	Jalalpur	32.67	73.42	11	10	Cheema *et al.*, 2000
405	Sangaum Village	32.74	75.09	11	10	Pickford & Gupta, 2001
406	Ladhyani	31.53	76.67	8	6	Sahni & Khare,

						1977; Pickford, 2007
407	Dera Gopipur	31.88	76.21	13	10	Gupta *et al.*, 1982

Appendix D

Bibliography for Appendix C

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Appendix E

Stenobiomic Late Miocene mammals

This appendix presents a list of Late Miocene stenobiomic mammal genera (BSI = 1 or 2) and their biome preferences.

Artiodactyla

Aepycamelus	Temperate deciduous broadleaf savanna
Amphiprox	Warm - temperate evergreen broadleaf and mixed forest
Antilope	Temperate deciduous broadleaf savanna
Bramatherium	Temperate grassland
Catagonus	Temperate deciduous broadleaf savanna
Cervus	Warm - temperate evergreen broadleaf and mixed forest
Cranioceras	Temperate deciduous broadleaf savanna
Criotherium	Warm - temperate evergreen broadleaf and mixed forest
Decennatherium	Warm - temperate evergreen broadleaf and mixed forest
Dicoryphochoerus	Warm - temperate evergreen broadleaf and mixed forest
Dorcadoryx	Temperate deciduous broadleaf savanna
Dystychoceras	Warm - temperate evergreen broadleaf and mixed forest
Dytikodorcas	Tropical savanna
Eotragus	Warm - temperate evergreen broadleaf and mixed forest
Helladorcas	Warm - temperate evergreen broadleaf and mixed forest
Hexobelomeryx	Warm - temperate evergreen broadleaf and mixed forest
Hippopatamodon	Tropical grassland
Hippopotamus	Tropical savanna
Hippotragus	Tropical savanna
Hispanodorcas	Warm - temperate evergreen broadleaf and mixed forest

Hispanomeryx	Warm - temperate evergreen broadleaf and mixed forest
Hyotherium	Tropical evergreen broadleaf forest
Kenyapotamus	Tropical savanna
Kobus	Tropical savanna
Listriodon	Warm - temperate evergreen broadleaf and mixed forest
Lucentia	Warm - temperate evergreen broadleaf and mixed forest
Merychyus	Temperate deciduous broadleaf savanna
Merycopotamus	Tropical grassland
Mesembriacerus	Warm - temperate evergreen broadleaf and mixed forest
Moschus	Tropical evergreen broadleaf forest
Nisidorcas	Warm - temperate evergreen broadleaf and mixed forest
Orasius	Temperate deciduous broadleaf savanna
Ouzocerus	Warm - temperate evergreen broadleaf and mixed forest
Pachytragus	Warm - temperate evergreen broadleaf and mixed forest
Palaeogiraffa	Warm - temperate evergreen broadleaf and mixed forest
Parabos	Temperate xerophytic shrubland
Parachleuastochoerus	Warm - temperate evergreen broadleaf and mixed forest
Paraoioceros	Warm - temperate evergreen broadleaf and mixed forest
Pavlodaria	Temperate deciduous broadleaf savanna
Platygonus	Temperate deciduous broadleaf savanna
Protragocerus	Warm - temperate evergreen broadleaf and mixed forest
Pseudotragus	Warm - temperate evergreen broadleaf and mixed forest
Samokeros	Warm - temperate evergreen broadleaf and mixed forest
Selenoportax	Tropical evergreen broadleaf forest
Shaanxispira	Temperate deciduous broadleaf savanna
Simatherium	Temperate evergreen needleleaf forest
Sivachoerus	Tropical savanna
Tetraconodon	Tropical grassland

Tragocerus	Warm - temperate evergreen broadleaf and mixed forest
Tragoreas	Warm - temperate evergreen broadleaf and mixed forest
Ustatochoerus	Temperate deciduous broadleaf savanna

