Global and regional assessment of Neogene climate and palaeoceanography using dinoflagellate cysts

by

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Declaration of authorship

The candidate confirms that the work submitted is her own and that appropriate credit has been given where reference has been made to the work of others.

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Abstract

The Neogene Period (23.03–2.59 Ma) has been referred to as ‘the making of the Modern world’, which eventually, via a relatively consistent cooling trend, culminated in the present day climate conditions on Earth. Researching the Neogene provides important information for understanding how modern patterns of atmospheric and oceanic circulation developed, and how sensitive they are to environmental change.

Climate and environmental parameter proxies are used to investigate past changes, and dinoflagellate cysts have great potential as their distribution can be limited by temperature, salinity, nutrient availability and sea ice cover. This project aims to use dinoflagellate cysts to study the evolution of the oceans over the Neogene and to further develop the potential of the climate proxy. This is achieved by collating all of the previously published literature on Neogene dinoflagellate cysts into a database and analysing the data on global and regional scales. This study allows for the first global synthesis, using dinoflagellate cysts, of changes that took place during the Neogene. It was found that, on a global scale, the distribution of Neogene dinoflagellate cysts was strongly controlled by temperature and can be correlated to the previously established cooling trend of the Neogene. However, short term climate changes superimposed on the overall cooling trend of the Neogene, cannot be observed. Changes to marine gateways have been shown to affect the composition of dinoflagellate cyst assemblages regionally, and caused allopatric speciation. New primary data from Cyprus demonstrates an increase in diversity in the Pliocene, which differs to the regional diversity. This reveals the importance of the difference between local and regional signals, and why it is important to understand, and to thoroughly explore, the datasets used in a global compilation.

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Abbreviations

ACC – Antarctic Circumpolar Current

AMOC - Atlantic Meridional Overturning Circulation

ANOSIM - ANalysis Of SIMilarity

CAS - Central American Seaway

CWS - Cold Water Species

G-cyst - Gonyaulax cysts

GCM - General Circulation Model

GSSP - Global Boundary Stratotype Section and Point

HF - Hydrofluoric acid

HCl - Hydrochloric acid

IN - Inner Neritic

JWIP - John Williams Index of Palaeopalynology

MDS - non-metric MultiDimensional Scaling

MMCO - Middle Miocene Climatic Optimum

MMCT - Middle Miocene Climate Transition

MOW - Mediterranean Outflow Water

MPWP - Middle Pliocene Warm Period

MSC - Messinian Salinity Crisis

NAC - North Atlantic Current

NADW - North Atlantic Deep Water

NHG - Northern Hemisphere Glaciation

ON - Outer Neritic

P-cyst - Peridinium cysts

PRIMER - Plymouth Routines In Multivariate Ecological Research

SST - Sea Surface Temperature

TEVIS - Tertiary Environment Vegetation Information System

TOPIS - Tertiary Oceanic Parameters Information System

WWS - Warm Water Species

Chapter 1: Introduction

1.1 Project rationale and aims

There is an increasing awareness of contemporary climate change, and the causes and consequences of it are constantly under investigation. Anthropogenic emissions of greenhouse gases are known to be causing global warming, and it is predicted that global mean annual surface temperatures will rise by 3.7–4.8 °C by the end of this century (IPCC, 2014). Understanding how environments change over time, and how different events influence the climate, is an important step in predicting future changes. Future climate change can be predicted with the use of General Circulation Models (GCMs), but in order to get the best, and most reliable results, it is vital to understand the parameters that are used in the models. To aid with this, deep time geological data are utilised.

When researching the past with regards to predicting future change, it is useful to select an interval that has the potential to provide information on the dynamics and processes associated with a warm climate regime. The Neogene Period (23.03–2.59 Ma) is an example of a warmer world and is considered to have been the 'making of the modern world' (Potter and Szatmari, 2009). During the Neogene, many important changes took place that resulted in the current climate and oceanic and atmospheric circulation. Such changes include alterations to marine gateways, uplifting of major mountain belts and the development of continental scale ice sheets in the high latitudes (see Section 1.2). These phenomena combined to change both the oceanic and the atmospheric circulation and hence, along with CO_2 fluctuations, altered the climate state. There is no true analogue for the future, due to, for example, changes in the palaeogeography, which makes it additionally important to understand the instances that are not analogous. To study these changes further, the geological record is utilised.

There are a plethora of ‘tools’ that can be used to study past changes, encompassing all of the major branches of geology. However, because oceans play an important role in climate change, due to their control on heat storage and transport, it makes sense to evaluate the changes in the marine realm (Winton, 2003). The marine realm is also particularly useful to research as, unlike for the terrestrial realm, it is often possible to study a continuous sediment record over millions of years, which contain abundant fossils. The study of micropalaeontology is an example of a discipline that is used to assess past changes. This is because microfossils are abundant, widespread, and some groups hold isotopic signatures in their shells/skeleton, which reflect the environment in which they lived (Corliss, 1985; Miller et al., 1987; Waelbroeck et al., 2002; Zachos et al., 2008; Henehan et al., 2013). Dinoflagellate cysts are one such group that is used in climate studies due to their specific environmental preferences, such as temperature, salinity, nutrient availability and ice cover (Marret and Zonneveld, 2003; Zonneveld et al., 2013a). The use of dinoflagellate cysts as a climate proxy is relatively recent (since the 1990s) and developing the proxy is important to aid with the continued understanding of climates and environments of the past. Since dinoflagellate cysts can be influenced by several factors, investigating their use as a proxy for a range of environmental parameters is necessary to discover their true potential and to understand exactly how they can be used to infer past change.

The broad aim of this project is to use dinoflagellate cysts to study the evolution of the oceans throughout the Neogene. Understanding the changes that took place during this dynamic period, and developing dinoflagellate cysts as a climate and environmental parameter proxy, is important to help understand the past, which can lead to an increased awareness of variability in the climate system. Dinoflagellate cysts are one such climate proxy that have been under-utilised, especially for the Neogene, and can provide valuable information on ocean and climate evolution. With an increased awareness of how and on what scale they are affected by oceanic changes, the proxy can be developed further and interpreted with a greater reliability.

In order to investigate the utility of dinoflagellate cysts, and to determine what information they can provide on Neogene climate and ocean circulation dynamics, the following research questions will be addressed:

Research question 1: Can dinoflagellate cysts be used to demonstrate a progressive global cooling during the Neogene (Chapter 3)?

It is known that the distribution of dinoflagellate cysts in the modern are controlled by sea surface parameters such as temperature, salinity, nutrient availability and sea ice cover, with temperature and nutrient availability being the primary controlling factors. It has also been demonstrated that pre-Quaternary dinoflagellate cysts also respond to the above mentioned environmental parameters. However, the use of a global dataset of Neogene dinoflagellate cysts has not been investigated as a temperature proxy, which this project aims to achieve.

Research question 2: Can a global compilation of Neogene dinoflagellate cysts detect shorter term variations in global/regional climate, which are superimposed on the long term cooling trend (Chapters 3 and 4)?

The majority of Neogene dinoflagellate cyst studies investigate only a few sites per publication, and very rarely are there assemblages representing the entire Neogene. This means that most of the literature investigates short term changes in local settings. This project aims to provide more long term global changes whilst investigating if it is possible to still determine the shorter changes that previously published literature have interpreted.

Research question 3: What were the regional effects of gateway changes on dinoflagellate cysts during the Neogene (Chapter 3)?

Gateway changes greatly impact the climate by altering ocean currents, and the Mediterranean had three important gateway changes that took place during the Neogene.

Again, the modern regional distribution of dinoflagellate cysts has been investigated, but research exploring regional and temporal changes to Neogene dinoflagellate cyst assemblages across the Mediterranean are limited to just a few data points. This project aims to determine the effects of gateway changes on Neogene dinoflagellate cyst assemblages throughout the Mediterranean.

Research question 4: Can changes in dinoflagellate cyst assemblages elucidate complex histories of the opening/closing of marine gateways (Chapters 3 and 5)?

By answering research question 3 (i.e. do gateway changes affect dinoflagellate cyst assemblages) it is possible to then investigate whether dinoflagellate cysts can be used to determine gateway changes. Again, by approaching this question with a regional dataset, the broad and long term changes can be determined, which can then be compared to more localised studies (such as chapter 5) to evaluate if the regional and localised trends show the same patterns. This aids in the understanding of what influences dinoflagellate cysts on a local versus regional scale. Many dinoflagellate cysts have known environmental preferences including whether they thrive in coastal or more oceanic regions. This means that they can be used to determine changing depositional environments. By including new primary data from a previously unsampled area (Cyprus; Chapter 5) the local versus regional effects can be further analysed, whilst also filling in a data sparse area of the Eastern Mediterranean.

To address these research questions the project is split into six chapters. Chapter 1 (this chapter) reviews the climate system of the Neogene as well as dinoflagellates, their cysts and their utility in the geological record. It also reviews the Mediterranean region in more depth. Chapter 2 provides an in depth description on the construction of the TOPIS database, which compiles previously published literature on Neogene dinoflagellate cysts. Chapter 3 uses the data compiled in TOPIS to investigate the changes to the global distribution of dinoflagellate cysts with known temperature preferences, to see if the alterations are related to climate change. Chapter 3 continues by investigating the potential of dinoflagellate cysts as a proxy for environmental parameters by examining other factors that affect their distribution and assemblage composition. It concentrates on exploring the variations caused by the isolation of the Mediterranean Sea as marine gateways to the Atlantic, Paratethys and Indian oceans closed. Chapter 4 provides a thorough evaluation of the data used in Chapter 3 and examines further constraints of dinoflagellate cysts as a climate proxy. Chapter 5 studies more localised alterations brought about by gateway changes in the Mediterranean and provides the first organic-walled dinoflagellate cyst data from Cyprus. The final chapter (Chapter 6) presents the overall conclusions from this project and discusses possibilities for future research.

1.2 The Neogene

1.2.1 Neogene chronology

The geological time scale is constantly evolving with more constrained dating and the establishment of new Global Boundary Stratotype Section and Points (GSSP). All age references are concurrent to the Gradstein et al. (2012) geological time scale (Figure 1.1).

The Neogene is particularly well dated with astronomical tuning resulting in all dates being accurate to a precession cycle (~20 Kyr; Hilgen et al., 2006; Gradstein et al., 2012). However, much (over half) of the estimated dates provided in the literature, and synthesised into TOPIS, are dated to stage or even sub-epoch level. As a result of this, the different stages of the Neogene as presented below. It is noted that the majority of the GSSPs can be found in the Mediterranean region, and are therefore particularly meaningful when discussing changes that took place in the Mediterranean and Paratethys regions (Sections 1.2.6 and 3.6).

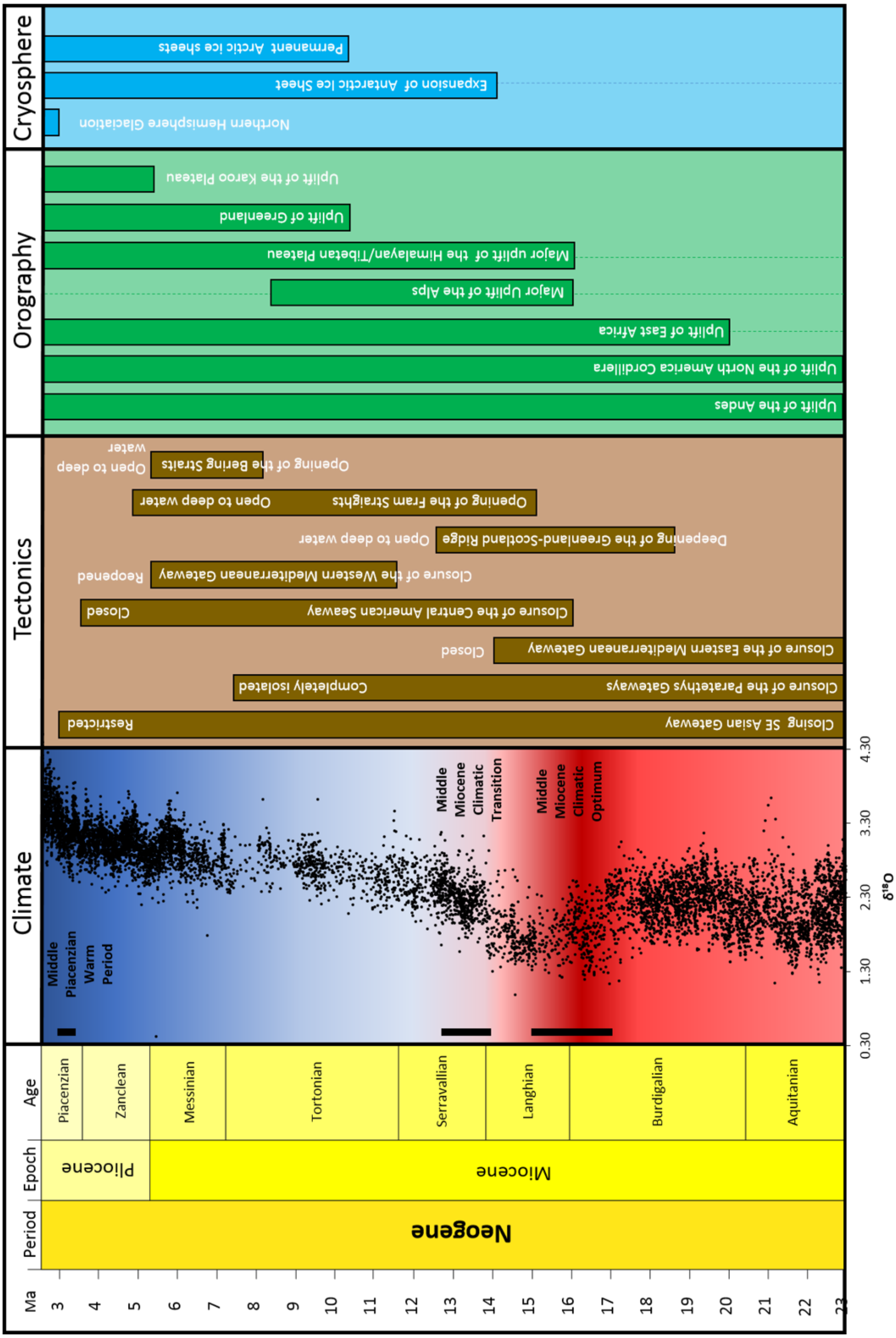


Figure 1-1: Neogene chronology and key events in the evolution of the Neogene. The $\delta^{18}O$ benthic oxygen isotope curve is from Zachos et al. (2001; 2008), other references can be found within the text in Sections 1.2.2 to 1.2.4 under the appropriate headings.

The Neogene (23.03–2.59 Ma), along with the Paleogene (66.0–23.03 Ma) and the Quaternary (2.589 Ma–present) make up the Cenozoic. The name Neogene comes from *Neo*, meaning new and *genēs* meaning born, of a specific kind. The Neogene is composed of two epochs, the Miocene (meaning “less recent” in Greek) and the Pliocene (meaning “more recent” in Greek). The Miocene is then further split into six stages and the Pliocene into two stages. The Miocene contains the Aquitanian, Burdigalian, Langhian, Serravallian, Tortonian and the Messinian stages and the Pliocene contains the Zanclean and Piacenzian stages.

The Aquitanian is the oldest stage of the Neogene (23.03–20.44 Ma) and along with the Burdigalian (20.44–15.97 Ma) makes up the early Miocene. The GSSP between the Aquitanian and the previous stage (the Chattian; 28.1–23.03 Ma) is Lemme-Carrosio in Northern Italy (Gradstein et al., 2012). However, there is no GSSP between the Aquitanian and the Burdigalian or between the Burdigalian and the Langhian. The Aquitanian was named after the Aquitaine region in France (Mayer-Eymar, 1858) and the Burdigalian after the city of Bordeaux, also in France (Depéret, 1893). The Langhian (15.97–13.82 Ma) follows on from the Burdigalian and is named after the Langhe area in northern Italy (Pareto, 1865). The GSSP between the Langhian and the next stage (the Serravallian; 13.82–11.62 Ma) is Rasil Pellegrin, Fomm Ir-Rih in Malta (Gradstein et al., 2012). The Serravallian is named after the Serravalle Scriva in northern Italy (Pareto, 1865) and along with the Langhian makes up the middle Miocene. The late Miocene is made up of the Tortonian (11.62–7.25 Ma) and the Messinian (7.25–5.33 Ma). There is a GSSP between the Tortonian and the Serravallian at Monte dei Corvi Beach, Ancora, Italy and one between the Tortonian and the Messinian at Oued Alcrech, Rabbat, Morocco (Gradstein et al., 2012). The Tortonian was named after the city of Torona in Italy and the Messinian after the city of Messina also in Italy (Mayer-Eymar, 1858). The top of the Miocene/the base of the Pliocene is at 5.33 Ma and its GSSP is at Eraclea Minoa, Sicily (Gradstein et al., 2012). The Zanclean follows this (5.33–3.60 Ma) and was named after Zancle, which was the pre-Roman name of Messina (Seguenza, 1868). Following the Zanclean comes the final stage of the Neogene, the Piacenzian (3.60–2.59 Ma). The GSSP between the Zanclean and the Piacenzian is at Punta Picola, Sicily (Gradstein et al., 2012). The Piacenzian was named after the city of Piacenza in Italy (Mayer-Eymar, 1858) and is followed by the first stage of the Quaternary, the Gelasian.

1.2.2 Neogene tectonics and ocean circulation

During the Neogene, the continental configuration was relatively similar to the present (Figure 1.2). Minor differences included a greater landmass in the Arctic and in Southeast Asia, and the presence of the Paratethys Ocean in Eastern Europe (Pound et al., 2012a). However, minor plate movements resulted in the opening and closing of ocean gateways (Figures 1.1 and 1.2), altering oceanic circulation (Berggren, 1982). Alterations to oceanic circulation can greatly impact climate, and changes in the Miocene are said to have resulted in the modification from the lingering greenhouse world of the early Cenozoic to the icehouse world of the late Cenozoic (Potter and Szatmari, 2009). A general trend of gateway changes in the Neogene is that high latitudes gateways, e.g. the Bering Strait, the Fram Strait and the Greenland Scotland Ridge, opened, while lower latitude gateways closed, e.g. the Eastern Mediterranean Gateway, the Indonesian Gateway and the Isthmus of Panama (Potter and Szatmari, 2009). This pattern could also be seen prior to the Neogene, for example both the high latitude gateways in the Southern Hemisphere, the Tasman Rise and the Drake Passage, opened (Hayes, 1973; Barker and Burrell, 1977; Gaina et al., 1998; Scher and Martin, 2006).

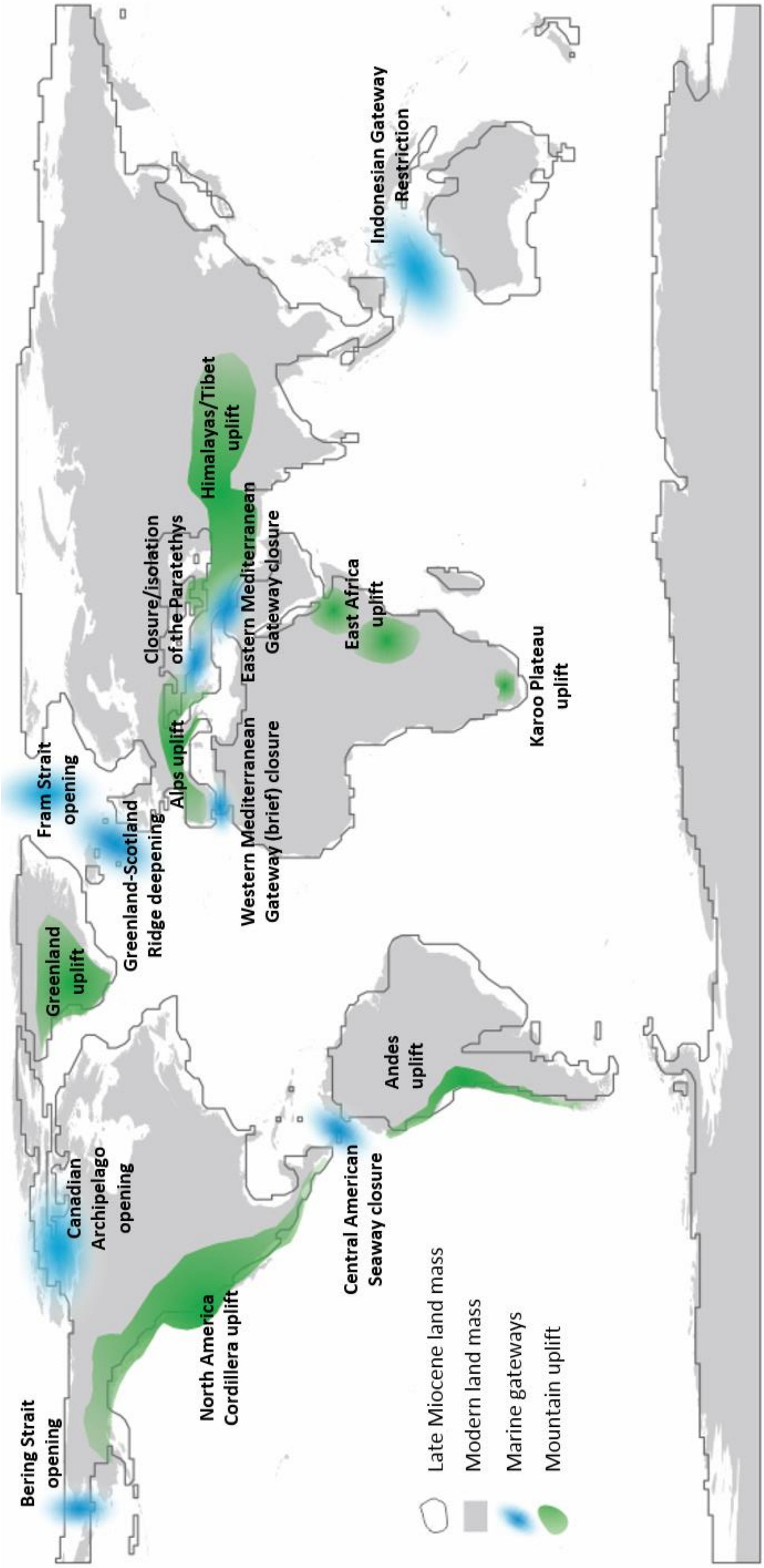


Figure 1-2: Location map of the key events of the Neogene. References can be found amongst the text in Sections 1.2.2-1.2.4. Late Miocene palaeogeography is from Markwick et al., (2000).

The Drake Passage opened between South America and Antarctic at ~41 Ma (Scher and Martin, 2006) and the Tasmanian Gateway opened between Australia and Antarctica at ~33.5 Ma (Kuhnt et al., 2004). Once both gateways were open, the Antarctic Circumpolar Current (ACC) initialised, forming a barrier to the warmer equatorial waters. This effectively isolated Antarctica and allowed further development of the East and West Antarctic ice sheets at roughly the Eocene-Oligocene boundary (Lawver and Gahagan, 2003; Barker et al., 2007). Although it has been postulated that the development of ice sheets on Antarctica may have begun prior to the Eocene-Oligocene boundary (Beerling and Royer, 2011), and was due to a decrease in CO_2 (DeConto and Pollard, 2003; Huber et al., 2004; Pagani et al., 2005; 2011; Pearson et al., 2009).

Following this, during the Late Oligocene (25 Ma), Australia began to collide with the Eurasian Plate, thereby reducing the width of the Southeast Asian gateway and decreasing marine throughflow in the Indonesian region (Hall et al., 2011; Pound et al., 2012a). This resulted in the ceasing of mixing of Pacific Ocean and Indian Ocean deep water by the early Miocene (23 Ma), although surface and intermediate water exchange between the ocean basins still occurs today (Hall, 2002; Kuhnt et al., 2004). The connection that still exists is a narrow band of warm, low salinity water and is regarded as the major switchboard in the global thermohaline circulation (You and Tomczak, 1993; Gordon and Fine, 1996; Kuhnt et al., 2004). Changes to this connection are thought to have dramatic repercussions on the circulation patterns in the Pacific, and hence global climate change (Kennett et al., 1985).

In the early Miocene, throughflow between the Eastern Mediterranean and the Indian Ocean was possible via the Tethys Seaway (Karami et al., 2009; Reuter et al., 2009). During the middle Miocene, this seaway restricted and the gateway was only intermittently open before it permanently closed in the middle Miocene (~14 Ma; Rögl, 1999; Harzhauser and Piller, 2007). The closure was due to the rotation of the African Plate causing a collision between the Arabian microplate and the Eurasian Plate (Krijgsman, 2002). This collision and subsequent gateway closure has been proposed as playing an important role in the Middle Miocene Climate Transition (MMCT; ~14 Ma, a period of rapid global cooling) because of its influence on meridional heat transfer and global thermohaline circulation (Reid, 1979; Bryden and Kinder, 1991). The Western Mediterranean also saw a gateway closure, this time between the North Atlantic Ocean and the Mediterranean Sea (Martín et al., 2001; Ivanovic et al., 2013). This closure occurred in the late Miocene, between ~5.96 and 5.33 Ma, and resulted in the precipitation of vast quantities of evaporites, an event called the Messinian Salinity Crisis (MSC; Hsü et al., 1973; Hsü et al., 1977; Flecker et al., 2015). Little is understood of the impact of the MSC on the climate. For example, pollen shows that it made no impact on the regional climate (Warny et al., 2003), but modelling studies suggest that it may have caused regional cooling (Schneck et al., 2010; Ivanovic et al., 2014b). At ~5.33 Ma water exchange became possible once more through the newly opened Strait of Gibraltar (Hsü et al., 1973). This allowed denser more saline water to flow out through the Strait of Gibraltar (Mediterranean Outflow Water; MOW), contributing warm and saline waters to the northern latitudes (Hernández-Molina et al., 2014). Without the MOW the Atlantic Meridional Overturning Circulation (AMOC) would decline by up to 15%, cooling the North Atlantic sea surface temperatures by up to 1 °C (Rahmstorf, 1998; Rogerson et al., 2012; Ivanovic et al., 2014a). The AMOC transports warm and saline water into the higher latitudes where it cools, sinks and flows southwards (Dickson and Brown, 1994; Stocker and Broecker, 1994).The added heat transport into the higher latitudes is the reason for the mild climate of Europe (Ganachaud and Wunsch, 2000). If the AMOC were suddenly to collapse, a significant cooling event would likely take place (Hemming, 2004; Gutjahr et al., 2010).

The Central American Seaway (CAS), a marine connection between the Atlantic and Pacific oceans, was a further low latitude gateway that closed during the Neogene. The timing of its closure is controversial with dates ranging from the middle Miocene (13–15Ma; Montes et al., 2015) to the late Pliocene (~3.5–2.5 Ma; Molnar, 2008). Emergence of land has been posited as occurring as early as 20–15 Ma (Montes et al., 2012; Montes et al., 2015) with a deep water connection closure at 10–7 Ma (Osborne et al., 2014; Sepulchre et al., 2014). The collision between North and South America closed down the circum-equatorial current, which had dominated throughout the Paleogene (Coates et al., 2004). Preceding this, North Atlantic Deep Water (NADW) formation, a key component of the AMOC, was relatively insignificant, and there was no evidence of its formation prior to 14.5 Ma (Lunt et al., 2008a; Butzin et al., 2011). The development of the NADW greatly strengthened in the late Neogene and resulted in the ACC accumulating silicates (entering from the Atlantic sector), which became trapped in both the water and the sediment (Berger, 2007). This resulted in the ACC becoming the dominant repository and redistribution centre for silicate and resulted in increased ocean productivity (Trégver et al., 1995; Pondaven et al., 2000). The increase (and strengthening of the NADW) in silcates is therefore proposed as being linked to the evolution of plankton, whales and other marine mammals (Fordyce, 1992; Berger, 2007).

In the late Miocene, the CAS closed sufficiently to restrict deep water flow between the Pacific and Atlantic oceans. This acted to intensify the Gulf Stream and initiated, or at least strengthened, NADW formation, redistributing ocean heat northeastwards in the North Atlantic (Raymo and Ruddiman, 1992). This event was highly significant because it brought about the present oceanic circulation pattern, enclosing the North Atlantic Basin and resulting in an AMOC similar to today. The exact timing of the final closure of the CAS is uncertain, but is likely to have occurred during the late Pliocene, between 3.5 and 2.7 Ma (Coates et al., 2004; Bartoli et al., 2005; Webb, 2006), or perhaps earlier, between 4.7 and 4.2 Ma (Haug et al., 2001; Steph et al., 2006). This may have contributed towards the onset of Northern Hemisphere Glaciation (NHG) in the Pleistocene (~3.6 Ma), along with a decrease in CO_2 (Mikolajewicz et al., 1993; Mudelsee and Raymo, 2005; Lunt et al., 2008a). Although, it has also been postulated that it delayed the intensification of the NHG by several million years and it was only due to mountain building, and a CO_2 reduction, that the intensification of glaciation occurred (Berger and Wefer, 1996).

Gateway changes in the high latitudes of the Northern Hemisphere included the opening of the Bering Strait, the Fram Strait and the subsidence of the Greenland-Scotland Ridge (Potter and Szatmari, 2009; Brierley and Fedorov, 2016). The Greenland-Scotland Ridge deepened between 18.0 and 15.5 Ma and again from 12.5 Ma (Wright and Miller, 1996). The deepening allowed the formerly isolated deep and cold Arctic waters to enter the Atlantic, modifying the global oceanic system (Wright and Miller, 1996). The Fram Strait, the link between Svalbard and Greenland (the Arctic and Norwegian-Greenland Sea), had a shallow water connection between 15 and 10 Ma (Engen et al., 2008). This connection opened to deep water between 7.5 and 5 Ma, and along with the Greenland-Scotland Ridge, allowed the exchange of water between the North Atlantic and the Arctic oceans. This caused the transition from poorly oxygenated waters to fully oxygenated and ventilated conditions in the Arctic (Jakobsson et al., 2007; Engen et al., 2008).

The final gateway that opened in the Neogene was the Bering Strait (De Schepper et al., 2015). The Bering Strait opened between 7.4 and 4.8 Ma (Marincovich and Gladenkov, 1999) and was an important oceanographic event of global significance (Reason and Power, 1994; Shaffer, 1994). It is proposed that its reconfiguration triggered the development of the modern circulation in the Nordic Seas, which is essential for NADW formation (De Schepper et al., 2015). Modelling studies demonstrate that a closed Bering Strait results in a strengthened AMOC, a warmer North Atlantic Ocean and reduced upper ocean water exchange between the Arctic and North Atlantic oceans (Hu et al., 2015), and an open Bering Strait weakens the AMOC (Brierley and Fedorov, 2016).

1.2.3 Neogene orography

Tectonic changes, including the uplift of mountain chains, can influence climate in a number of ways. For example, mountain height influences the climate by perturbing atmospheric circulation and altering monsoon patterns (Quade et al., 1989; Guo et al., 2002; Spicer et al., 2003; Harrison and Yin, 2004). An increase in elevation may also cause an increase in snow cover, resulting in a higher albedo and reduced heat absorption (Molnar et al., 2010). Furthermore, mountain uplift exposes more fresh rock to both physical and chemical processes. This enhances silicate weathering and sequesters CO_2 from the atmosphere on millennial timescales, leaving lower greenhouse gas concentrations in the atmosphere (Retallack, 2002). An increase in silicate weathering can lead to the amount of biolimiting nutrients (those necessary to sustain life), such as phosphates, in the oceans to rise (Filippelli, 1997). This can elevate the ocean productivity, i.e. result in blooms of phytoplankton, which in turn contributes towards a rise in organic burial and hence an increase in the drawdown of atmospheric CO_2 (Filippelli, 1997). Furthermore, uplifting of the sea floor can increase the amount of shelf areas, where many dinoflagellates and other organisms thrive, also providing further nutrients to the microfauna/flora and encouraging them to flourish (Marret and Zonneveld, 2003).

Many of the current major mountain chains were initiated during the Neogene (Figure 1.1 and 1.2), aiding in cooling of the climate and changing atmospheric circulation (Raymo et al., 1988; Pound et al., 2012a). Specifically, the Tibetan Plateau and the Himalayan Range rose during the Neogene, extensively increasing in height in the late Tortonian (8 Ma), which is thought to have contributed to the initiation of the Asian monsoon (Griffin, 2002). The uplift of the Himalayas caused increased amounts of physical and chemical weathering of the Himalayan and Tibetan Plateau, which destabilised the climate system and helped to produce the intense cooling seen throughout the Neogene (Filippelli, 1997). The rapid uplift was a result of the increase in the intensity of the collision of India into Asia during the middle and late Miocene (Rowley et al., 2001; Molnar et al., 2010). By the earliest Pliocene (5 Ma) some areas in the Himalayas had reached above 7000 m, which enabled ice fields to develop (Rowley et al., 2001; Molnar et al., 2010). Further uplifting, which resulted in the establishment of ice, took place in Greenland. Uplifting in Greenland occurred during the late Miocene and resulted in increased ice sheet growth, raising the albedo, which increased the inception of ice sheets and produced additional cooling (Japsen et al., 2006; Lunt et al., 2008a; Solgaard et al., 2013; Knies et al., 2014a; Knies et al., 2014b).

An example of uplifting that altered the atmospheric circulation, and hence regional climate patterns, is given in Rech et al. (2006), where it is suggested that the uplift of the Andes blocked moisture coming from the South American Summer Monsoon and caused the initiation (between 19 and 13 Ma) of hyperaridity in the Atacama Desert. Hyperaridity can increase the amount of iron transported into the ocean via aeolian dust. Iron fertilises the water providing micronutrients for phytoplankton, allowing blooms (Meskhidze et al., 2005). Iron fertilisation also reaches the oceans from volcanic ash, and strong links have been shown to exist between iron fertilisation and the productivity of the oceans (Abrajevitch et al., 2014). The Andes have been rising since the middle Miocene, uplifting consistently by 0.2–0.3 mm per year since the late Miocene (Tortonian, 10.7 Ma), when they were at half their current height of 3600 m (Hooghiemstra and van der Hammen, 1998; Gregory-Wodzicki, 2000; Jiménez-Moreno et al., 2008). Other mountain chains that uplifted during the Neogene included the Alps. During the early Miocene, the Alps were islands between the Paratethys and the Western Tethys oceans. They began to uplift during the Langhian (14 Ma), reaching 3500 m above sea level by the Tortonian (8 Ma; Jiménez-Moreno et al., 2008).

The back bone of the Americas is the North America Cordillera and is made up of mountain chains such as the Alaska Range, the Rocky Mountains, the Cascades and the Coast Ranges (Foster et al., 2010). Without the North American Cordillera the northeast of North America would have significantly warmer winters and the continental interior would have increased precipitation (Kutzbach et al., 1989; Seager et al., 2002). Most of the North American

Cordillera ranges have been at a high elevation (over 2 km) since before the Neogene, having formed in the early Cenozoic and, if anything, have reduced in height during the Neogene (Wolfe et al., 1998; Horton et al., 2004; Kent-Corson et al., 2006). However, the Coastal Mountain Ranges, such as the Cascade in northwest of North America, did not develop until the middle to late Miocene and did not reach their present height of ~ 1.5 km until ~7–9 Ma (Denton and Armstrong, 1969; Clague, 1991).

1.2.4 Neogene climate and cryosphere development

Throughout the Neogene, global temperatures were warmer than they are today. The Neogene marks the transition between the warmer greenhouse world of the Paleocene, to the colder temperatures seen today, with ice sheets on both poles (Figures 1.1 and 1.2; Zachos et al., 2001; 2008; Lawver and Gahagan, 2003; Hönisch et al., 2012). The cooling trend was established prior to the Neogene, beginning in the Eocene with the development of ice on Antarctica at the Eocene-Oligocene boundary (~34 Ma) due to CO_2 levels falling below a critical threshold (Kennett, 1976; Barrett, 2008; Zachos et al., 2008; Pearson et al., 2009; Lear et al., 2015). This cooling trend is marked by a 1.5‰ positive shift of oxygen isotope values, and atmospheric CO_2 levels, determined from boron isotopes, were between ~450 and ~1500 ppmv (Pearson et al., 2009). However, with increased development of CO_2 proxy methods, there is now only a twofold discrepancy between the different methods used (Beerling and Royer, 2011). At this time, ice rafted debris suggests that the ice was semi-permanent, but on a continental scale (Zachos et al., 1992; Scher et al., 2011). The cause of ice development is partly attributed to the breaking up of Gondwana where the ocean gateways widened (e.g. the opening of the Drake Passage), isolating the continent and partially leading to the southern polar glaciation (Livermore et al., 2007; Lagabrielle et al., 2009). In the Northern Hemisphere, only ephemeral glaciers were present in Greenland at the Eocene-Oligocene boundary (Eldrett et al., 2009).

Global cooling continued and a second stage of ice growth occurred just prior to the Oligocene-Miocene boundary (~23 Ma) with a ~1‰ positive excursion in marine benthic foraminifera $\delta^{18}O$ records (Beddow et al., 2016). The global cooling event resulted in large scale ice sheet expansion on Antarctica (Mi-1) and a decrease of high latitude deep ocean temperatures (Woodruff and Savin, 1989; Miller et al., 1991; Zachos et al., 1997). It separated the low amplitude climate variability, with relatively warm global temperatures of the late Oligocene, from the high amplitude rapid climate variability, with large temperature and ice fluctuations, of the early Miocene (Miller et al., 1991; Zachos et al., 2001; Billups et al., 2004; Holbourn et al., 2005; Pälike et al., 2006; Shevenell and Kennett, 2007; Liebrand et al., 2011).

The Miocene continued the cooling trend established during the Oligocene, with reductions in CO_2 levels and the aridification of continental interiors (Zachos et al., 2008; Potter and Szatmari, 2009; Beerling and Royer, 2011). However, the steadily-cooling early Miocene was interrupted by the Middle Miocene Climatic Optimum (MMCO), where temperatures peaked following a 3–7 °C increase in deep-sea temperatures (Raymo and Ruddiman, 1992). The MMCO was a period of global warmth that occurred towards the end of the Burdigalian and the start of the Langhian, between 17 and 15 Ma (Savin et al., 1975; Zachos et al., 2001; Böhme, 2003; You et al., 2009). Although it began earlier in Europe (between 42 and 45° N), at around 18 Ma, and lasted longer (until 14 Ma; Böhme, 2003). Böhme (2003), used ectothermic vertebrates and bauxite records to calculate a lower and upper limit of mean annual temperatures of 17.4 °C and ~22 °C respectively for the MMCO. Global temperatures of the MMCO were thought to have been 3 °C higher than today, with an atmospheric CO_2 concentration between 460 and 580 ppmv (You et al., 2009). In Japan, molluscan assemblages suggest that temperatures were ~6 °C warmer than present (Itoigawa and Yamanoi, 1990; Tsuchi, 1990) and mean annual temperatures in Alaska/North West Canada reached 9 °C higher than present (White et al., 1997). The MMCO led to a 2000 fold increase in two species of dinoflagellate cysts (*Operculodinium centrocarpum* and *Pyxidinopsis braboi*) preserved in Antarctica, showing the peak of the MMCO in Antarctica was between 15.7–15.5 Ma (Warny et al., 2009). The enormous increase of these two species has been related to a peak in productivity due to warmth causing the ice to retreat (Warny et al., 2009). West Greenland also saw an increase in dinoflagellate cyst abundance and diversity over the MMCO (Piasecki, 2003).

Estimates of atmospheric CO_2 levels over the MMCO (from palaeosols, stomatal indices and marine CO_2 proxies) range from 180 to 700 ppmv (Cerling, 1991; Pagani et al., 1999; Pearson and Palmer, 2000; Royer et al., 2001; Kürschner et al., 2008). The lower levels from this range, as calculated by Pagani et al. (1999) and Pearson and Palmer (2000), suggest that CO_2 may have become decoupled from sea surface temperatures. Whilst numerous temperature proxy records show global warmth during this time (Zachos et al., 2001; Böhme, 2003; Kürschner et al., 2008; Sun and Zhang, 2008), climate models are so far unable to recreate the deep water warmth under low CO_2 conditions (You et al., 2009; Herold et al., 2012). Along with the debate over exactly what the CO_2 levels over the MMCO were, the cause is also debated (You et al., 2009; Henrot et al., 2010; Herold et al., 2012), and may be linked to changes in ocean circulation and heat transport due to ocean gateway evolution (Woodruff and Savin, 1989; Flower and Kennett, 1994; Ramsay et al., 1998; Shevenell and Kennett, 2004; Poore et al., 2006). For example, both the CAS and the Eastern Mediterranean Gateway were open at this time, resulting in different ocean patterns (Herold et al., 2008; Henrot et al., 2010).

The MMCO was followed by the MMCT (~14 Ma), and a further major phase of cooling and ice development in Antarctica (Holbourn et al., 2005). The MMCT took place in several stages, Miocene isotope events Mi-3 to 7 (Quaijtaal et al., 2014), and represents an important step between the initiation of global cooling, and the modern ocean and climate system of the present (Flower and Kennett, 1994). The largest cooling step was Mi-3b, at ~13.82 Ma (Abels et al., 2005), which resulted in an increased production of cold Antarctic deep water, major ice sheet growth and a decrease of 2 °C of deep ocean temperatures (Flower and Kennett, 1994; Billups and Schrag, 2002; Shevenell et al., 2004; 2008). A decrease of 6 to 7 °C is postulated for Pacific sea surface temperatures (Shevenell et al., 2004). Like the MMCO, causes of the MMCT are debated and have been attributed to a drawdown of CO_2 and/or changes in oceanic circulation (Shevenell and Kennett, 2004; Kürschner et al., 2008; Pagani et al., 2009; Badger et al., 2013). Back stripping evidence shows that during the MMCT sea levels fell between 53 and 69 m (John et al., 2011), and evidence from glacial landforms suggest that larger than modern ice sheets overrode the Transantarctic Mountains (Lewis et al., 2007).

After the rapid cooling during the MMCT, temperatures resumed their steady decline throughout the remainder of the Miocene. However, the rate of cooling and ice growth slowed (Zachos et al., 2001; 2008). Despite this sustained Miocene global cooling, vegetation evidence from global reconstructions shows that the late Miocene (Tortonian) had warmer and wetter climates than today (Pound et al., 2011; 2012a; 2012b), and a nearly ice free Northern Hemisphere (Zachos et al., 2001; Ruddiman, 2010). Significant ice cover on Greenland was not possible until mountain uplift, beginning at 10 Ma, resulted in parts of southern and eastern Greenland reaching two kilometres above sea level (Japsen et al., 2006; 2010). Even at this time, only southern Greenland was glaciated (Wolf and Thiede, 1991). The development of ice in both hemispheres helped regulate the climate by driving changes to eustatic sea level and deep-ocean circulation (Anderson, 1999; Lear et al., 2015). The increasing amount of ice resulted in a higher surface albedo, further reducing temperatures and reinforcing cooling, particularly in the high latitudes (Curry et al., 1995).

During the Pliocene, compared to the modern, meridional temperatures were reduced, the tropics were expanded towards the high latitudes and poleward ocean heat transport was increased (Brierley et al., 2009; Pagani et al., 2010). In the early Pliocene, the east-west temperature gradient of the Pacific was approximately 1.5 °C, compared to 5 °C today (Wara et al., 2005; Dowsett and Robinson, 2009). The latitudinal temperature gradient was also reduced, for example oxygen isotopes and annual tree rings depict that the Pliocene Arctic had mean annual temperatures ~19 °C warmer than the modern (Ballantyne et al., 2010). At the Zanclean-Piacenzian boundary (3.6 Ma) there was an intensification of glaciation, which peaked at 3.3 Ma (Mudelsee and Raymo, 2005; Contoux et al., 2015), and during the late Pliocene there was a relatively brief, but significantly warmer interval, the middle Piacenzian Warm Period (MPWP, 3.29–2.97 Ma; Haywood et al., 2002). During the MPWP, temperatures were ~3 °C higher than pre-industrial levels, with atmospheric CO_2 concentrations of ~400 ppm and sea levels 10–20 m higher than today (Raymo et al., 1996; Ravelo and Andreasen, 2000; Haywood et al., 2009; Seki et al., 2010; Salzmann et al., 2013). During this time, the ice sheets were reduced and the eastern Arctic Ocean was seasonally ice free (Knies et al., 2002; Dolan et al., 2011).