Lagomorpha

Amphilagus	Warm - temperate evergreen broadleaf and mixed forest
Eurolagus	Warm - temperate evergreen broadleaf and mixed forest
Ochotona	Temperate deciduous broadleaf savanna
Ochotonoides	Temperate deciduous broadleaf savanna
Proochotona	Temperate deciduous broadleaf savanna
Lepoides	Temperate deciduous broadleaf savanna
Notolagus	Warm - temperate evergreen broadleaf and mixed forest
Pronotolagus	Temperate deciduous broadleaf savanna

Lipotyphla

Alluvisorex	Temperate deciduous broadleaf savanna
Amphechinus	Warm - temperate evergreen broadleaf and mixed forest
Anouroneomys	Temperate deciduous broadleaf savanna
Asoriculus	Warm - temperate evergreen broadleaf and mixed forest
Dinosorex	Warm - temperate evergreen broadleaf and mixed forest
Gaillardia	Temperate deciduous broadleaf savanna
Hesperoscalops	Temperate deciduous broadleaf savanna
Heterosorex	Tropical evergreen broadleaf forest
Lemoynea	Temperate deciduous broadleaf savanna
Metacordylodon	Warm - temperate evergreen broadleaf and mixed forest
Mysorex	Temperate evergreen needleleaf forest
Paenelimnoecus	Warm - temperate evergreen broadleaf and mixed forest
Paranourosorex	Temperate deciduous broadleaf savanna

Parasorex	Warm - temperate evergreen broadleaf and mixed forest
Plesiodimylus	Warm - temperate evergreen broadleaf and mixed forest
Postpalerinaceus	Warm - temperate evergreen broadleaf and mixed forest
Proscapanus	Warm - temperate evergreen broadleaf and mixed forest
Scalopoides	Temperate deciduous broadleaf savanna

Notoungulata

Typotheriopsis	Tropical savanna
Xotodon	Tropical savanna

Perissodactyla

Anisodon	Warm - temperate evergreen broadleaf and mixed forest
Aphelops	Temperate deciduous broadleaf savanna
Calippus	Temperate deciduous broadleaf savanna
Chilotheridium	Tropical grassland
Diceros	Warm - temperate evergreen broadleaf and mixed forest
Lartetotherium	Warm - temperate evergreen broadleaf and mixed forest
Ningxiatherium	Temperate deciduous broadleaf savanna
Protohippus	Temperate deciduous broadleaf savanna
Pseudhipparion	Temperate deciduous broadleaf savanna
Shansirhinus	Temperate deciduous broadleaf savanna
Sinohippus	Warm - temperate evergreen broadleaf and mixed forest
Stephanorhinus	Temperate deciduous broadleaf savanna

Proboscidea

Amebelodon	Tropical savanna
Loxodonta	Tropical grassland
Mammuthus	Temperate evergreen needleleaf forest

Prodeinotherium	Warm - temperate evergreen broadleaf and mixed forest

Rodentia

Anomalomys	Warm - temperate evergreen broadleaf and mixed forest
Baiomys	Temperate deciduous broadleaf savanna
Blackia	Warm - temperate evergreen broadleaf and mixed forest
Blancomys	Temperate deciduous broadleaf savanna
Brachyrhizomys	Tropical evergreen broadleaf forest
Brachyscirtetes	Temperate deciduous broadleaf savanna
Cardiomys	Tropical savanna
Castillomys	Temperate xerophytic shrubland
Castromys	Temperate deciduous broadleaf savanna
Ceratogaulus	Temperate deciduous broadleaf savanna
Chalicomys	Warm - temperate evergreen broadleaf and mixed forest
Collimys	Warm - temperate evergreen broadleaf and mixed forest
Cricetulodon	Warm - temperate evergreen broadleaf and mixed forest
Democricetodon	Warm - temperate evergreen broadleaf and mixed forest
Dryomys	Warm - temperate evergreen broadleaf and mixed forest
Eomyops	Warm - temperate evergreen broadleaf and mixed forest
Epimeriones	Warm - temperate evergreen broadleaf and mixed forest
Eucastor	Temperate deciduous broadleaf savanna
Eumyarion	Warm - temperate evergreen broadleaf and mixed forest
Euroxenomys	Warm - temperate evergreen broadleaf and mixed forest
Fahlbuschia	Warm - temperate evergreen broadleaf and mixed forest
Geomys	Temperate deciduous broadleaf savanna
Glis	Warm - temperate evergreen broadleaf and mixed forest
Graphiurops	Warm - temperate evergreen broadleaf and mixed forest
Gyriabrus	Tropical savanna