An increase in glaciation followed the MPWP culminating in the Northern Hemisphere Glaciation (NHG) at 2.74 Ma (Lear et al., 2015). At this time the extent of the North American ice-sheet far exceeded that of today, a Eurasian ice sheet grew and the Antarctic ice sheet was considerably thicker than at present, before it waxed and waned throughout the Pleistocene (Ingólfsson, 2004; Bartoli et al., 2005; Mudelsee and Raymo, 2005; Pagani et al., 2010; Knies et al., 2014b). The cause of the NHG is not fully understood and possible hypotheses include the closure of the CAS and decreases in CO_2 levels during the late Pliocene (Lunt et al., 2008a).

1.2.5 Plankton evolution

The development of the modern climate and oceanic circulation that took place during the Neogene had important consequences for the distribution and evolution of plankton, and large turnover events can often be related to major palaeoceanographic changes (Tappan and Loeblich, 1973; Wei and Kennett, 1986). For example, the diversity of planktonic foraminifera increased during the early Miocene, probably due to an increased polar to equatorial thermal gradient, and remained steady during the middle and late Miocene. It then decreased between the Pliocene and present day, due to the large scale palaeoceanographic fluctuations and high frequency climatic oscillations that resulted in the NHG (Wei and Kennett, 1986). Radiolarians also saw a similar pattern of diversity changes (Lazarus, 2002).

Controlling factors of the distribution and diversity of different microfossil planktonic groups are complex, and are not all associated with temperature. For example, radiolarians have an inverse correlation to productivity. High diversities are found in regions with few nutrients, whereas a high diversity of diatoms is often associated with high productivity (Lazarus, 2002; 2014). The increasing diversity of diatoms through the Neogene has been related to the increased continental weathering, which resulted in an increased strength of the biological pump (Cermeño et al., 2015).

The Oligocene-Miocene transition is marked by a major change in the global distribution of planktonic groups, which has been attributed to the development of the ACC (Kennett, 1978). This development aided in the establishment of modern planktonic distributions, which are often arranged into latitudinal bands, with a steep latitudinal diversity gradient (Rutherford et al., 1999; Crame, 2001). Environmental changes also can influence the size of plankton. For example, through the Neogene, planktonic foraminifera increased in size, whereas there was a decrease in size in the coccolithophores (Schmidt et al., 2006). The increase in size of the foraminifera is attributed to the cooling Neogene, whereas the decreasing size of the coccolithophores is attributed to an increase in the stratification of the waters, which influences the amount of nutrients that reach the surface waters (Schmidt et al., 2006). Dinoflagellates are an additional group that have been affected by the environmental changes that took place during the Neogene, and their responses are discussed throughout this thesis.

1.2.6 Geological development of the Mediterranean Basin

This section provides more detailed information on the changes that took place during the Neogene that specifically influenced the Mediterranean and Paratethys regions (Figure 1.3). The Mediterranean region underwent great change during the Neogene making it an excellent case study for investigating the climate proxy potential of dinoflagellate cysts (see Section 3.6).

During the late Palaeozoic and early Mesozoic eras all the continents converged and formed the supercontinent Pangaea. The breakup of Pangaea, beginning around the Permian-Triassic boundary, lasted several hundred million years starting with the breakup of Gondwana and Laurasia (Bosworth, 2015). The Tethys Ocean was situated between Gondwana and Laurasia and, through continental rifting, stretched through to the newly emerging Atlantic Ocean in the Early Jurassic (Stampfli and Borel, 2002). The opening of the Indian Ocean began towards the end of the Late Jurassic with the detachment of the Indian Plate from Gondwana (Stampfli and Borel, 2002). It collided with Asia during the Eocene (Rögl, 1999). The movement of India resulted in the western end of the Tethys Ocean being reduced to the size of the Mediterranean of today (Rögl, 1999). It also caused the formation of the intercontinental Paratethys Sea, which was situated in the region of present day Austria, Hungary and Romania (Rögl, 1999); an area now emerged above sea level.

In the Late Cretaceous, the northward movement of the Arabian Plate and India narrowed the Tethys Seaway (Golonka et al., 1994; 2004) and eventually, around 14 Ma, the Eastern Mediterranean Gateway closed, preventing water from being exchanged between the Indian Ocean and the Mediterranean (Rögl, 1997; Hüsing et al., 2009). Earlier estimates for the timings of the closure are described below. What was once the Tethys Seaway continued to

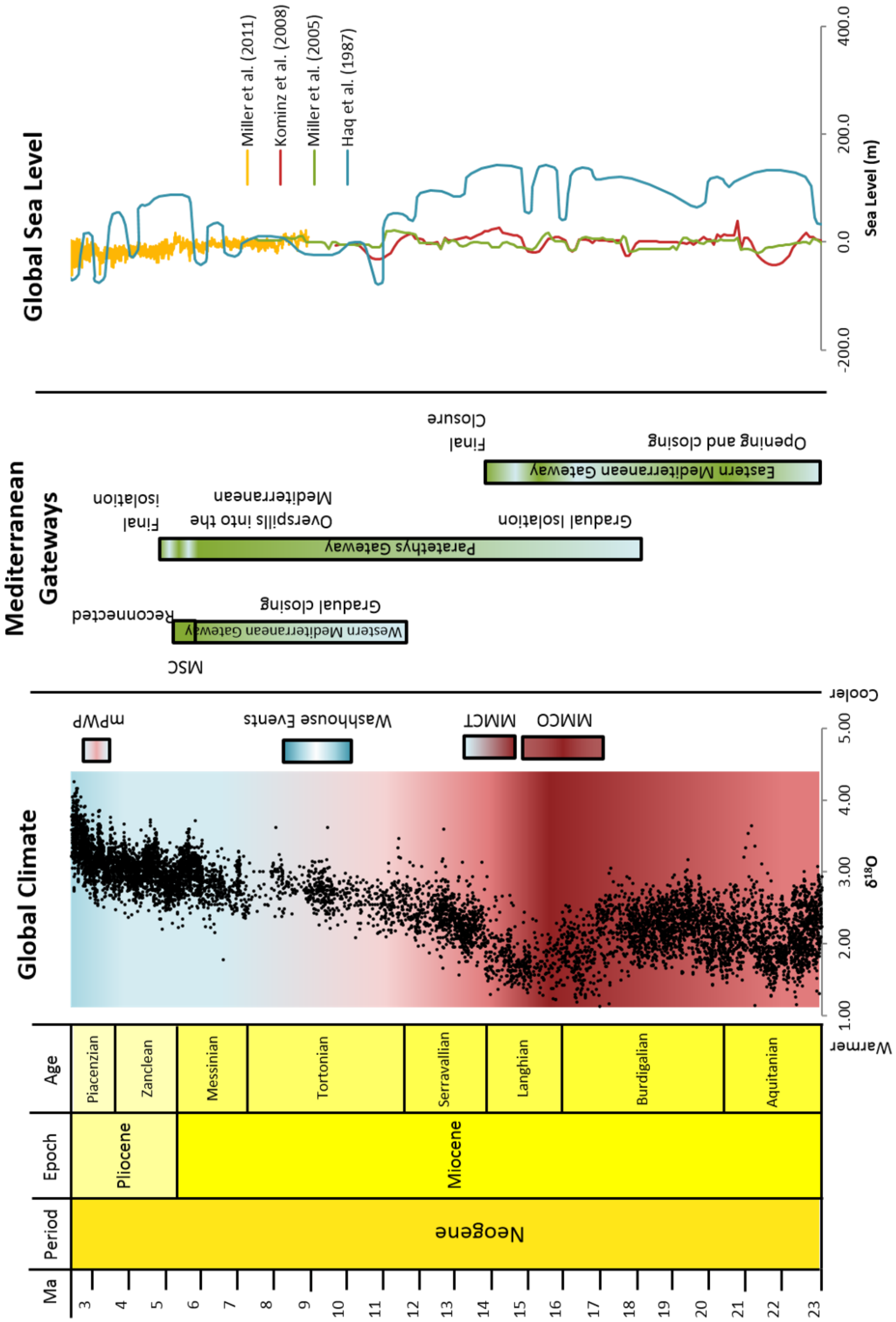


Figure 1-3: Summary of the major changes that took place in the Mediterranean and Paratethys during the Neogene. The benthic δ^{18}O curve is adapted from Zachos et al. (2008) and reflects bottom water temperatures. Data for the Sea level curves comes from Haq et al. (1987); Miller et al. (2005; 2011) and Kominz et al. (2008). All other references can be found in the text (Section 1.2.6). Sea level (m) is relative to present.

close with the subduction of the Arabian Plate under the Eurasian Plate, and the gateways between the Paratethys and the Mediterranean eventually closed. Today, only the Black and Caspian Seas represent the ancient Paratethys Sea (Rögl, 1999; Popov et al., 2006; Harzhauser and Piller, 2007). The shrinkage of the Tethys Seaway also resulted in triggering the North African aridity, establishing the Sahara Desert (Zhang et al., 2014). Connections between the Mediterranean Sea and the Atlantic Ocean were briefly interrupted during the Messinian (5.97–5.33 Ma), with the closure of the Western Mediterranean Gateways causing huge salinity fluctuations and the mass precipitation of evaporites during an event known as the Messinian Salinity Crisis (MSC; Hsü et al., 1973; 1977; Krijgsman et al., 1999a; Flecker et al., 2015), also described in more detail below.

Thus, the Mediterranean Sea has changed greatly since its formation, from being connected to both the Indian and the Atlantic oceans to being completely isolated before partially reopening, and this evolution has significantly altered regional flora and fauna, circulation, depth, sediment type and climate. The gateway changes of the Mediterranean during the Neogene (23.03–2.59 Ma) helped to develop the modern world's oceanic and atmospheric circulation (Potter and Szatmari, 2009). Several studies suggest a link between the closing of the Eastern Mediterranean Gateway (Woodruff and Savin, 1989; Flower and Kennett, 1993a; Rögl, 1999), which stopped water exchange between the Indian Ocean and the Mediterranean, and the MMCT (~14 Ma); a time of global cooling (Flower and Kennett, 1993a; Zachos et al., 2001; 2008; Shevenell et al., 2004). Furthermore, because the Mediterranean has a very different hydrological balance than the open ocean, producing relatively warm and salty water, exchange through its marine gateways has an important influence on water temperature and salinity in the connected basins. It therefore affects circulation of both the Mediterranean and the open oceans (Ivanovic et al., 2014a). For example, warm waters of the Atlantic are exchanged for the cooler and saltier intermediate to deep waters of the Mediterranean, which amplifies the Atlantic Meridional Overturning Circulation (Rogerson et al., 2010).

1.2.6.1 Eastern Mediterranean Gateway

The timing of the closure of the gateway between the Indian Ocean and the Mediterranean Sea is less certain than for the later Western Mediterranean Gateway closure that caused the MSC (Rögl, 1999; Popov et al., 2004; Harzhauser and Piller, 2007; Allen and Armstrong, 2008; Hüsing et al., 2009; Okay et al., 2010). The Eastern Mediterranean Gateway closure was caused by the rotation and collision of the Arabian plate with Eurasia, preventing the exchange of water between the Mediterranean Sea and the Indian Ocean (Rögl, 1999). Evidence for the final collision between the Arabian and Eurasian plates gives a range of dates between the late Eocene (~35 Ma; Allen and Armstrong, 2008) and the early Tortonian (~11 Ma; Hüsing et al., 2009).

The progressive restriction of the Tethys Ocean was due to the northward movement of both the Indian and Arabian plates (Rögl, 1999; Hüsing et al., 2009). What was once a wide and deep gateway became more restricted until it was a subtidal marine environment by the end of the Oligocene (23 Ma; Rögl, 1999; Hüsing et al., 2009). By the middle Miocene, biostratigraphical evidence indicates that a shallow water gateway emerged in response to the subduction of the Arabian Plate under the Eurasian Plate (Hüsing et al., 2009). This connection was situated north of the Arabian Plate and is thought to have been between 300–600 m deep. It remained open until the seafloor of the gateway re-emerged and the connection between the Mediterranean and the Indo-Pacific closed permanently at 11 Ma (Hüsing et al., 2009), although other authors suggest it was already closed by this time (Rögl, 1999; Popov et al., 2004; Harzhauser and Piller, 2007; Vincent et al., 2007; Allen and Armstrong, 2008; Okay et al., 2010).

The oldest estimate for the final collision of the Arabian and Eurasian plates, is ~35 Ma and Allen and Armstrong (2008) provided evidence for this from compressional deformation, major surface uplift, onset of terrestrial sediments and changes in palaeobiogeography. Vincent et al. (2007) agreed with this timing and showed that the uplift of the Greater Caucasus, Europe's largest mountain belt, located on the northern margin of the Arabia-Eurasian collision zone, began during the initial collision of the Arabian and Eurasian plates at ~35 Ma. Based on regional stratigraphy, ~20 Ma is the date given for the collision of the plates (Okay et al., 2010), but the presence/absence of Mediterranean and Indian fauna suggests that marine exchange ended much later; ~14 Ma (Rögl, 1999; Popov et al., 2004; Harzhauser and Piller, 2007). The youngest possible date of water exchange between the Indian Ocean and the Mediterranean Sea is 11 Ma, when the end of deposition of deep water sediments is thought to represent the ceasing of continental plate subduction (Hüsing et al., 2009).

The general consensus is that the Indian Ocean and Mediterranean Sea were intermittently connected until at least the middle Miocene, and that the final closure took place at ~14 Ma (Woodruff and Savin, 1989; Rögl, 1999; Popov et al., 2004; Harzhauser, 2007; Harzhauser and Piller, 2007; Hüsing et al., 2009; Hamon et al., 2013). Faunal changes (molluscs, echinoids and foraminifera) concur with this theory, and it is thought that the water basins reconnected due to sea level fluctuations during the MMCO, a period of global warmth between ~17 and 15 Ma (Rögl, 1999; Meulenkamp and Sissingh, 2003; Harzhauser, 2007; Harzhauser and Piller, 2007; Allen and Armstrong, 2008; Hüsing et al., 2009; Reuter et al., 2009; Okay et al., 2010; Hamon et al., 2013).

1.2.6.2 Atlantic Gateway and Messinian Salinity Crisis

The Atlantic-Mediterranean connection is still present today, although this has not always been the case and the nature of the connection has evolved. The Eastern Mediterranean Gateway closed during the collision of the African and Eurasian plates (see previous section) and during the late Miocene the Mediterranean Sea became increasingly isolated due to the tectonic uplift related to the Africa-Europe convergence (Hüsing et al., 2010). The uplift along the continental margins of Africa and Iberia caused the two remaining passages connecting the Mediterranean Sea and the North Atlantic to become narrower and shallower, restricting the throughflow between the two basins (Weijermars, 1988; Garcés et al., 1998; Krijgsman et al., 1999a). These corridors, called the Rifian Corridor, through Northern Morocco, and the Betic Corridor (Iberian Seaway) in Southern Spain (Benson et al., 1991; Krijgsman, 2002; Krijgsman et al., 2002; Betzler et al., 2006), had complex geometries, although broadly they were much wider (and longer) than the current Straits of Gibraltar.

The Betic Corridor was the first of the two corridors to close and was made up of four distinct elements: the North Betic Strait, the Granada Basin, the Guadix Basin and the Guadalhorce Corridor (Flecker et al., 2015). These four passages/basins connected the Guadalquivir Basin to the Mediterranean Sea, and all four closed prior to the MSC (Flecker et al., 2015). The first of the Betic connections to close was the Guadix Basin at ~7.8 Ma (Betzler et al., 2006), followed by the North Betic Strait at ~7.6 Ma (Krijgsman et al., 2000) and then the Granada Basin between 7.37 and 7.24 Ma (Corbí et al., 2012). These dates all result from the discovery of continental deposits in the corridor, indicating the emergence of the surface above sea level (Flecker et al., 2015). The last Betic Corridor to close was the Guadalhorce Corridor, although little is known regarding the timing of its closure. However, Pérez-Asensio et al. (2012) put its closing at ~6.18 Ma (~200 Ka before the onset of the MSC) from changes to the deep-sea benthic foraminiferal oxygen-isotope curve.

Initial restriction between the North Atlantic and the Mediterranean Sea at the Rifian Corridor began at ~ 7.3 Ma, restriction increased between ~6.26 Ma and ~5.4 Ma primarily due to tectonic uplift (Warny et al., 2003). By 6.5 Ma, the Rifian Corridor had experienced enough tectonic uplift that the only movement of water between the North Atlantic and the Mediterranean occurred during small glacioeustatic fluctuations (Warny et al., 2003). The

Rifian Corridor is split into two main connections, the North Connection and the South Connection. The timing of the southern margin of the Rifian Corridor is better constrained, through astronomical tuning of the transition from marine to continental sedimentation, and shows a closure between 6.7 and 6 Ma (Krijgsman et al., 1999b; Krijgsman and Langereis, 2000). Mammal exchange was possible by 6.1 Ma, providing further evidence for closure by 6.0 Ma (Krijgsman, 2002; Van der Made et al., 2006). Dating for the closing of the Northern Connection is poorly constrained, 11.6–5.3 Ma. This estimate is provided by biostratigraphy and the presence/absence of open marine and highly diverse assemblages (Wernli, 1988). Additional timings of the Rifian Corridor closure are provided from pollen and dinoflagellate cyst analyses. The restriction is thought to have further intensified at ~5.4 Ma shown by an increase in the amount of pollen found compared to dinoflagellate cysts at the site (Salé, North West Morocco; Warny et al., 2003). Further, more constrained timings are provided by neodymium isotopes and show a change of hydrographic situation at 7.2 Ma, with a final closure of the Rifian Corridors between 6.64 and 6.44 Ma (Ivanovic et al., 2013).

Once throughflow between the North Atlantic and the Mediterranean was no longer possible, the Mediterranean became completely isolated. It is thought that because the influx of freshwater from rivers could not fully compensate for total evaporation, the evaporites of the MSC were precipitated (Martín et al., 2001). The precipitation of evaporites was synchronous across the whole of the Mediterranean Basin (Krijgsman, 2002; Krijgsman et al., 2002) and was associated with a sea level fall of over 1000 metres (Gómez, 2006), with the precipitation of several kilometres of salt beginning at 5.97 Ma and ending ~5.33 Ma (Riding et al., 1998; Martín et al., 2001; Krijgsman, 2002; Krijgsman et al., 2002; Manzi et al., 2013; 2015). It is thought that several kilometres of salt could only be precipitated if there were periodic incursions of saltwater into the Mediterranean Basin from the North Atlantic Ocean and results from a neodymium isotope record north of Morocco cannot rule this out (Ivanovic et al., 2013).

The MSC is considered one of the most dramatic ocean events of the Neogene (Krijgsman, 2002) and reduced the world's ocean salinity by 6% (Hsü et al., 1977; Warny et al., 2003). Large salinity fluctuations took place, reaching three to ten times higher than present day conditions, and brackish and near fresh water conditions occurred towards the end of the MSC in the ostracod-rich Lago Mare facies (Decima and Wezel, 1973; Krijgsman et al., 1999a). The near drying up of the Mediterranean Basin and precipitation of vast quantities of evaporites also had profound impacts on the biota of the time and wiped out/diminished many taxa due to the loss of marine habitats and the increasingly hostile environment (Hsü et al., 1977; Logan et al., 2004; Domingues et al., 2005; Kouwenhoven et al., 2006).

The salinity crisis had three distinct stages (Figure 1.4; CIESM, 2008; Manzi et al., 2013). In the first stage (5.97 to 5.60 Ma), selenites precipitated in shallow sub basins while euxinic shales and dolostones were found in the deep basins. In the second stage (5.60 to 5.55 Ma), local desiccation of some of the salt basins occurred, resulting in resedimentation of the evaporites. Selenite and laminar gypsum were deposited in the third stage (5.55 to 5.42 Ma). After the main phase of precipitation, the final stage of the MSC (5.42 to 5.33 Ma) witnessed the progressive establishment of brackish to freshwater aquatic environments throughout the Mediterranean, which is known as the 'Lago Mare' event, characterised by ostracods and molluscs of brackish affinity (Carnevale et al., 2006; Roveri et al., 2008a; 2014). The Lago Mare event was an environmental change where non-marine sediments were deposited, possibly due to intense runoff from continental areas resulting from a more humid climate and the draining of the relatively fresh Paratethys Sea (Carnevale et al., 2006).

Marine conditions were re-established at the start of the Pliocene (~5.33 Ma) after further tectonic activity/erosional collapse resulted in the opening of the Strait of Gibraltar and Atlantic water flowing back into the Mediterranean Sea (Hsü et al., 1973; Comas et al., 1999; Blanc, 2002; Krijgsman, 2002; Krijgsman et al., 2002; Fauquette et al., 2006). However, it has been suggested that reflooding of the Mediterranean may have taken place earlier at 5.46

Ma, ~130 Kyrs before the Messinian/Zanclean boundary (Popescu et al., 2009). Carnevale et al. (2006) also gave dates for the reflooding of the Mediterranean preceding the Messinian-Zanclean boundary. They found fully marine fish present amongst the Lago Mare facies, suggesting that there were normal marine conditions (and there was an episodic if not sustained connection to the Atlantic) at least during the upper interval of the Lago Mare event.

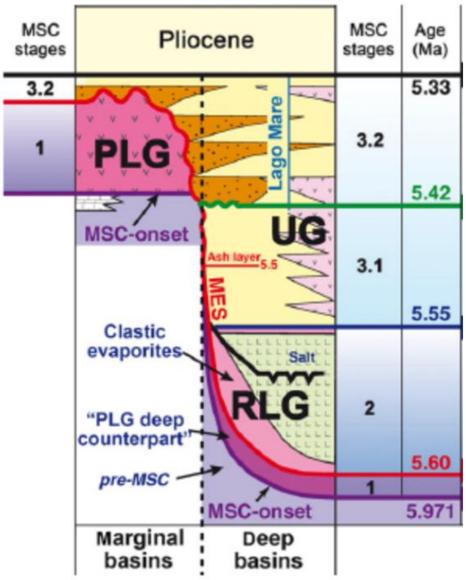


Figure 1-4: The three major stages of the MSC from CIESM, (2008) and Manzi et al. (2014). The three main evaporate units are labelled PLG (Primary Lower Gypsum), UG (Upper Gypsum) and RLG (Resedimented Lower Gypsum).

After the flooding event, at the beginning of the Pliocene, new niches opened up in the Mediterranean, allowing species to migrate into the region from the Atlantic, replenishing the diversity (Bianchi and Morri, 2000; Logan et al., 2004). Today, 67% of marine Mediterranean species are also present in the Atlantic (Fredj et al., 1992).

1.2.6.3 Paratethys Sea and Lake Pannon

The Paratethys was an epicontinental sea that, at its maximum extent, spanned from the Rhône Basin in France towards Inner Asia (Harzhauser and Piller, 2007). Its development began in the late Eocene to Oligocene, due to the northward movement of the Arabian Plate, and its separation from the Mediterranean Sea is strongly linked to the Alpine orogeny (Kroh, 2007). The newly formed Paratethys was split into two main sub-basins, which underwent different histories due to differing geotectonic events and timings (Harzhauser and Piller, 2007). The two sub-basins were not equal in size; the smaller of the two consisted of the western and central Paratethys and the larger was the Eastern Paratethys (Harzhauser and Piller, 2007). Both had a complex history of connection and disconnection with the Mediterranean (Rögl, 1999; Harzhauser and Piller, 2007).

In the early Miocene, normal marine conditions prevailed and the Rhine Graben, the central segment of the Cenozoic rift system (Ziegler, 1992; 1994), connected what is now the Mediterranean Sea to the North Sea. This connection ceased during the lower Aquitanian, and freshwater environments developed in the western tip of the Paratethys. In the late Aquitanian and early Burdigalian there were broad connections between the Paratethys and the Mediterranean and mollusc, echinoid and bryozoans faunas spread via the gateways (Mandic and Steininger, 2003; Harzhauser, 2007; Kroh, 2007). The middle Burdigalian had normal marine conditions and rare patchy corals could be found. The uplift of the Alpine Foreland resulted in connections with the west terminating (Rögl, 1997; Harzhauser and Piller, 2007) and a fluvial-lacustrine environment established in the western Alpine foreland basin (Berger, 1996; Harzhauser and Piller, 2007).

The beginning of the Paratethys isolation was accentuated in the middle Burdigalian by a global sea level fall (Haq et al., 1988). During the late Burdigalian there was a low diversity of mollusc fauna, but during the MMCO (Zachos et al., 2001; 2008), taxa migrated northwards into the Paratethys. The migration occurred through a new broad gateway connecting the Paratethys and the Mediterranean, the Trans-Tethys Trench Corridor (Bistricic and Jenko, 1985), and resulted in high diversities during this time (Harzhauser and Piller, 2007). For example, the diversity of gastropods in the Paratethys was 277 in the late Burdigalian and rose to 772 species in the Langhian (Harzhauser and Piller, 2007). A similar pattern was seen in the foraminifera record (Harzhauser and Piller, 2007). The migration of species between the Mediterranean and the Paratethys is also evident in decapod (crustaceans) assemblages

(Gatt and De Angeli, 2010). In the Langhian there is evidence of strong affinities with decapod assemblages from Maltese and those from Hungary, Poland and Ukraine (Gatt and De Angeli, 2010). After peaking towards the end of the Langhian, the diversity of both the gastropods and foraminifera groups declined (Harzhauser and Piller, 2007) in correlation with the MMCT. The MMCT culminated in the development of ice in Antarctica, which caused a sea level fall around 14 Ma of between 53 and 69 m (Flower and Kennett, 1993a; Shevenell et al., 2004; John et al., 2011). The sea level fall occurred at roughly the same time as the loss of the final connection between the Mediterranean Sea and the Indian Ocean as well as the closure of the seaway between the Mediterranean and the Central Paratethys (Rögl, 1999).

In the Serravallian, there was a further hiatus due to sea level fall and by the Tortonian (11.6 Ma) further continentalisation had resulted in the restriction of the aquatic realm to Lake Pannon. Lake Pannon was a vast brackish to fresh water lake in the Western Paratethys (currently Hungary) that had a high percentage of endemic species (Müller et al., 1999). The assemblages differed greatly to those found in the Eastern Paratethys and Mediterranean instigating rapid evolutionary radiations (Müller et al., 1999; Harzhauser and Piller, 2007).

The Paratethys is thought to have over spilled into the Mediterranean Sea on two occasions after the basin became semi isolated; once before the end of the MSC (top of the marginal evaporites) and once in the lower most Zanclean (Clauzon et al., 2005). These over spills can be traced by a sudden increase in the number of species thought to be endemic to the Paratethys, such as the dinoflagellate cyst complex *Galeacysta etrusca* (Popescu et al., 2009). Other endemic surges that are found in the Mediterranean include molluscs and ostracods (Clauzon et al., 2005).

1.2.6.4 Overview of the modern Mediterranean region

The diversity of the modern Mediterranean region is very high, with approximately 12,000 macroscopic marine species (Boudouresque, 2004). There are several hypotheses as to why the diversity of the Mediterranean region is so high compared to the rest of the marine realm, particularly when considering its relatively small size. The simplest explanation is that it has been studied for longer than other regions and thus has more material to draw from (Bianchi and Morri, 2000). Other reasons relate more to its variable geological history (connections to or isolation from different ocean basins at different times, changes in hydrological balance etc.), which created a variety of different niches and hence many invasions and speciation events (Bianchi and Morri, 2000). For example, the Mediterranean Sea was once part of the Tethys Seaway, and was connected to the Indopacific Ocean, whereas today it is only connected to the Atlantic Ocean. This means that as well as its endemic species, which make up 25% of the total species (Fredj et al., 1992), it has palaeomigrants from numerous previous ocean connections (Bianchi and Morri, 2000).

The change in Cenozoic climate has also influenced the diversity of the Mediterranean (Bianchi and Morri, 2000) and its variable climate allowed both temperate and sub-tropical biotas to migrate into the area (Sara, 1985). The Mediterranean is strongly influenced by the North Atlantic Ocean, meaning climate transitions that have taken place in the Atlantic are reflected in changes to Mediterranean fauna (Bianchi and Morri, 2000). Subtropical species migrated into the Mediterranean during interglacials, while temperate and boreal species migrated into the region during colder glacial periods, such as the Younger Dryas between 12.9 and 11.7 Ka (Broecker et al., 2010). The Pliocene ‘diversity dump’ from the North Atlantic, caused by the reopening of the Western Mediterranean Gateway (~5.33 Ma) also increased diversity (Bianchi and Morri, 2000), as did the more recent reconnecting of the Red Sea and Mediterranean Sea via the Suez Canal in 1869 (Galil, 2000; Galil et al., 2015). This man-made gateway between the Red Sea and the Mediterranean Sea allowed the migration of so many species that a separate biogeographical province has been proposed for the southeast Mediterranean (Por, 1999).

The current position of the Mediterranean means that it is highly susceptible to climate change. It is situated in the mid latitudes with a strong North Atlantic influence from the high latitudes and a strong monsoonal influence from lower latitudes (Dormoy et al., 2009). This means that it is particularly sensitive to short term climate changes; such as the Younger Dryas, arguably the last major climatic fluctuation of the last glaciation (Broecker et al., 1988; Alley et al., 1993; Bakke et al., 2009); which can have major impacts on the diversity both directly and indirectly. A change in water temperature can affect the survival and reproduction of a species and thus increase species competition. However, an increase in water temperature can also have indirect effects, such as changes to ocean currents, salinity and sea level, which may result in serious consequences to the diversity (Bianchi and Morri, 2000).

The modern climate of the Mediterranean region has a strong seasonality, with warm to hot dry summers and mild, wet winters (Quézel and Médail, 2003). It has had an extremely varied climatic history and today has a west to east gradient of decreasing precipitation (Dormoy et al., 2009). In the Miocene the latitudinal precipitation gradient was significantly stronger than today. The latitudinal temperature gradient has also evolved, increasing from ~0.48 °C per degree of latitude in the latest Miocene, to ~0.6 °C per degree of latitude today (Böhme et al., 2006' Fauquette et al., 2007).

1.3 Dinoflagellates

1.3.1 Dinoflagellates and the tree of life

The word dinoflagellate is derived from the Greek word *dino* meaning a whirl or eddy and the Latin word *flagellum,* meaning a small whip (Fensome et al., 1996a). Their name describes their distinctive morphology, which is comprised of two flagella (Figure 1.5). Dinoflagellates are single-celled eukaryotic organisms that typically range from 15-100 µm in length (de Vernal and Marret, 2007) and as part of their reproduction, ~15% of species form fossilisable cysts, which can be traced back to the Middle Triassic (Fensome et al., 1996b).

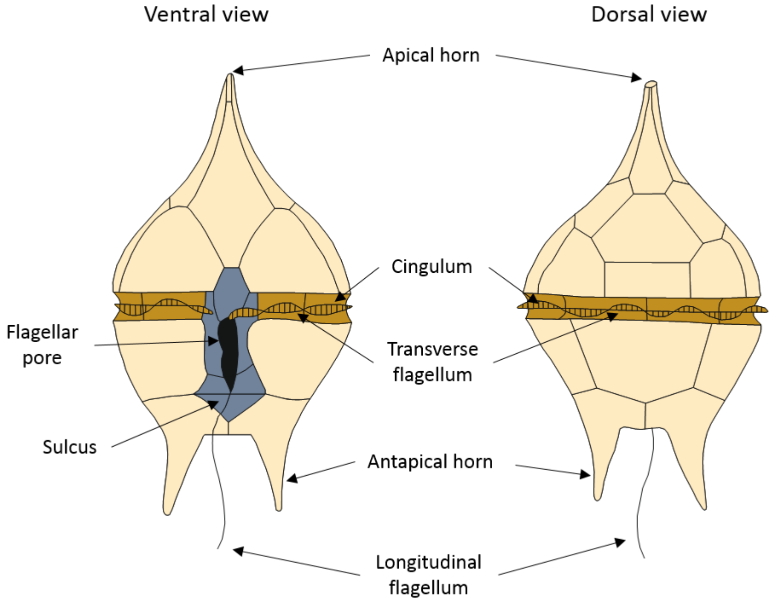


Figure 1-5: General morphology of a thecate motile cell. Adapted from Evitt, (1985) and Fensome et al., (1996).

Dinoflagellates are classified as protists, within the division Dinoflagellata (Fensome et al., 1993), and form a major constituent of the marine food chain. Their anatomy is complex as they share both plant and animal characteristics (Jeong, 1994). Generally, they are considered to be plants due to the cellulose in their cell wall and chlorophyll pigments in their protoplasm, and so plant nomenclature is used in reference to them (Taylor, 1987).

The taxonomic rank for the majority of the dinoflagellate cysts used in this project is listed below (Figure 1.6):

Domain - Eukarya

Kingdom - Alveolata

Division – Dinoflagellata (Bütschli, 1985) Fensome et al., 1993

Subdivision – Dinokaryota (Fensome et al., 1993)

Class- Dinophyceae (Pascher, 1914)

Subclass – Peridiniphycidae (Fensome et al., 1993)

Order – Gonyaulacales (Taylor, 1980) and Peridiniales (Haeckel, 1894)

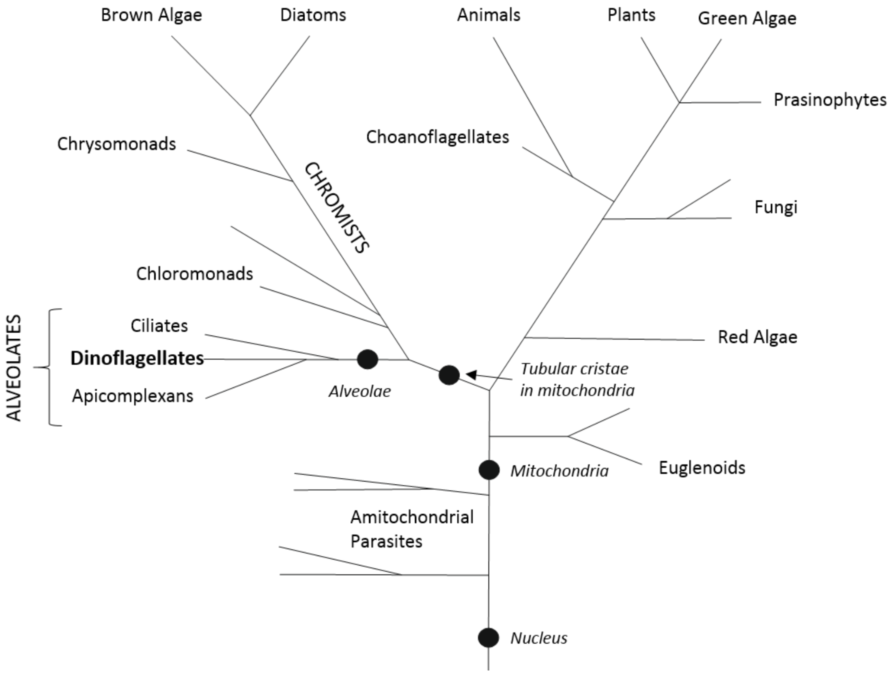


Figure 1-6: Demonstrating where dinoflagellates are on the tree of life. Adapted from Taylor, (1994) and Fensome et al., (1999).

1.3.2 Brief history

Fossil dinoflagellate cysts were first described by Ehrenberg, 1836, and are used in biostratigraphy, palaeoclimatology and palaeoecology. The majority of earlier studies on dinoflagellate cysts were undertaken by petroleum exploration companies who used them as biostratigraphical markers.

The research of dinoflagellate cysts can be split into four main stages (Stover et al., 1996). First was the initial discovery and curiosity stage from 1836 to 1954, followed by stage two, which was the development and documentary stage, from 1955 to 1967. Stage three was the compilation and application stage (from 1968 to 1977) and from 1977 onwards, refinement of data took (and is still taking) place (the fourth stage). One of the major steps in the documentation of the ranges of dinoflagellate cysts was when Woollam and Riding (1983) calibrated Jurassic dinoflagellate cysts with the standard European ammonite zonation, helping to define zones and dates for the various assemblages.

It was not until the early 1960s that the biological affinity with modern motile dinoflagellates was discovered; prior to this the cysts were thought of as representing the thecae or were assigned to the hystrichospheres (de Vernal and Marret, 2007). Once the dinoflagellate cysts were related to their motile equivalents, it became possible to use them for purposes other than biostratigraphy. Their use in palaeoceanography is still relatively new as the modern dinoflagellate taxonomy is still progressing. From the 1980s and onwards, the development of modern databases (Harland, 1983; Rochon et al., 1999; de Vernal et al., 2001; Marret and Zonneveld, 2003; Zonneveld et al., 2013a) helped to improve the understanding of their distribution and environmental preferences. Today, research continues, developing both biostratigraphy, in order to calibrate timings, and their use in palaeoecology, to aid in reconstructing palaeoenvironments.

1.3.3 Life cycle/reproduction

Dinoflagellates have three life stages including the motile stage, the growth stage and the cyst stage (Figure 1.7). The cyst stage happens for one of two reasons, as part of their reproductive cycle or because environmental conditions turn unfavourable. Dinoflagellates can remain encysted for as long as eight years (Mizushima and Matsuoka, 2004), although they can remain encysted for longer. For example, in one study, McQuoid et al. (2002) were able to hatch *Lingulodinium polyedra* from 20 to 55 year old sediment, and Ribeiro et al., (2011) demonstrate survival after a century of dormancy. The encystment stage often occurs seasonally and frequently follows periods of great abundance where the population increases exponentially (Stover et al., 1996).

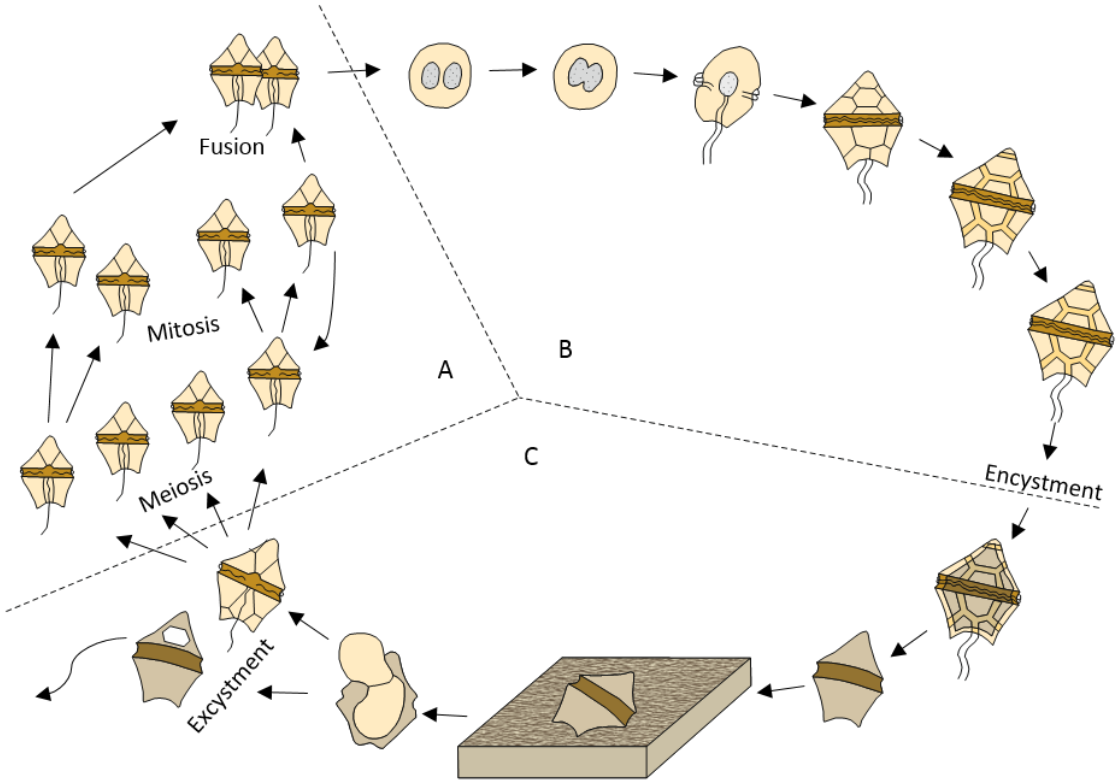


Figure 1-7: The life and reproduction cycle of the majority of the dinoflagellate cysts used in this study. Adapted from Evitt (1985) and Fensome et al. (1996).

The majority of dinoflagellates reproduce simply via asexual division of one parent cell into two daughter cells; a process that commonly includes the shedding of all, or part of, the parent wall (Fensome et al., 1993). However, dinoflagellates that reproduce asexually generally only have a motile stage and do not form cysts. Dinoflagellates that form a resting cyst do so by sexual reproduction. A resting cyst is any non-motile cell that possesses a resistant cell wall. They are made of dinosporin, a preservable complex organic polymer (Fensome et al., 1993). However, more recently studies (e.g. Versteegh et al., 2012; Bogus et al., 2012; 2014) have demonstrated that dinosporin is carbohydrate based, and represents a variety of chemically distinct biopolymers, which may differ between species. Siliceous and calcareous cysts can also form, but are less common (Stover et al., 1996).

Starting with the cyst (stage C, Figure 1.7), an idealised life cycle would be the following: excystment takes place (i.e. the motile form hatches) where a motile form, with two sets of chromosomes (diploid), emerges from the cyst. This cell would then undergo meiosis, which reduces the number of chromosomes by half (stage A, Figure 1.7). This results in motile and haploid cells that then undergo mitosis (where identical copies are made of each cell). At a certain time, normally autumn, two of the motile and haploid cells act as gametes, undergo fusion and form a zygote. The zygote forms a new theca, which is both motile and diploid, and becomes a planozygote (stage B, Figure 1.7). Eventually a cyst begins to form and the theca falls away leaving just the cyst, which is diploid, non-motile and called a hypnozygote or resting cyst. The cyst overwinters, and in the spring excystment takes place, and the cycle repeats (Evitt, 1985).

1.3.4 Morphology

Motile dinoflagellates have a distinctive morphology (Figure 1.5), which comprises two flagella and a unique nucleus called a dinokaryon (Dodge and Greuet, 1987; Fensome et al., 1996b). The flagella are orientated perpendicular to each other and cause the cell to move forward whilst rotating. The cell surface has two furrows known as the cingulum (transverse) and the sulcus (longitudinal) and within each furrow lies one of the flagella, which arise from pores (Taylor, 1987). The term theca is used to describe the non-resistant organic wall of the motile stages and often forms plates (Taylor, 1987; Fensome et al., 1993). The thecae are split into two main groups: armoured/thecate or unarmoured/naked. In armoured dinoflagellates, the cell has a rigid tabulate layer below the outer layer of the theca, while naked dinoflagellates have no plates in the theca.

1.3.4.1 Dinoflagellate (cyst) plates and their nomenclature

Both the motile form and the cyst have similar plate configuration (tabulation), which is different depending on the genus etc. Tabulation refers to the arrangement of the plates, which form in the amphiesmal vesicles in the theca. Plate boundaries are joined together along sutures. Tabulation is split into 6 main groups: gymnodinioid, suessioid, gonyaulacoid-peridinioid, nannoceratopsioid, dinophysioid and prorocentroid (Fensome et al., 1996b). The main tabulation types in this study are peridinioids and gonyaulacoids, which consist of five to six latitudinal bands and are often shortened to P- and G-cysts (Figures 1.8 and 1.9).