Hispanomys	Warm - temperate evergreen broadleaf and mixed forest
Huerzelerimys	Warm - temperate evergreen broadleaf and mixed forest
Irhoudia	Tropical savanna
Kanisamys	Warm - temperate evergreen broadleaf and mixed forest
Liodontia	Temperate deciduous broadleaf savanna
Marmota	Temperate deciduous broadleaf savanna
Megacricetodon	Warm - temperate evergreen broadleaf and mixed forest
Microtocricetus	Warm - temperate evergreen broadleaf and mixed forest
Microtodon	Temperate deciduous broadleaf savanna
Microtoscoptes	Temperate deciduous broadleaf savanna
Miodryomys	Warm - temperate evergreen broadleaf and mixed forest
Myoglis	Warm - temperate evergreen broadleaf and mixed forest
Mystromys	Temperate evergreen needleleaf forest
Neoepiblema	Tropical savanna
Neotoma	Temperate deciduous broadleaf savanna
Paenemarmota	Temperate deciduous broadleaf savanna
Palaeocavia	Temperate deciduous broadleaf savanna
Pampamys	Temperate deciduous broadleaf savanna
Paraglirulus	Warm - temperate evergreen broadleaf and mixed forest
Paraglis	Warm - temperate evergreen broadleaf and mixed forest
Paralactaga	Temperate deciduous broadleaf savanna
Parapliosaccomys	Temperate deciduous broadleaf savanna
Phoberomys	Tropical savanna
Phtoramys	Tropical savanna
Pliogeomys	Temperate deciduous broadleaf savanna
Pliosaccomys	Temperate deciduous broadleaf savanna
Promimomys	Warm - temperate evergreen broadleaf and mixed forest
Prosomys	Temperate deciduous broadleaf savanna

Prospalax	Warm - temperate evergreen broadleaf and mixed forest
Prosiphneus	Temperate deciduous broadleaf savanna
Protalactaga	Temperate deciduous broadleaf savanna
Protatera	Temperate xerophytic shrubland
Ramys	Warm - temperate evergreen broadleaf and mixed forest
Reigechimys	Temperate deciduous broadleaf savanna
Rhinocerodon	Temperate deciduous broadleaf savanna
Rotundomys	Warm - temperate evergreen broadleaf and mixed forest
Scirtodipus	Temperate deciduous broadleaf savanna
Spermophilinus	Warm - temperate evergreen broadleaf and mixed forest
Stephanomys	Temperate xerophytic shrubland
Stertomys	Warm - temperate evergreen broadleaf and mixed forest
Vasseuromys	Warm - temperate evergreen broadleaf and mixed forest

Xenarthra

Acantharodeia	Tropical savanna
Aspidocalyptus	Temperate deciduous broadleaf savanna
Coscinocercus	Temperate deciduous broadleaf savanna
Doellotatus	Temperate deciduous broadleaf savanna
Elassotherium	Temperate deciduous broadleaf savanna
Hoplophractus	Temperate deciduous broadleaf savanna
Macroeuphractus	Temperate deciduous broadleaf savanna
Neoglyptatelus	Tropical savanna
Paleuphractus	Tropical savanna
Parahoplophorus	Tropical savanna
Pliomorphus	Tropical savanna
Plohophorus	Tropical savanna
Stromaphorus	Tropical savanna

Urumacotherium	Tropical savanna
Vassallia	Tropical savanna