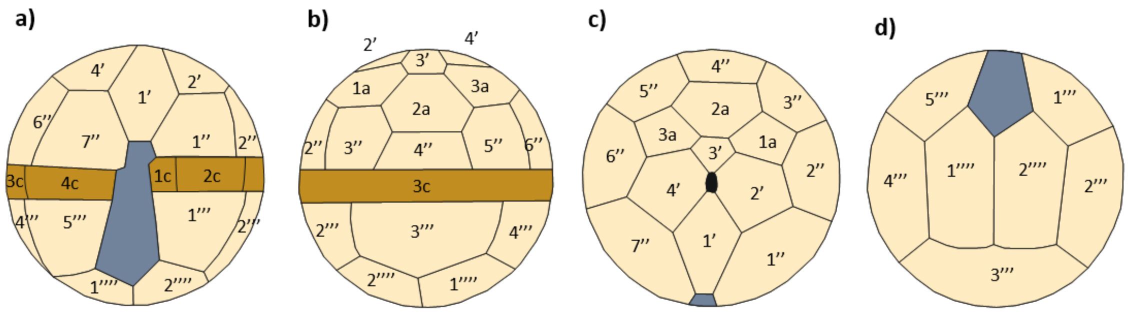


Figure 1-8: Standard peridinialean tabulation (as projected onto a sphere), labelled according to the Kofoid tabulation system (Table 1-2), different views of the same cysts are provided: (a) Ventral, (b) dorsal, (c) apical, (d) antapical. After Evitt (1985) and Fensome et al. (1996b).

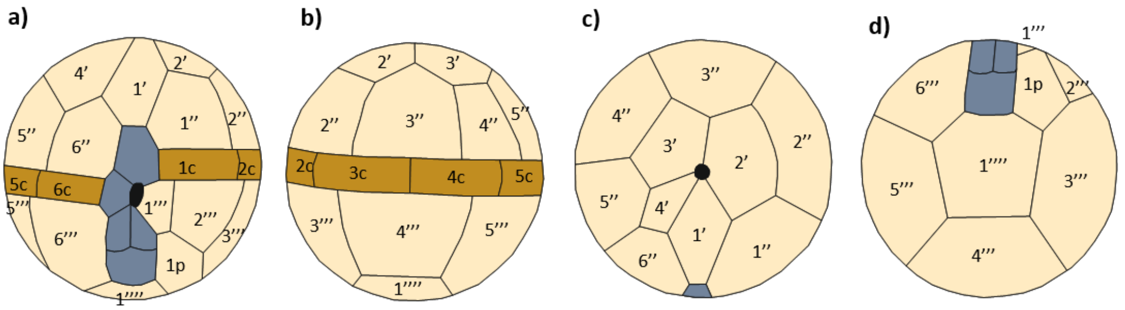


Figure 1-9: Standard gonyaulacalean tabulation (as projected onto a sphere), labelled according to the Kofoid tabulation system (Table 1-2), different views of the same cysts are provided: (a) Ventral, (b) dorsal, (c) apical, (d) antapical. After Evitt (1985) and Fensome et al. (1996b).

The most widely used system to label the plates is the Koifoid tabulation system (Table 1.2), which has been used since the early 1900s. It uses a suffix to designate each of the latitudinal series, for example: apical plates (′), precingular plates (″) cingular plates (c), postcingular plates (‴) and antapical plates (⁗). Anterior intercalary plates are denoted by (a) and posterior intercalary plates by (p). If a dinoflagellate has a tabulation that does not quite fit into the Koifoid tabulation system an asterisk is used and the plate is called a homologue.

Cyst type	Koifoid tabulation
P-cysts, or Peridinium cysts (Figure 1.8)	4′, 3a, 7″, 4c, 5‴, 0p, 2⁗
G-cysts, or Gonyaulax cysts (Figure 1.9)	4′, 0a, 6″, 6c, 6‴, 1p, 1⁗

Table 1-1: The Koifoid tabulation system for the two main dinoflagellate cyst types used in this study

There are three main cyst types (Fensome et al., 1996b). These are: temporary, vegetative and resting cysts. Temporary cysts form when conditions turn unfavourable and motile cells with a well-developed pellicle (an additional wall layer) shed their flagella and outer wall. These cysts are short lived and are not preserved in the fossil record. Vegetative cysts are also not usually fossilised and form as part of the life cycle of some parasitic and symbiotic dinoflagellates. It is resting cysts that are thought to comprise the vast majority of the fossil record; they are dormant and virtually exclusively result from sexual fusion. The taxa that form resting cysts are commonly the orders peridiniales and gonyaulacales (Figure 1.8 and 1.9).

The dinoflagellate cyst fossil record appears to be highly selective, and it is not known what proportion of species were cyst-producers in the geological past (Evitt, 1981; 1985). Today only 15–20% of the extant dinoflagellate species form cysts, and it is assumed that the ratio of pre-Quaternary cyst-producers to non-cyst-producers was approximately similar (Fensome et al., 1996b). However, not all of the cysts that do form can be preserved. It is those cysts that are formed from dinosporin that are preserved best in the fossil record and are used in this project. Since cysts form in the theca, their morphology often reflects that of its motile counterpart. However, there are cases in the modern (e.g. *Gonyaulax spinifera*) where a single motile form can produce more than one type of cyst (Wall, 1971; Head et al., 1996).

Cysts have six main features which are mostly also represented in the motile stage (Figure 1.5). The main feature are: the dorsal and ventral sides, the apex (anterior) and antapex (posterior), the sulcus and the cingulum. If the motile form has excysted, then an archeopyle is also present. The sulcus is where the two flagellae emerge and is situated on the ventral side running roughly from the apex end to the antapex end.

1.3.4.2 Archeopyle/Operculum

If an archeopyle is present, it is often one of the best ways to distinguish a cyst from its motile form. It also is often used as a key feature in differentiating one species from another. The archeopyle is present in dinoflagellate cysts when excystment has taken place. The archeopyle is the hole left behind and the operculum is the ‘door’ though which the dinoflagellate cytoplasm hatches. The operculum may be either left attached to the cyst (adnate operculum or a theropylic archeopyle), or completely lost (a saphopylic archeopyle). The operculum nearly always results from the loss/opening of one or more plates, and is often found in the apical half of the dinoflagellate on the dorsal side (Figures 1.5). However, archeopyles do not always form as the result of a loss of plates. If they are theropylic then the motile form escaped through a split that follows the plates, whereas a chasmic archeopyle means the split was random. Sometimes the archeopyle is reduced or enlarged, meaning that the hole is either slightly smaller or larger than the plate(s) in which it formed (Evitt, 1967; 1985).

1.3.4.3 Wall layers, structures and textures

The walls of dinoflagellate cysts are generally multi-layered (Figure 1.10), although the majority are formed from one or two layers, and can consist of: an autophragm (single wall), endophragm (inner wall), mesophragm (middle wall), periphragm (outer wall), ectophragm (extreme outer wall) and/or exophragm (when the wall formed externally to the theca). Other features of cysts are the sutures, crests and ridges that run along the plate boundaries or at least suggest where the plate boundaries of the theca were.

If a cyst has two or more wall layers, it is known as cavate, whereas if it has a single layer, it is termed acavate. Other examples of cavation are circumcavate, where cysts have a continuous cavity surrounding them, and bicavate, where cavities are only around the apex and antapex, and not around the equatorial region (the cingulum; Evitt, 1985).

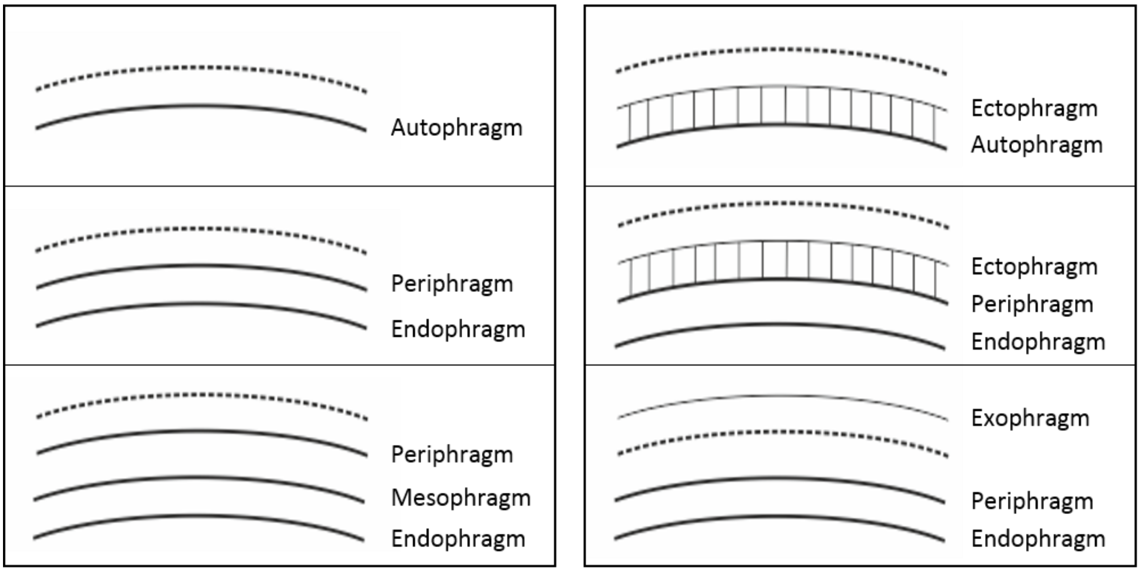


Figure 1-10: The basic terminology of wall layers of dinoflagellate cysts. The dotted line represents the position of where the theca would have been. Redrawn from Fensome et al. (1996b).

1.3.4.4 Processes (cyst protrusions)

As previously stated, dinoflagellate cysts can have a very similar morphology to that of their motile counterparts. Cysts can either be proximate (no long protrusions, also known as processes), chorate (close to round in shape with processes or crests) or somewhere in between (proximochorate).

Processes can occur anywhere on the cysts surface although certain genera (e.g. *Spiniferites*) only have processes on the gonal points and in some species on their intergonal points (gonal points refer to triple junctions where three plates meet, while intergonal points are situated between junctions). In *Spiniferites,* gonal processes trifurcate and intergonal processes bifurcate at their distal ends. In genera such as *Lingulodinium* and *Operculodinium* processes are randomly distributed (nontabular). Processes or other ornaments can also be arranged within the margin of each plate (penitabular) and in some cases, such as with *Cannosphaeropsis*, processes are distally linked together by trabeculate. There are several theories as to why dinoflagellates might form processes, including: to increase buoyancy, to avoid sinking too deep into the water column, and to deter predators (Sarjeant et al., 1987).

1.3.5 Evolution

Dinoflagellates are known to have existed from the Middle Triassic (247.1–237.0 Ma; Helby et al., 1987) although cytological and geochemical evidence strongly indicates a Late Precambrian origin for the group (Moldowan et al., 1996; Medlin and Fensome, 2013). There is evidence from Late Silurian Africa of a species showing dinoflagellate tabulation (*Arpylorus antiques).* This is, however, a controversial issue, was not widely accepted, and has recently been discredited as untrue (Le Hérissé et al., 2012). If it is the case that dinoflagellates were present during the Paleozoic, it is likely that they did not then have the capability to produce cysts, and thus are not found in the geological record from this time (Sarjeant and Downie, 1974).

However, acritarchs, which means "of uncertain origin", a name coined by Evitt (1963), were very abundant in the Paleozoic. They are an artificial group and include any organic-walled microfossil that cannot be assigned to a natural group. They are thought to have algal affinities and are valuable biostratigraphical markers. While they have high diversities in the Paleozoic, their diversity declined and the dinoflagellates 'took over' in the Late Triassic (~235 Ma; Riegel, 2008). The Triassic was an important time period for dinoflagellates. The first modern corals, scleractinians, appeared, and for them, the radiation of dinoflagellates was important, as some species of dinoflagellate and scleractinians are symbiotic with each other (Fensome et al., 1996b). Also during the Triassic, the Pangaean supercontinent was breaking up, which lead to new niches being exploited by the dinoflagellates due to an increasing number of shallow seas (Stover et al., 1996).

The Permian-Triassic mass extinction (~252 Ma), which left many empty niches, is thought to have been the reason for the radiation of dinoflagellate cysts in the Triassic (Fensome et al., 1996b). However, at the end of the Triassic a further mass extinction resulted in the loss of close to 60% of dinoflagellate cyst (Figure 1.11) species. The diversity radiated once more after this event, and continued to diversify into the Jurassic, as is recorded by many fossil groups at this time (Fensome et al., 1996a; MacRae et al., 1996).

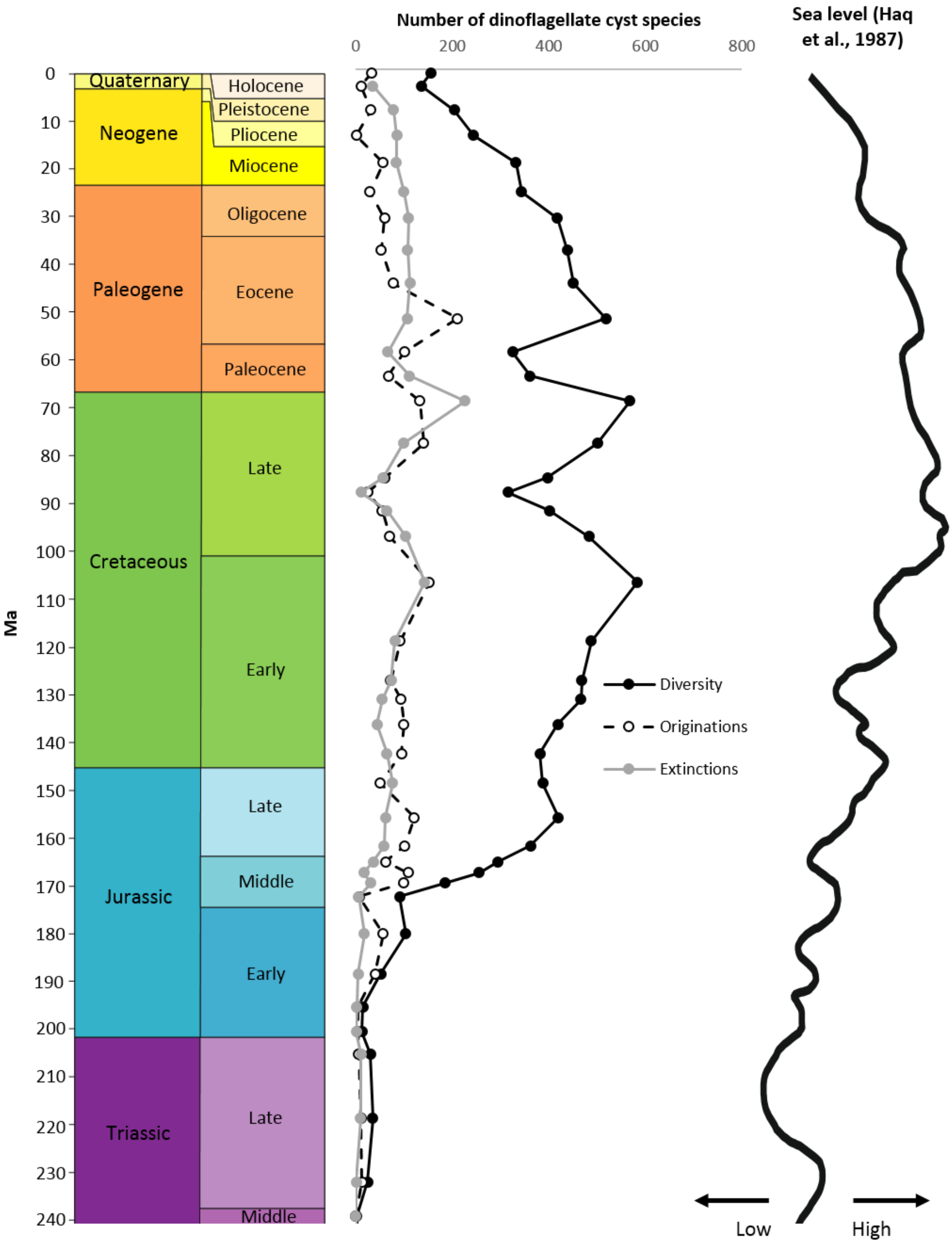


Figure 1-11: The number of dinoflagellate cyst species present and the number of extinctions/originations. Adapted from MacRae et al. (1996). The sea level curve is plotted after Haq et al. (1987) and Sluijs et al. (2005).

The early Jurassic (~201 Ma) was a time of slow recovery for dinoflagellate cysts with very low diversities (Figure 1.11; MacRae et al., 1996). Speciation suffered again during the early Toarcian Oceanic Anoxic Event (~183 Ma; Jenkyns, 1988). Open-ocean dwelling dinoflagellates (oceanic species) were forced to move into tidal areas due to the vertical stratification of the oceans. However, diversity quickly recovered afterwards, and by the end of the Jurassic nearly all families were present (Fensome et al., 1996a). The Middle Jurassic (174.1–163.5 Ma) was an important interval for dinoflagellates, with the gonyaulacacean lineage rapidly radiating (Fensome et al., 1996a). One of the key evolutionary events for dinoflagellate cysts took place during the Middle Jurassic, which was when major dinoflagellate genera experimented with different archeopyle styles (Stover et al., 1996). By the Late Jurassic (163.5–145.0 Ma), diversification was still taking place, but not as rapidly, and archeopyle experimentation resulted in most gonyaulacacean having precingular or apical archeopyles (Stover et al., 1996).

The Lower Cretaceous (145.0–100.5 Ma) was characterised by high sea levels due to there being little terrestrial ice, and there was widespread continental flooding as the Gondwanan supercontinent started to break up. The dinoflagellate cyst floras were of high diversity with chorate forms becoming more prominent (Stover et al., 1996). The maximum number of species occurred in the Albian (113–100.5 Ma; Figure 1.11); a time of particularly high sea levels, providing more space in which the dinoflagellates could live (MacRae et al., 1996).

By the late Cretaceous (~100 Ma), South America and Africa had separated, and the Atlantic was steadily increasing in size. Sea levels were still high, and temperatures were warm enough to have allowed crocodiles to reach the polar regions (Tarduno et al., 1998). Dinoflagellates had to survive another mass extinction at the end of the Cretaceous-Paleogene boundary (66.1 Ma) as a combination the Deccan Traps (a large igneous province in Indian) and a giant meteorite struck the Earth, wiping out 34–37% of marine genera (Sepkoski Jr, 1996; Bambach et al., 2004). Although, dinoflagellates did not undergo the rapid extinction rates that other microfossil groups, such as planktonic foraminifera, and nannofossils did (Brinkhuis and Zachariasse, 1988). After the Cretaceous-Paleogene boundary, dinoflagellate cyst evolution was fairly stable, although diversity decreased from the Eocene onwards possibly as a result of the decreasing sea levels and cooling climate, especially during the Neogene (Stover et al., 1996).

1.3.6 Ecology

Dinoflagellates are found globally and can be very abundant. Consequently they are one of the most important primary producers of the world's oceans (Taylor et al., 2008), and today there are 2,377 dinoflagellate species within 259 genera (Gómez, 2012). They are a widespread group found in a range of environments including: freshwater, sand, snow and ice (Marret and Zonneveld, 2003; Taylor et al., 2008). They also have diverse life strategies, for example their feeding habits can be autotrophic (self-feeding), heterotrophic (feed on other organisms/nutrients), phagotrophic (intracellular digestion), mixotrophic (mix of food sources), symbiotic (mutual advantage of living together), parasitic (benefitting at the expense of the host) or a combination of these (Marret and Zonneveld, 2003; Taylor et al., 2008).

The vast majority of dinoflagellates are marine, living in both fully oceanic and neritic waters (shelf), with only ~270 fresh water species (Taylor et al., 2008). Species preferring neritic environments are most common and can also live at the bottom of the euphotic zone (water depths that can receive enough light that photosynthesis can occur). They have particularly high diversities (and abundances) near the shelf edge where both shelf and oceanic species can coexist (de Vernal and Marret, 2007). High diversities are also found in intertropical areas and diversity generally decreases into the higher latitudes. However, the polar regions have a relatively high diversity compared to other microfossils because some taxa can tolerate extensive sea-ice cover (Matthiessen et al., 2005). This global abundance makes dinoflagellate cysts a particularly powerful proxy archive and allows them to record temperature/environmental changes at all latitudes, and in a range of water depths from coastal to fully marine.

1.3.7 Utility of Dinoflagellate cysts

1.3.7.1 Modern

Dinoflagellates are not only important in today's oceans because they are primary producers, but 75 to 85% of all toxic phytoplankton species are dinoflagellates (Cembella, 2003). When conditions such as nutrient availability and temperature are optimal, the species bloom during their asexual reproduction phase and, if the species composing the blooms are toxic, the sheer quantity harm the organisms feeding on them (Fensome et al., 1996b; de Vernal and Marret, 2007). These toxins ascend the food chain to fish populations and can thus have severe consequences on human health, including food poisoning and paralysis (Van Dolah, 2000). The blooms also impact fisheries and tourism as vast numbers of fish are killed by consuming the toxins and wash ashore, ruining the beaches. Blooms also result in the dinoflagellates using up the available oxygen, and therefore blooming of non toxic species can also harm the ecosystem. Dinoflagellates are not only known for the devastation they can cause; they also have a certain appeal in the form of bioluminescence; that is, they produce light. It is unknown why some species of dinoflagellates bioluminesce, but it may be part of their reproduction, it may serve to attract larger predators to deter smaller predators that are a direct threat to dinoflagellates, or it may have no function and could simply be a response to movement (Abrahams and Townsend, 1993).

Another important factor is the symbiosis with certain species of scleractinian corals, allowing the corals to thrive in nutrient-poor waters, e.g. the dinoflagellate genus *Symbiodinium* (Pochon et al., 2004). It is the dinoflagellates that give the corals their colour, and their bleaching, if conditions turn unfavourable, is a result of the zooxanthellae dying or moving away.

1.3.7.2 The fossil record

The benefits of dinoflagellates in the fossil record comes from the preservable cysts that some of the species form during reproduction. The cysts are used for biostratigraphical purposes and increasingly by the oil industry to help date the cores they drill, for inter- and intra-basin correlation, to test sequence stratigraphic concepts and to assess the maturity of the hydrocarbon field. They are increasingly used in palaeoecological reconstructions (Powell, 1992; Head, 1994; 1997; Versteegh and Zonneveld, 1994; De Schepper et al., 2009; 2011; 2015; Warny et al., 2009; Schreck and Matthiessen, 2013; Verhoeven and Louwye, 2013; Hennissen et al., 2014). The cysts have specific features that can be related to its motile form and if the ecological preferences of the motile form in the modern are known, the law of uniformitarianism can be applied to hypothesise that it preferred similar conditions in the past. For extinct species, the relationship is more ambiguous as their motile forms are not preserved. The following sections discuss the different environmental parameters that dinoflagellate cyst can be used for and how the proxy can be applied.

The use of dinoflagellate cysts as palaeoecological indicators is recent (within the last three decades). It is know that their distributions and relative abundances are governed by temperature, seasonality, salinity, nutrient upwelling and/or sea ice cover (i.e. light availability), making them excellent proxies for these past ocean conditions (Harland, 1983; Zonneveld, 1995; 1997; Rochon et al., 1999; Marret and Zonneveld, 2003; Pospelova et al., 2008; Radi and de Vernal, 2008; de Vernal et al., 2013). The biogeographical distributions, which reflect the preferred environmental conditions of living dinoflagellate cyst species, have been well documented (Harland, 1983; Rochon et al., 1999; Marret and Zonneveld, 2003; Radi and de Vernal, 2008; Zonneveld et al., 2013a). Marret and Zonneveld (2003) was the first global compilation of modern dinoflagellate cyst data recording the distribution of 61 extant species, and reports their relationships to nitrate and phosphate concentrations, salinity, sea surface temperatures and sea ice. This dataset was recently updated by Zonneveld et al. (2013a). Radi and de Vernal (2008) documented the distributions of 76 living dinoflagellate cyst species in the Arctic, the northeastern Pacific and the North Atlantic Oceans.

With the combination of modern distribution maps (with abundance data) it is possible to compare known sea surface parameters with the relative abundance of individual species to obtain quantitative optimal sea surface parameters of individual dinoflagellate cyst taxa. Multivariate statistical techniques such as detrended correspondence analysis and canonical correspondence analysis enables investigation into which sea surface parameters influence the dinoflagellate cysts. These statistical techniques compare the variation in modern dinoflagellate cyst distributions and abundances with the variations in known sea surface parameters, such as temperature and salinity (Marret and Zonneveld, 2003; Zonneveld et al., 2013a). Multivariate statistics show that the most important environmental variable is temperature followed by nitrate concentrations, salinity, phosphate concentrations and bottom water oxygen (Zonneveld et al., 2013a). It is therefore possible to use the information obtained from the modern to quantitatively interpret changes in the fossil record, providing that the species are still extant today and abundance counts are provided (Mudie, 1992; Peyron and de Vernal, 2001; de Vernal et al., 2005; Mudie and McCarthy, 2006). Quantitative controls on extinct species are increasing as known surface parameters (from other sea surface parameters proxies such as foraminifera) are compared to dinoflagellate cyst assemblage data (De Schepper et al., 2011).

Another approach to developing the utility of modern dinoflagellate cysts as proxies is the detailed analysis of morphological parameters, including the use of process length in chorate (spine-bearing) taxa to model salinity levels (Mertens et al., 2009a; 2012). By collecting and comparing all these types of modern dinoflagellate cyst data with the fossil record, it is possible to reconstruct the palaeoenvironmental significance of pre-Quaternary dinoflagellate cyst assemblages, and hence interpret past oceanic conditions.

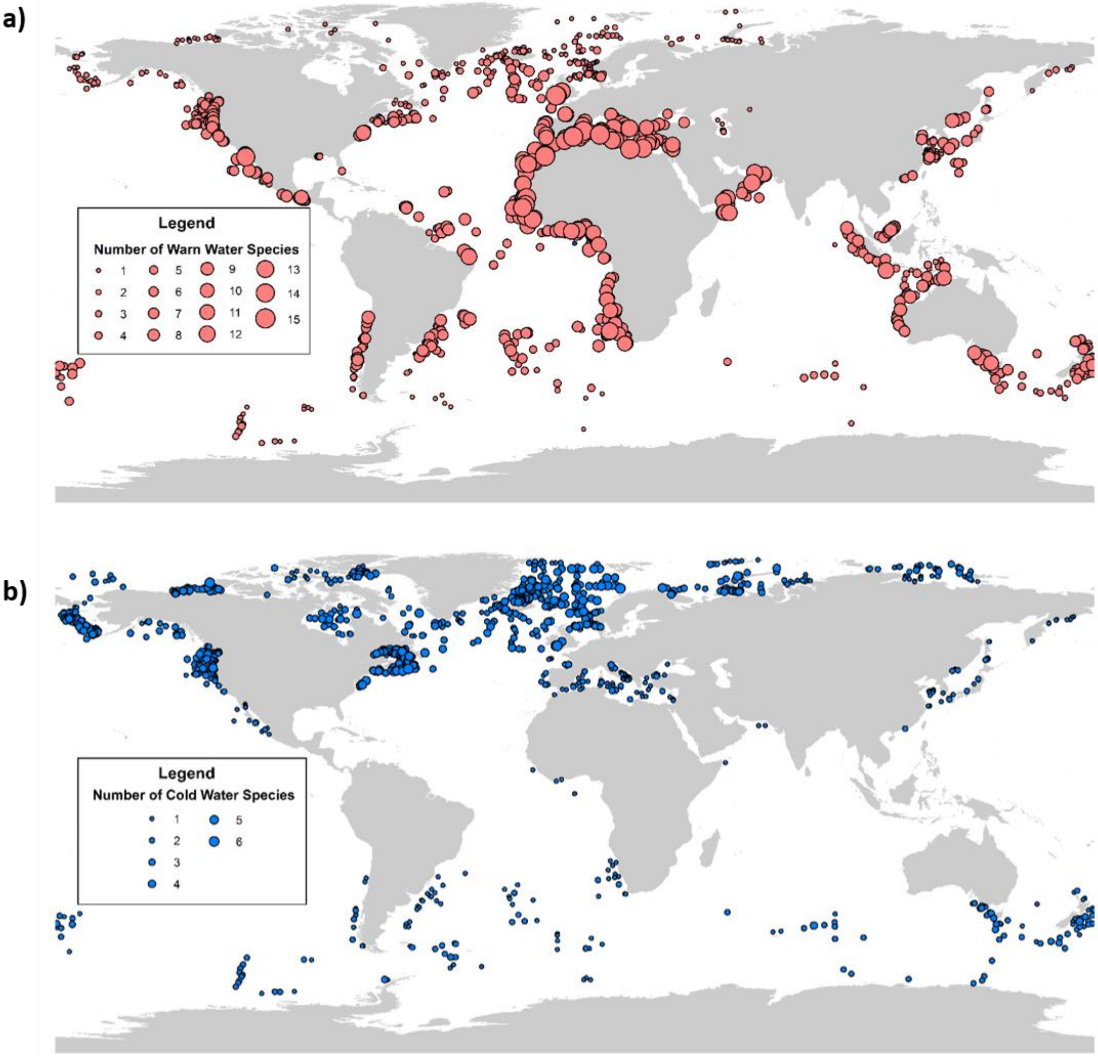


Figure 1-12: The modern distribution of (a) species with warm water preferences and (b) species with cold water preferences. Data is from Zonneveld et al., (2013b). Larger circles represent a higher diversity of dinoflagellate cysts.

1.3.7.2.1 Temperature

Sea Surface Temperature (SST) is one of the most important parameters in the Earth's climate system because it is a principal driver of atmospheric circulation, generating winds and weather as well as influencing evaporation rates and controlling the hydrological cycle (Henderson, 2002). It also helps govern seawater density, driving the deep ocean circulation (Covey and Barron, 1988). Globally, there is generally a clear distinction between polar species versus tropical dinoflagellate cyst species (Figure 1.12). The assemblages are mainly related to summer SST and whilst they can be found in a wide range of temperatures, they are often only really abundant within a much smaller range. Diversity is highest in tropical regions and generally decreases towards the poles (Figure 1.13). However, compared to many non-dinoflagellate marine groups, there is a relatively high diversity of dinoflagellate cysts found in polar regions (de Vernal et al., 2001).

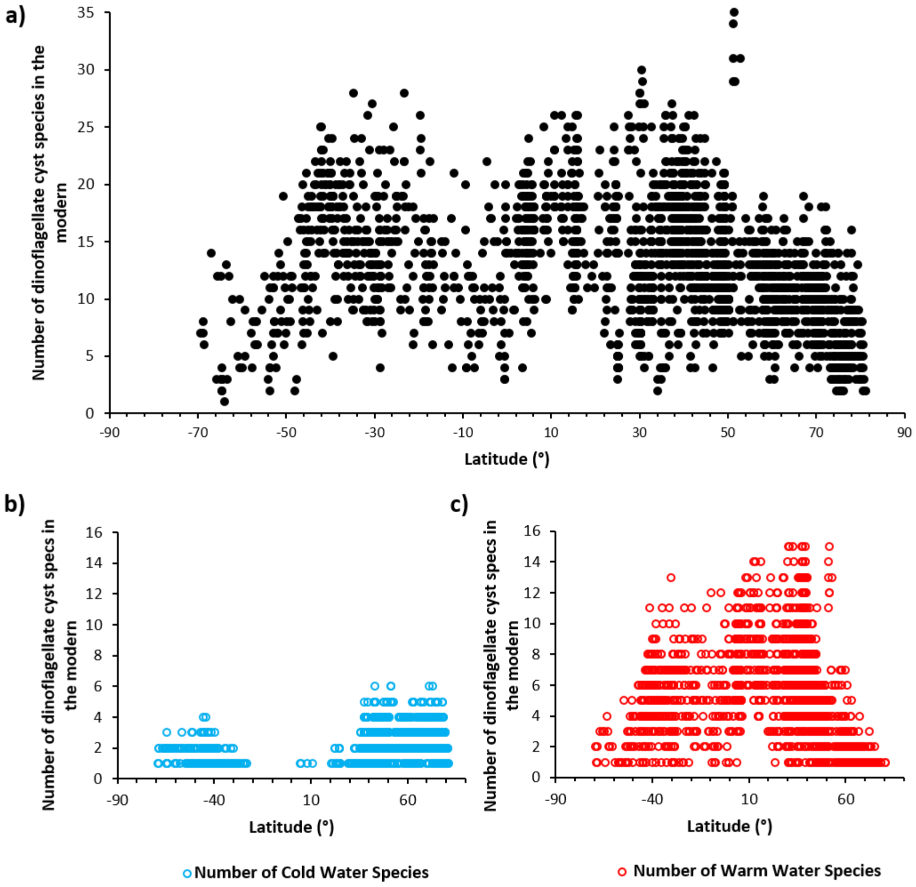


Figure 1-13: (a) The number of species found in the modern at each latitude. (b) The number of species with cold water preferences found at each latitude in the modern. (c) The number of species with warm water preferences found at each latitude in the modern. Data is replotted from Zonneveld et al., (2013b).

Similar patterns of diversity related to temperature are seen in both the Southern and Northern hemispheres (Figure 1.13). Over 60 cyst taxa are found in the Northern Hemisphere and only 10–12 of these are common in the Arctic (de Vernal and Marret, 2007). This 10–12 includes cosmopolitan species such as *Operculodinium centrocarpum* sensu Wall and Dale (1966). Examples of species that mainly thrive in cooler waters include *Islandinium minutum* and *Impagidinium pallidum.* Both are bipolar species (Figure 1.14a and d) and *Islandinium minutum* is a temperate to polar species while *Impagidinium pallidum* is a polar species (Zonneveld et al., 2013a). *Islandinium minutum* has relative abundances of over 10% when winter SST are less than 0 °C and summer SST are less than 5 °C (Figure 1.14 b; Zonneveld et al., 2013a) and *Impagidinium pallidum* has its highest relative abundances between -1.7 and

5.4 °C (Figure 1.14c; Zonneveld et al., 2013a). Examples of species that thrive in warm waters include *Polysphaeridium zoharyi* and *Operculodinium israelianum.* Both species are examples of subtropical to tropical species (Figures 1.15a and d). *Polysphaeridium zoharyi* can survive in regions with summer SST above 14 °C whereas *Operculodinium israelianum* can survive in summer SST above 10 °C, they are abundant in temperature in excess of 29.1 °C (Figure 1.15b) and 28.8 °C (Figure 1.15c) respectively (Zonneveld et al., 2013a).

1.3.7.2.2 Salinity

Salinity is an important environmental parameter as it is the other contributor to ocean density and hence a driver of large scale (deep) ocean currents. Unlike other microfossils used for reconstructing palaeoenvironmental parameters, such as foraminifera and calcareous nannoplankton, the majority of dinoflagellates are euryhaline (tolerant of widely fluctuating salinity), meaning that regions other than the oceanic realm, which has a relatively stable salinity, can be studied. In brackish environments (for example, the Baltic Sea), the species present often have a high morphological variability, but with low diversities (eight or less species; Dale, 1996; Mudie et al., 2001; Marret et al., 2004). Morphological differences can include the length of processes. For example, if *Lingulodinium machaerophorum* is found with short processes, the waters are likely to be low salinity, whereas larger/longer processes indicate a higher salinity (Mertens et al., 2009a; 2012).

Spiniferites cruciformis is an example of a species that is endemic to the Caspian, Aral, Black and Eastern Mediterranean seas. It is principally present in regions affected by river discharge with lower salinities (Figure 1.16a and b; Zonneveld et al., 2013a). An example of a species that has its highest relative abundances in higher salinities is *Impagidinium strialatum* which is a fully marine species thriving in sea surface salinities (spring-autumn) between 31.1 and 39.3 psu (Figure 1.16c and d; Zonneveld et al., 2013a).

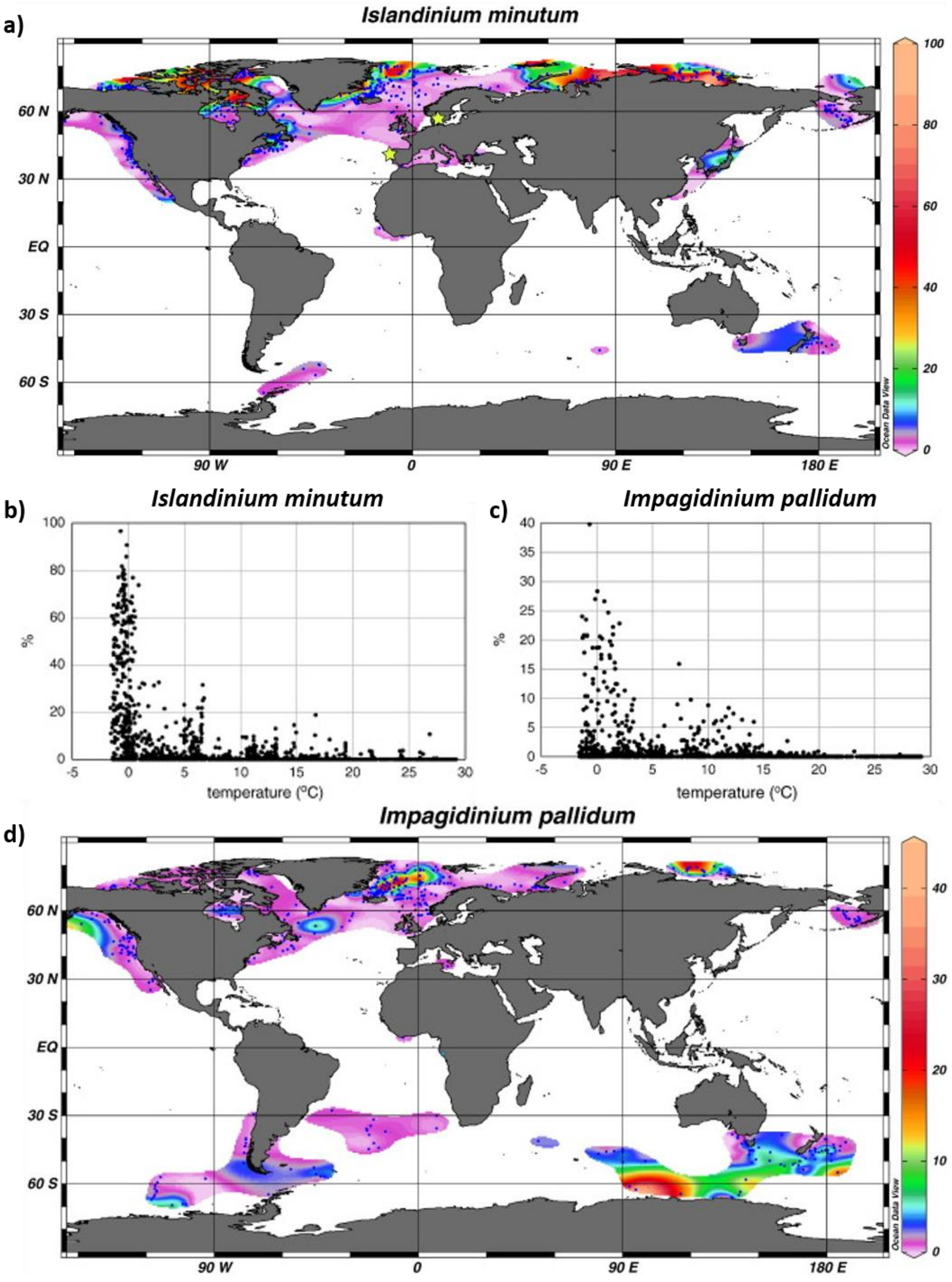


Figure 1-14: (a) The modern distribution of the temperate to polar species *Islandinium minutum.* (b) The relative abundance of *Islandinium minutum* in relationship to annual sea surface temperature. (c) The relative abundance of *Impagidinium pallidum* in relationship to annual sea surface temperature. (d) The modern distribution of the polar species *Impagidinium pallidum.* All Figures are from Zonneveld et al., (2013a). Colours represent the relative abundance.

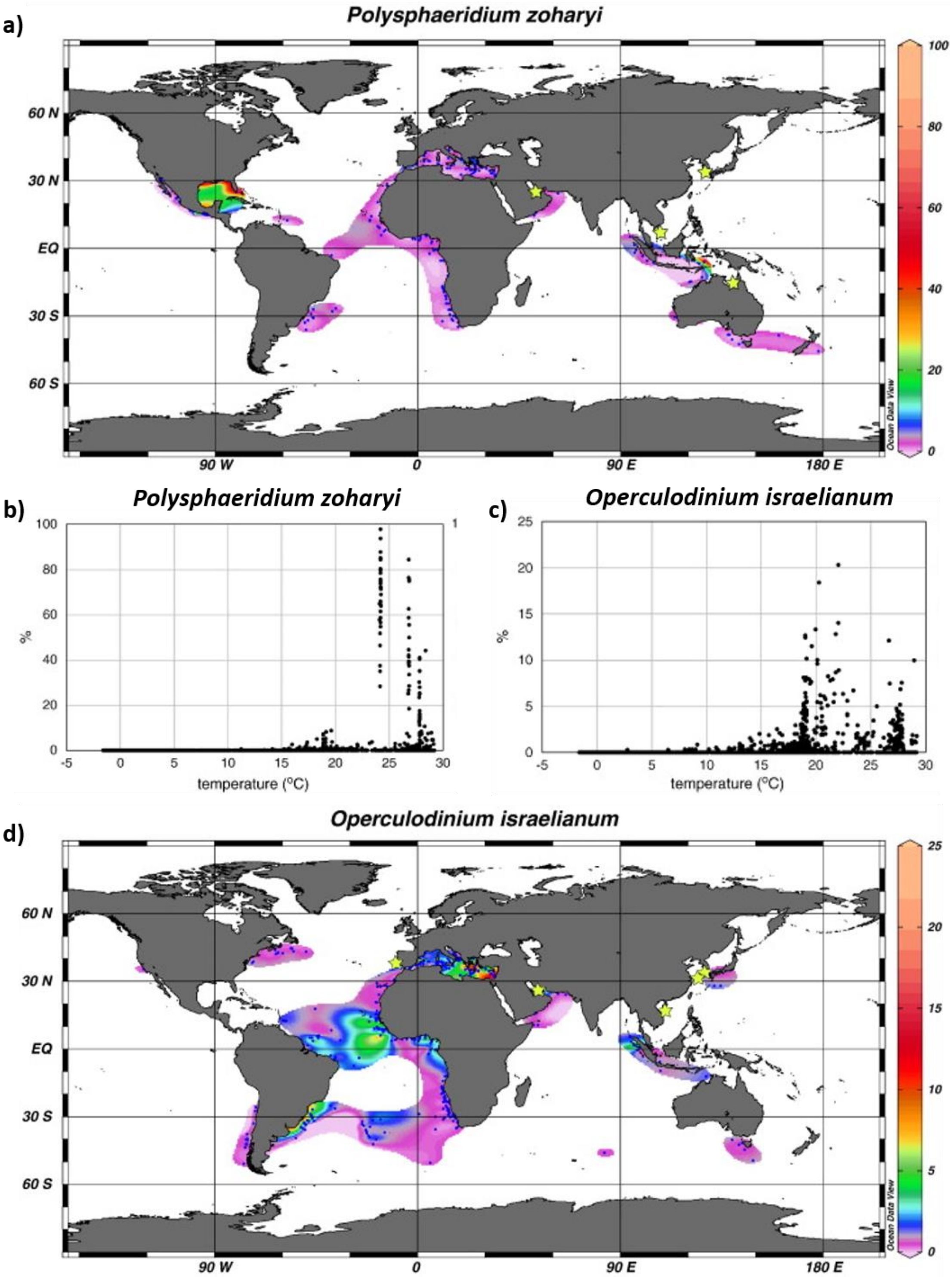


Figure 1-15: (a) The modern distribution of the subtropical to tropical species *Polyspaeridium zoharyi.* (b) The relative abundance of *Polyspaeridium zoharyi* in relationship to annual sea surface temperature. (c) The relative abundance of *Operculodinium israelianum* in relationship to annual sea surface temperature. (d) The modern distribution of the subtropical to tropical species *Operculodinium israelianum.* All Figures are from Zonneveld et al., (2013a). Colours represent the relative abundance.

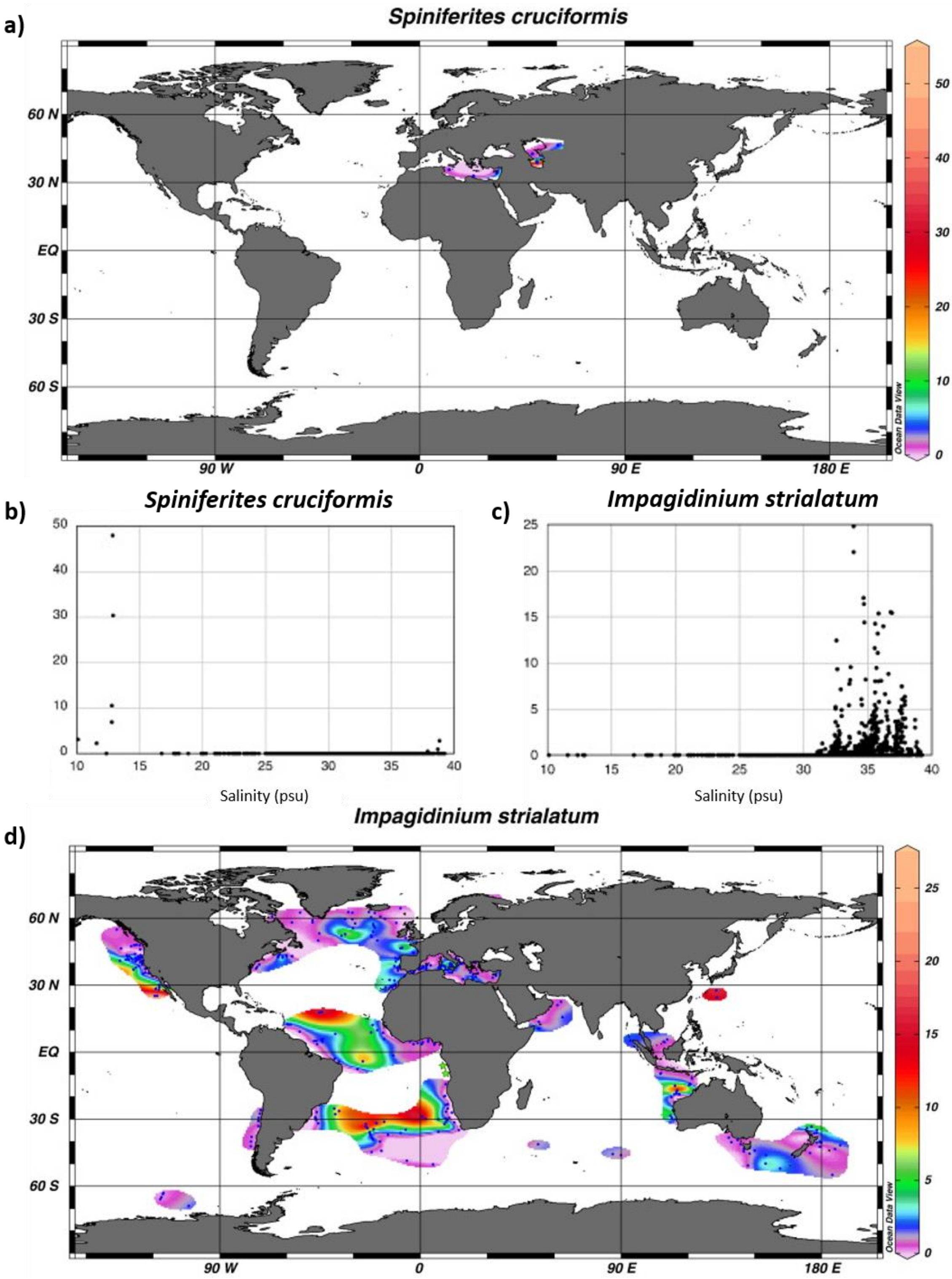


Figure 1-16: (a) The modern distribution of *Spiniferites cruciformis.* (b) The relative abundance of *Spiniferites cruciformis* in relationship to annual sea surface salinity. (c) The relative abundance of *Impagidinium strialatum* in relationship to annual sea surface salinity. (d) The modern distribution of *Impagidinium strialatum.* All Figures are from Zonneveld et al., (2013a). Colours represent the relative abundance.

1.3.7.2.3 Nutrients

As mentioned previously (Section 1.3.4) there are two main groups of dinoflagellate cysts, these are peridinioids (P-cysts) and gonyaulacoids (G-cysts). The majority of P-cysts are heterotrophic while G-cysts are autotrophic. This results in P-cysts thriving in regions with a high nutrient content, such as areas of upwelling, as the nutrients attract organisms such as diatoms that the heterotrophic taxa can feed on. Therefore the P-cyst to G-cyst ratio can be utilised to indicate a region of higher productivity (Harland et al., 1973) where high values indicate a predominance of P-cysts and therefore higher productivity. However, this method has been criticised because not all of the modern peridinioids are heterotrophic, because of this the ratio between heterotrophic and autotrophic species is often applied instead (Dale and Fjellså, 1994; Dale 1996).

An increase of nutrients, in modern settings, is often related to human activity and eutrophication. *Lingulodinium machaerophorum* is an example of a dinoflagellate cyst species that is used as an eutrophication indictor, particularly in European fjords and lochs (Dale and Fjellså, 1994; Thorsen and Dale, 1997). Nutrients that have been associated to dinoflagellates are nitrates and phosphates, but so far only regional patterns have been observed (de Vernal and Marret, 2007).

1.3.7.2.4 Sea ice Cover

Autotrophic species that rely on light to photosynthesise to produce food cannot survive both an extended period of sea ice cover occluding the sun and having to compete with other autotrophic plankton. Samples are generally barren if they come from an area with perennial pack-ice (Rochon et al., 1999; de Vernal et al., 2005). However, some taxa can thrive in polar environments with seasonal ice, e.g. *Islandinium* spp. (de Vernal et al., 2005). This is because species of the genera *Islandinium* are heterotrophs, meaning they prey on other organisms (often diatoms), and so can survive the cold temperatures and dark winters. This is also the explanation as to why the diversity of dinoflagellate cysts in the high latitudes is relatively high (Mudie and Rochon et al., 2001) compared to other microfossil groups (Figure 1.13).

Chapter 2: Construction of the TOPIS database

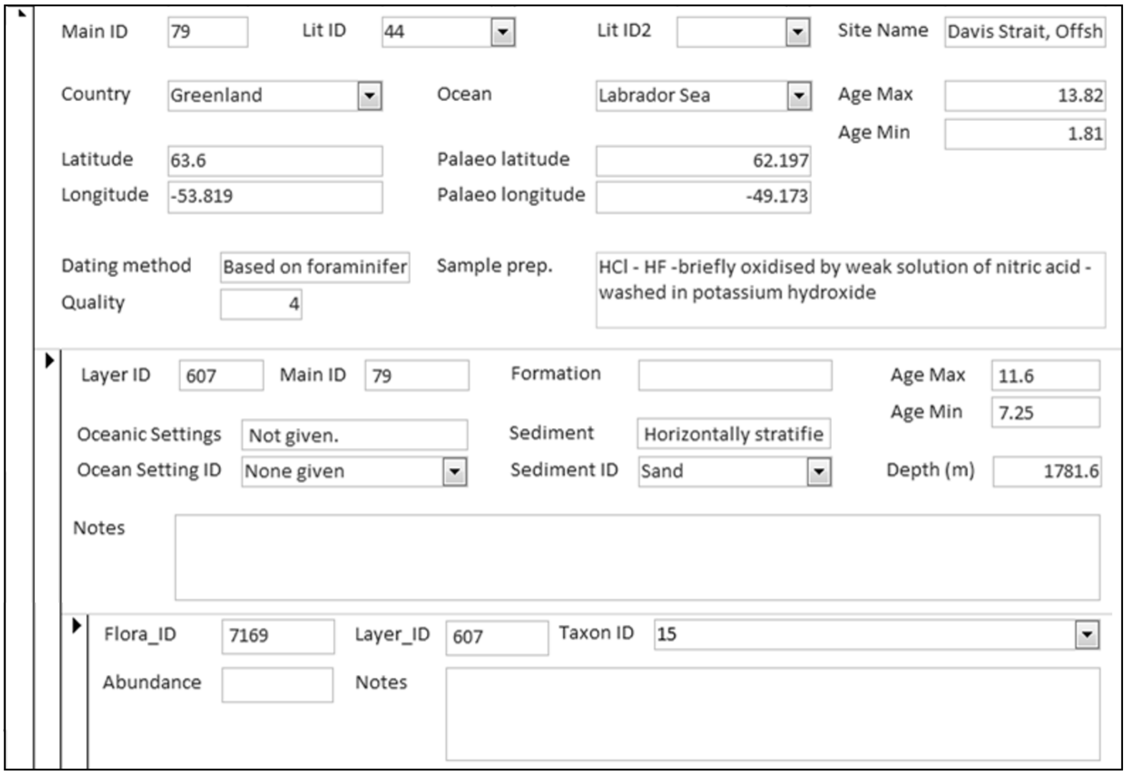
2.1 The TOPIS database

The Tertiary Oceanic Parameters Information System (TOPIS) is a Microsoft Access - ArcGIS database containing public domain literature on Neogene dinoflagellate cysts. A total of 275 items are included, totalling 500 globally distributed sites. The database was produced by compiling and entering data from published studies into three forms: ‘main’, ‘layer’ and ‘flora’ (Figure 2.1). In the ‘main’ form, key information (including the bibliographic references, location and approximate age of the samples, and dating methods) is entered with the option to include information on the nearest country and ocean basin to the sample site. The ‘main’ form also include an option to input the sample preparation technique utilised. The ‘layer’ form is where the lithotype, formation, depth and a more refined age model are entered. This format allows more accurate ages to be given by breaking down the overall cores/outcrop sections into smaller divisions. Therefore, once the third and final form (the ‘flora’ form) is completed, the dinoflagellate cysts can be shown as part of a smaller and more constrained age range, representing individual assemblages. The ‘flora’ form is the smallest, and it simply contains dinoflagellate cyst taxonomy and, if available, the relative abundance as a percentage of the total dinoflagellate cyst assemblage. In order to avoid duplication caused by typographical errors, each dinoflagellate cyst species is given its own unique number. The numbering system is recorded in a separate form where additional information, such as the climate or the habitat that the species preferred and if the species is extinct or extant, can be added. The database therefore collates all the published data in an internally consistent framework.

There is some spatial bias in TOPIS as a large proportion of the sites are situated in coastal areas in the Northern Hemisphere, particularly in the North Atlantic and Mediterranean regions. The Southern and Indian oceans have poorer sampling coverage due to fewer drilling sites and studies having been undertaken.

2.1.1 Literature sources

The literature entered into the TOPIS database are from a broad range of authors, journals and countries. The John Williams Index of Palaeopalynology (JWIP; Riding et al., 2012) was interrogated in order to ensure that the coverage is as comprehensive as possible. The JWIP is the most comprehensive reference catalogue on palaeopalynology in the world, and contains 23,350 references as of February 2012 (Riding et al., 2012). Therefore, confidence can be placed on TOPIS including the vast majority of the available published literature on Neogene dinoflagellate cysts.



Main ID	79	Lit ID	44	Lit ID2		Site Name	Davis Strait, Offsh
Country	Greenland	Ocean	Labrador Sea			Age Max	13.82
						Age Min	1.81
Latitude	63.6	Palaeo latitude	62.197				
Longitude	-53.819	Palaeo longitude	-49.173				
Dating method	Based on foraminifer	Sample prep.	HCl - HF -briefly oxidised by weak solution of nitric acid - washed in potassium hydroxide				
Quality	4						

Layer ID	607	Main ID	79	Formation		Age Max	11.6
						Age Min	7.25
Oceanic Settings	Not given.			Sediment	Horizontally stratifie		
Ocean Setting ID	None given			Sediment ID	Sand	Depth (m)	1781.6
Notes							

Flora_ID	7169	Layer_ID	607	Taxon ID	15
Abundance		Notes			

Figure 2-1: Screen shot of the Microsoft Access database; Tertiary Oceanic Parameters Information System (TOPIS).

2.1.2 Dating

The diverse nature of the literature used in the TOPIS database means that several different dating methods were employed. Not all of the papers state the method of dating used, adding some uncertainty to any interpretation. The majority of age assessments were derived biostratigraphically, typically using calcareous nannofossils, foraminifera and palynomorphs, with fewer based on diatoms, mammals and molluscs (see references in Appendix A). Some publications have used magnetostratigraphy and radiometric methods. The dating method in each paper is given a numbered confidence coefficient between zero (low) and five (high) in order to document the reliability of the dating in a semi quantitative fashion. The number is based on assessment of the published stratigraphical data. If no dating method was provided then a value of zero was assigned. Papers that use dinoflagellate cysts as their dating method are deliberately given a low confidence to avoid circular reasoning.

As TOPIS contains such a large number of publications, all of which had different aims and objectives, the resolution of the assemblage is very varied, ranging from ages estimates less than 0.001 Myr to over 25 Myr (Figure 2.2 and 4.1). Consequently the assemblages with a very low resolution are not useful to include in any analysis. The majority of the assemblages are dated to within one or two stages and assemblages with a maximum and minimum age range spanning longer than two stages are excluded from the analysis (Chapter 3) to avoid using poorly constrained data that may influence the results. A maximum of two stage was chosen as TOPIS does contain assemblages that have a relatively high dating resolution, but happen to span two stage boundaries.

While making this compilation, it has been important to take note of the date of publication and the specific geological time scale referenced, due to its evolving nature (Gradstein et al., 2012). If the geological time scale employed was not stated in a publication it was assumed that the most up to date time scale of the time was utilised. Any changes between previous versions and the 2012 version were noted and if necessary the estimated age range of the assemblages were altered to represent the 2012 geological time scale (Gradstein et al., 2012). The majority of the publications affected were those that did not give quantitative age controls and only provided the stage(s) as the estimate age range of the assemblages. The most major change to the calibration of the Neogene in the last few decades was the transition of the Gelasian from the Pliocene into the Pleistocene, effectively shortening the Pliocene to 2.58 Ma (Gradstein et al., 2010). This meant that the age estimates of any publications published prior to 2010, which dated assemblages to the Pliocene, were altered to 5.333–1.806 Ma rather than the shorter 5.333-2.59 Ma range of the Pliocene of the more modern geological time scale. Incidentally the only difference, for the Neogene, between the 2012 version and the most recent 2016 version is the Serravallian-Tortonian boundary changing from 11.62 Ma to 11.63 Ma.

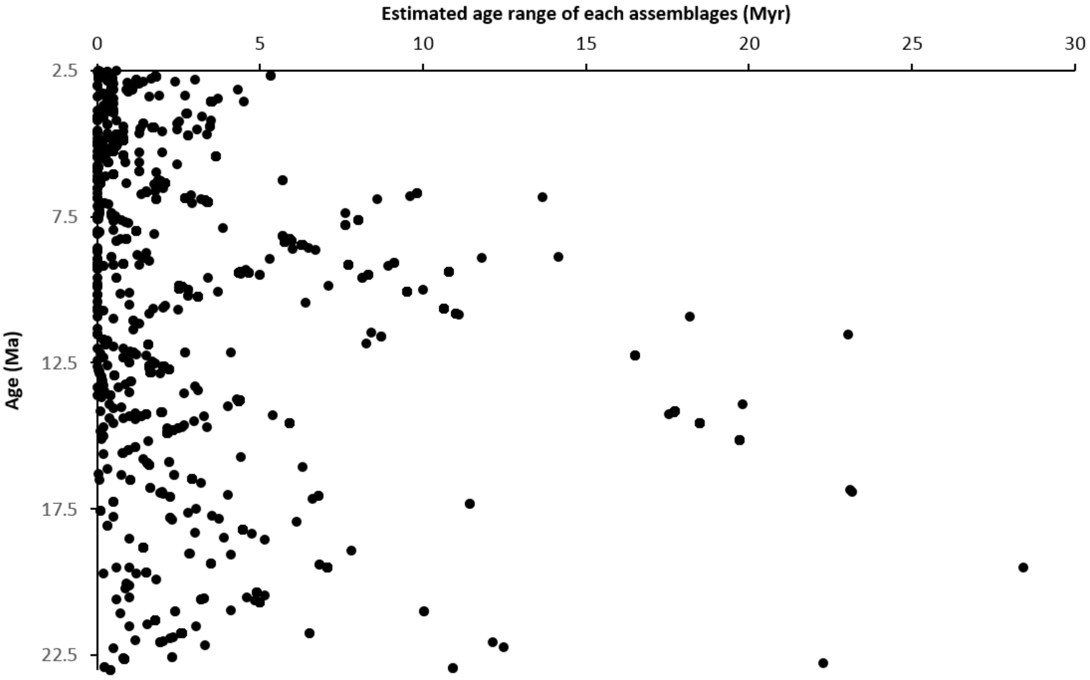


Figure 2-2: Example of the varied resolution of the dating, where each point represents an assemblage (layer) in TOPIS. The position on the x-axis represents the estimated ages range for each assemblage (the larger the number the poorer/lower the resolution of the dating). The position on the y-axis is the mean of the maximum and minimum ages range.

2.1.3 Location

Site locations are given as latitude and longitude coordinates, either taken directly from the published literature (when provided), or projected onto a map using online cartographic resources (such as Google Earth). If the location was not provided with sufficient resolution, the notes section of the database states that it is approximate. Sites are rotated to their palaeoposition using a plate rotation model that is compatible with the underlying palaeogeography of Markwick et al., (2000).

2.1.4 Taxonomy and reworking

The rationale of the TOPIS database follows that of the Cenozoic vegetation Tertiary Environmental Vegetation Information System (TEVIS database; Salzmann et al., 2008; Pound et al., 2012a) and the Bartonian/Rupelian dinoflagellate cyst database of Woods et al. (2014). As in these previously published databases, TOPIS undertakes little reinterpretation of the primary data in order to allow rapid construction and interpretation of large scale trends. However, in order for the TOPIS database to be effective at detecting real phenomena and trends, it is essential that the taxonomy is robust. To maintain a consistent dinoflagellate cyst taxonomy and to disregard synonyms, the taxonomy from Fensome et al. (2008) was used throughout, resulting in the species used having their most recently assigned genus. Obvious synonyms were combined/disregarded and where doubt existed, species were checked against published plates or were not included in any further analysis. Taxa not defined to species level were also not included in any analysis, and neither were questionably assigned species (i.e. species that are not confirmed with complete confidence – usually indicated with a question mark). However, the large amount of data collated, and the broad scale of the analysis, helps militate against any problematic taxonomy (Woods et al., 2014).

2.1.5 Stratigraphy

Any species thought to have been reworked were removed. Reworked species were established by the authors indicating a reworked species and/or by checking with previously published range charts produced for the Neogene (e.g. de Verteuil and Norris, 1996; Munsterman and Brinkhuis, 2004; De Schepper and Head, 2008). There is a possibility that some reworked species were still included. However, as for taxonomic problems, the large quantity of data analysed suggests that it this unlikely to bias any results. In the modern only 7% of cysts recorded in the Quaternary are affected by reworking. This substantiates the claim that the few reworked species, which may or may not be included in the analysis, will not affect the results (Mertens et al., 2009b; Verleye and Louwye, 2010).

2.1.6 Abundance data

The papers used in the TOPIS database are from a variety of sources, and have focused on different aspects of research including hydrocarbon exploration, palynology, palaeoecology, sedimentology and taxonomy. This diversity has resulted in uncertainties in the dataset, such as the dating (as several different methods were applied with different precision) and consistency of identification (since it was carried out by so many different authors). It also results in the absence of data with abundance counts in many of the publications. Therefore, for consistency, only presence and absence data is analysed in the following chapters. Where abundance counts have been calculated and included in the literature, many different methods have been used and may not give comparable results.

Chapter 3: The response of Neogene dinoflagellate cysts to global and regional climate dynamics

3.1 Introduction

The Neogene Period (23.03–2.59 Ma) has been referred to as ‘the making of the modern world’ (Potter and Szatmari, 2009), which eventually, via a relatively consistent cooling trend and changes to the Earth’s palaeogeography and atmospheric CO_2 concentration, culminated in the present day climate conditions on Earth (Raymo and Ruddiman, 1992; Zachos et al., 2001; Ruddiman, 2013; Sijp et al., 2014; De Schepper et al., 2015). It has provided important information for understanding how modern patterns of atmospheric and oceanic circulation developed, and how sensitive they are to environmental change (Potter and Szatmari, 2009).

To further research past climate changes, temperature proxies are used. The development and discovery of new proxies for climate variables is essential because the utility of both geochemical and non-geochemical proxy techniques can be limited by: post-depositional alteration; overprinting of the original signal through diagenesis and the absence or rarity of key fossils in open and deep ocean settings (de Vernal and Marret, 2007). This means that it is valuable to continually develop established temperature proxies and to find new proxies, methodologies and applications. Furthermore, the application and development of climate proxies and our understanding of palaeo sea surface parameters improves our ability to evaluate the performance of coupled ocean-atmosphere climate model simulations, especially when considering ocean circulation. One such climate and oceanic parameter proxy that is used increasingly for palaeoclimate studies is dinoflagellate cysts (Section 1.3; Head, 1994; 1997; Versteegh and Zonneveld, 1994; De Schepper et al., 2009; 2011; 2015;

Warny et al., 2009; Schreck and Matthiessen, 2013; Verhoeven and Louwye, 2013; Hennissen et al., 2014).

The distribution of dinoflagellate cysts is affected by a wide array of factors, and understanding how they react to changing environmental parameters is complex. With a better understanding, it would be possible to expand their climate proxy potential. The aim of this study is to investigate the changes to the global distribution of Neogene dinoflagellate cysts, and to understand the role and influence of climate change. Specifically, can dinoflagellate cysts be used to determine global cooling in the Neogene, was the cooling uniform at all latitudes and can anything be said regarding the rate of cooling? The investigation is then taken further to compare the differences between global and regional scale datasets as well as additional factors that control the distribution and composition of dinoflagellate cyst assemblages.

This study uses the synthesised previously published work on Neogene dinoflagellate cysts from the newly created database TOPIS (Tertiary Oceanic Parameters Information System; Chapter 2). The new database makes it possible to analyse and compare the results of published research on a global scale, and enables global analysis of the development of Neogene oceans over a long time scale.

3.2 Methods

Dinoflagellates and their cysts make excellent temperature proxies, and as such, numerous papers provide evidence of their temperature preferences (Head, 1997; Marret and Zonneveld, 2003; Wijnker et al., 2008; De Schepper et al., 2009; Schreck et al., 2013; Zonneveld et al., 2013a). Using TOPIS Appendix B was compiled and presents the complete list of literature from which the temperature preference for each dinoflagellate cyst was obtained. Both modern and palaeontological studies were used to ascertain dinoflagellate temperature preferences of the Neogene. Temperature categories used in the literature, to name a few, include: tropical, warm temperate to tropical, temperate, cool temperate and sub polar. However, to simplify, and to avoid unnatural category breaks, this study uses just two categories:

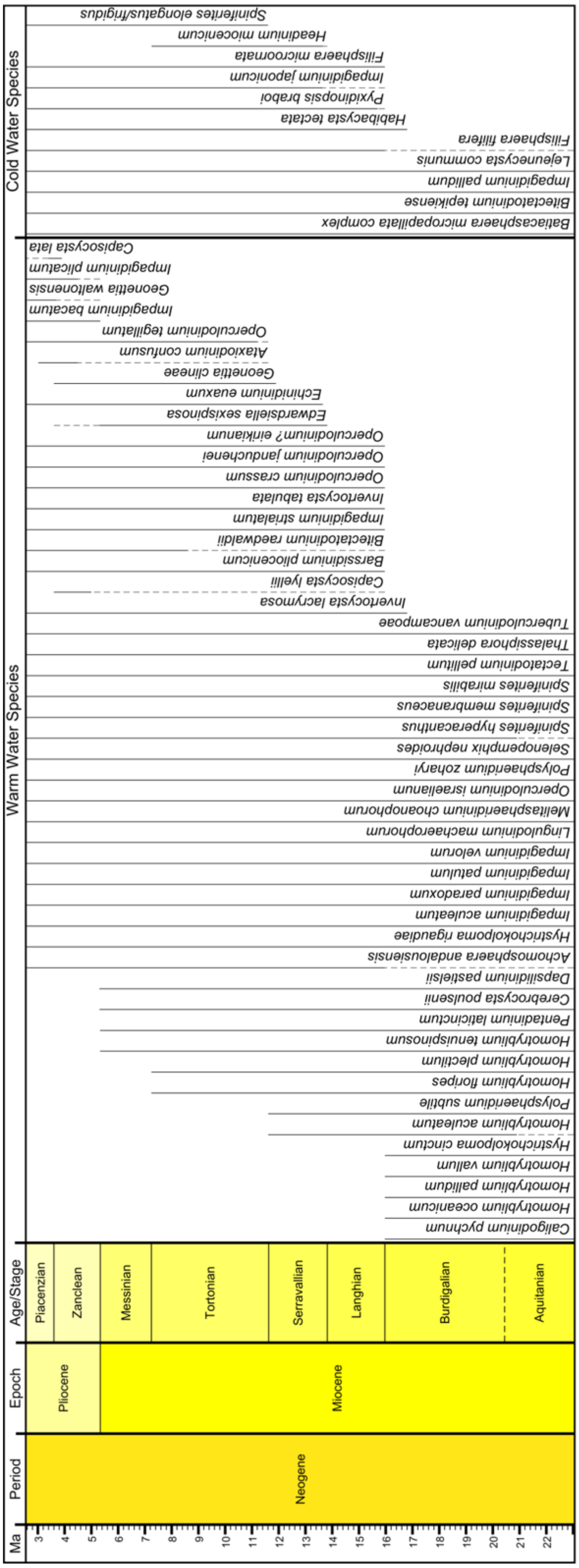


Figure 3-1: Age ranges of the species with known temperature preferences used in this study for the Neogene. Dashed lines represent ages where species are known to have lived, but are not represented in this study. References are provided for the temperature preference in Appendix B.

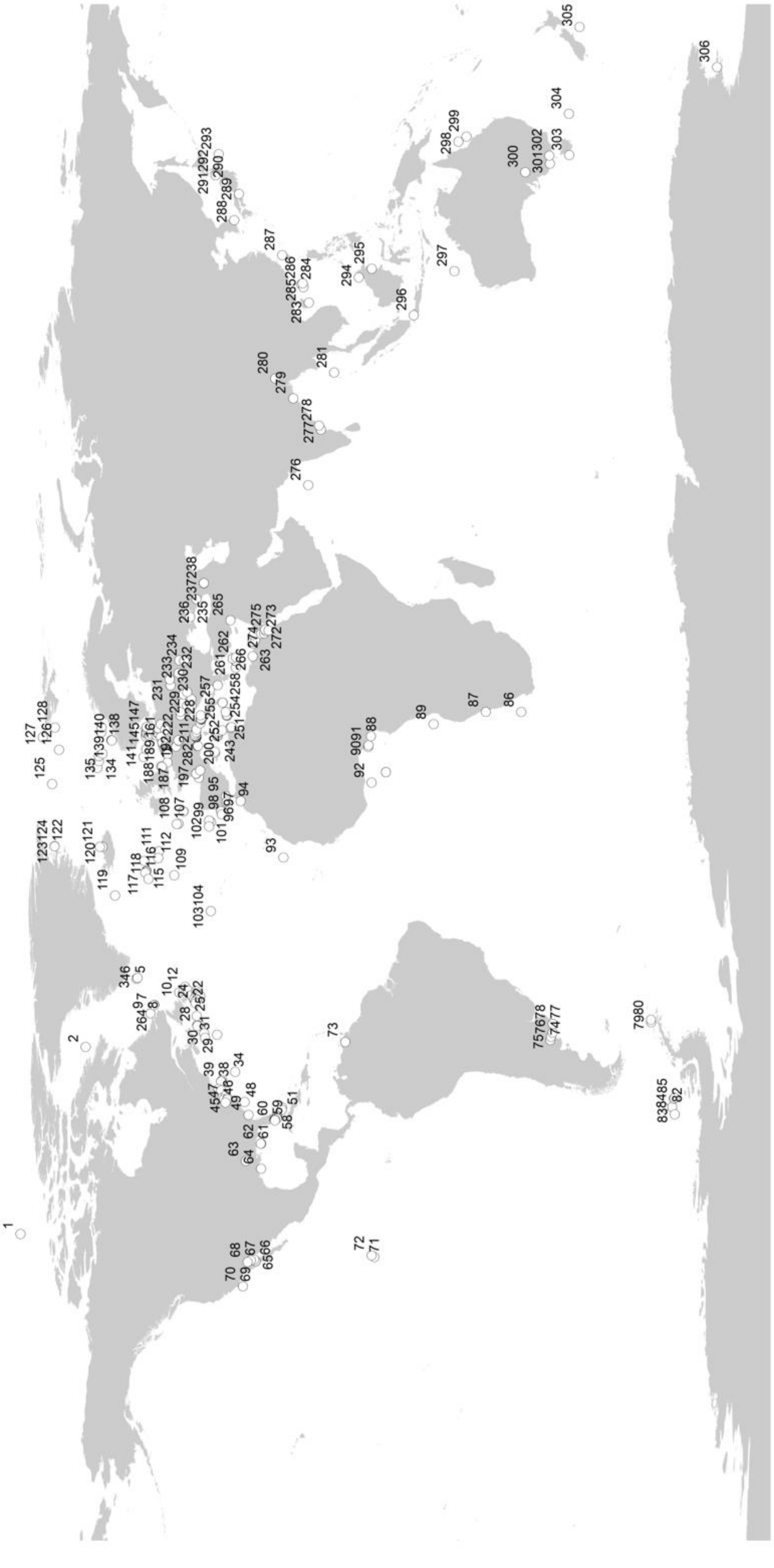


Figure 3-2: Distribution of all of the records used in this study for the Neogene. Sites are plotted at their modern latitude and longitude and references can be found in Appendix A.

Warm Water Species (WWS) and Cold Water Species (CWS). Warm Water Species include species within the warm temperate to tropical categories and CWS from within the cool temperate to polar categories.

Once a list was created of all the species found in the Neogene with known temperature preferences (Figure 3.1; Appendix B), sites with those species present were extracted from TOPIS (Figure 3.2; Appendix A). The list contains 11 CWS and 48 WWS in the Neogene. Any species that have been questionably assigned were ignored (as were cf. species, such as *Xandarodinium cf. xanthum*) for the purpose of having the most reliable and consistent taxonomy. Synonyms were combined with the use of Dinoflaj2 (Fensome et al., 2008). Synonyms that are combined that are not included in the current version of Dinoflaj2 include: *Barssidinium pliocenicum* and *Barssidinium wrennii* (De Schepper et al., 2004); *Dapsilidinium pseudocolligerum* and *Dapsilidinium pastielsii* (Mertens et al., 2014) and *Operculodinium tegillatum* and *Operculodinium antwerpensis* (Louwye and De Schepper, 2010). Sub-species were treated on a species level; for example, *Achomosphaera andalousiensis andalousiensis* was entered in the database as *Achomosphaera andalousiensis.* The stratigraphic range for each species was checked, and if reworking was suspected, the species in question was removed. It is possible that some reworked species may have been included. However, according to Woods et al. (2014), reworking is unlikely to bias any results due to the large quantity of data analysed combined with limited evidence of reworking in younger sediments (Mertens et al., 2009b; Verleye and Louwye, 2010). Several of the species used have been grouped into complexes (Appendix B); for example, *Spiniferites elongatus* and *Spiniferites frigidus* have been grouped due to gradations in morphology (Rochon et al., 1999) as were *Batiacasphaera micropapillata* and *Batiacasphaera minuta* (Schreck and Matthiessen, 2013).

Once the taxonomy was confirmed, the data were further filtered to remove any record that had an age range spanning longer than two geological stages, to avoid using poorly constrained data that may influence the results. A record is defined as one or more species, with a known temperature preference, from a site with a specific age range. A maximum of two stages (e.g. Zanclean–Piacenzian) was chosen to avoid losing data that span two consecutive stages. This resulted in a dataset of 733 records (Figure 3.2; Appendix A). The records stem from 306 sites (183 publications) and as some sites contain several records of different ages they have different palaeo latitudes and longitudes. As many of the publications did not provide abundance counts, only presence and absence data were used for all published datasets. This results in inferred sea surface temperature changes being qualitative rather than quantitative (see Section 1.3.7 for a full explanation).

The results are presented in two different styles; the first is by plotting the records on separate maps for each stage (Figure 3.3a-i), while the second displays all the data on one figure, separated into latitudinal bins of 5° (Figure 3.4). Figure 3.3a-i shows maps for each stage where points represent the palaeo latitude and longitude for each record, which were calculated using a palaeo-rotation model based on the palaeogeography of Markwick et al., (2000). As the majority of the records have estimated age ranges spanning entire stages, the analysis concentrates on investigating stages separately to attempt to match the quality of the data (e.g. Figures 3.3, 3.5 and 3.6). However, the estimated age range for each assemblages is also provided to visualise the spread and quality of the data (Figure 3.4a and b). Chapter 4 provides a more thorough evaluation of both dinoflagellate cysts as a proxy for environmental change and databasing, as well as possible limitations of the methodology and data utilised.

More temperature preferences are known for extant species than extinct species as studies can be done showing exactly where the cysts collect, under what conditions and in what abundances, providing reliable environmental parameters. Further back in geological time there are fewer species that are still extant today (Versteegh and Zonneveld, 1994), which can result in a ‘pull of the recent’ in an ecological sense. The pull of the recent was originally conceived for diversity studies, particularly in the Cenozoic (Raup, 1979; Jablonski et al., 2003), and results in the number of species with known temperature preferences decreasing with increasing sample age. It is for this reason that, while the number of CWS in each record is represented by the size of the points, the main analysis concentrates on the proportion of CWS relative to WWS for each record.

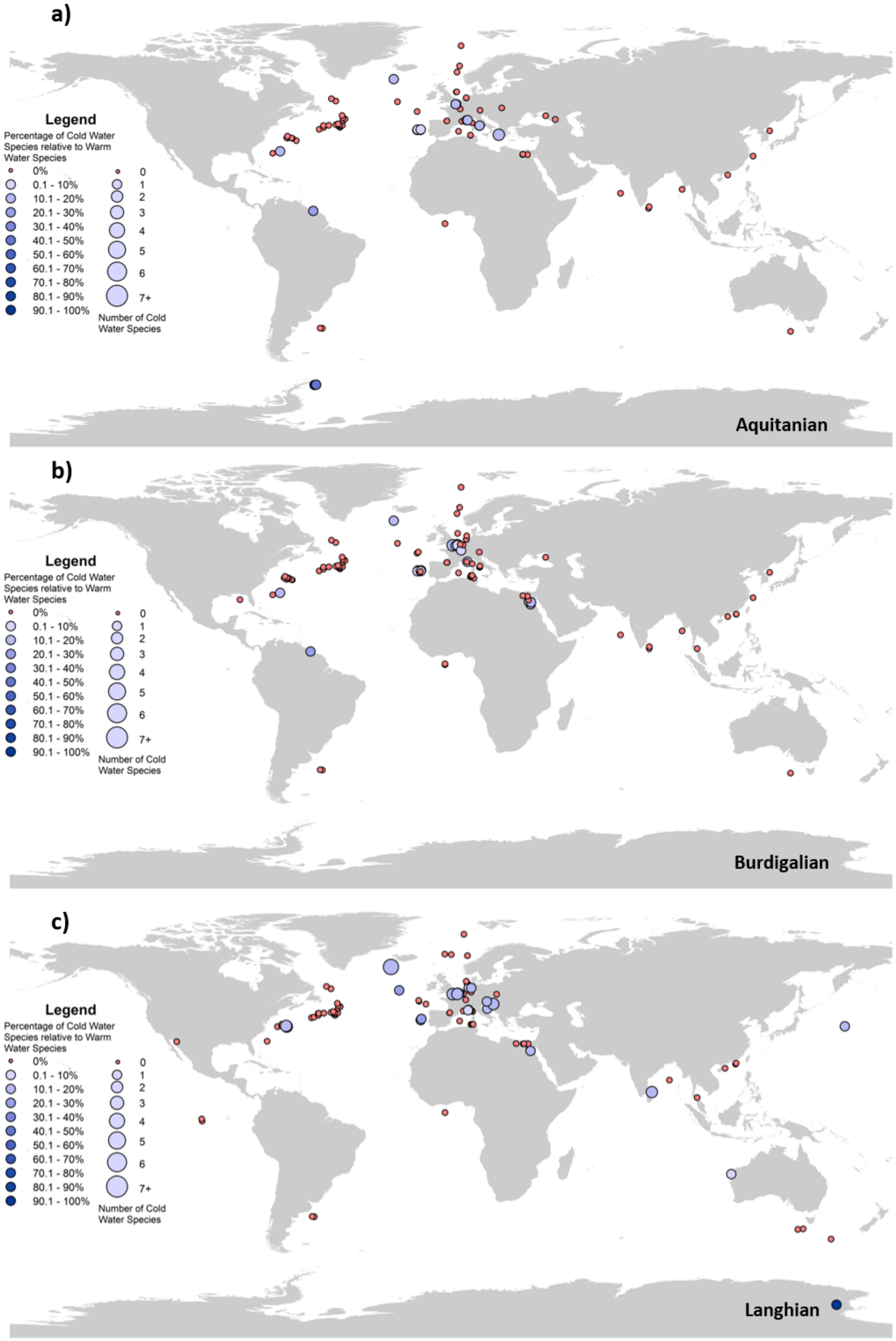
A different dataset was used for the modern era and was obtained from Zonneveld et al. (2013b). It provided details for 33 WWS and 10 CWS. Seventeen of the WWS and five of the CWS were also found in the Neogene, but the remaining species were present in the records from the modern only. Once records that had no species with known temperature preferences were removed, there were 1,784 records remaining for the modern.

To aid visualisation and understanding of any patterns, the data were analysed in latitudinal bins of 5° (Figure 3.4). The percentages of CWS used is the same as for Figure 3.3a-i. To help explore uncertainties, the number of records found within each latitudinal bin is represented by the shading. The darker the shading, the more data there are, and therefore the more reliable the signal is likely to be. Red dashed lines represent the records with no CWS present.

To demonstrate change over time and space, the mean percentage of CWS for each stage and latitude was analysed (Figures 3.5 and 3.6). As the majority of the data are located in the Northern Hemisphere much of the analysis ignores the Southern Hemisphere due to a lack of data from the publications used. This is an unfortunate limitation that can be addressed as the literature expands to include more Southern Hemisphere study sites.

3.3 Results

The records for each stage of the Neogene, as well as for the modern, are presented on individual distribution maps (Figures 3.3a-i). An overview Figure is also included to compare the differences in the percentage of CWS through the Neogene (Figure 3.4a and b). Where the percentage of CWS is mentioned, it is the percentage of CWS relative to the number of species with known temperature preferences for that record.


a)
Legend
Percentage of Cold Water Species relative to Warm Water Species
0%
0.1 - 10%
10.1 - 20%
20.1 - 30%
30.1 - 40%
40.1 - 50%
50.1 - 60%
60.1 - 70%
70.1 - 80%
80.1 - 90%
90.1 - 100%
0
1
2
3
4
5
6
7+
Number of Cold Water Species
Aquitanian
b)
Legend
Percentage of Cold Water Species relative to Warm Water Species
0%
0.1 - 10%
10.1 - 20%
20.1 - 30%
30.1 - 40%
40.1 - 50%
50.1 - 60%
60.1 - 70%
70.1 - 80%
80.1 - 90%
90.1 - 100%
0
1
2
3
4
5
6
7+
Number of Cold Water Species
Burdigalian
c)
Legend
Percentage of Cold Water Species relative to Warm Water Species
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0.1 - 10%
10.1 - 20%
20.1 - 30%
30.1 - 40%
40.1 - 50%
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60.1 - 70%
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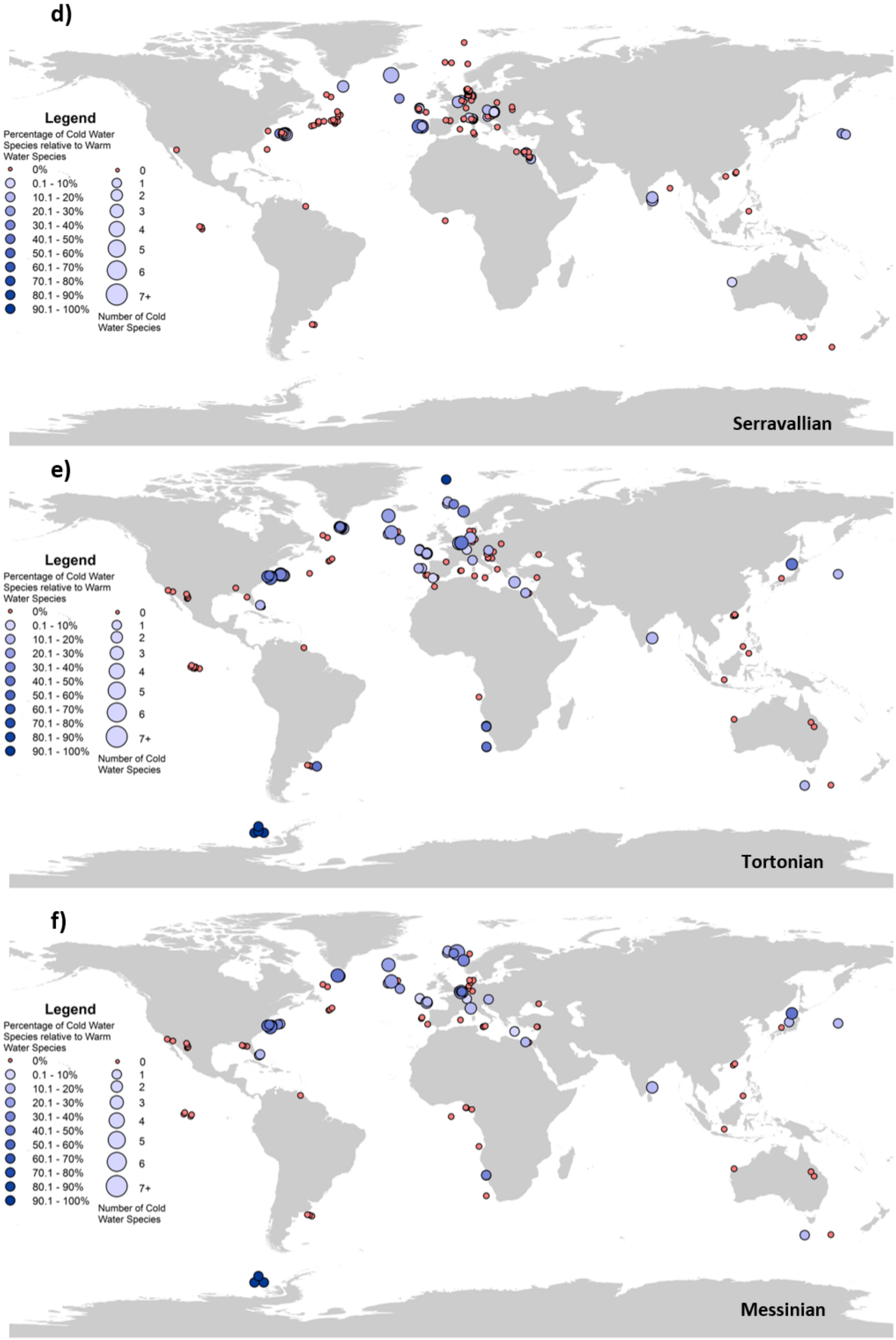
6
7+
Number of Cold Water Species
Langhian


d)
Legend
Percentage of Cold Water Species relative to Warm Water Species
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40.1 - 50%
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70.1 - 80%
80.1 - 90%
90.1 - 100%
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3
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5
6
7+
Number of Cold Water Species
Serravallian
e)
Legend
Percentage of Cold Water Species relative to Warm Water Species
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0.1 - 10%
10.1 - 20%
20.1 - 30%
30.1 - 40%
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50.1 - 60%
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Number of Cold Water Species
Tortonian
f)
Legend
Percentage of Cold Water Species relative to Warm Water Species
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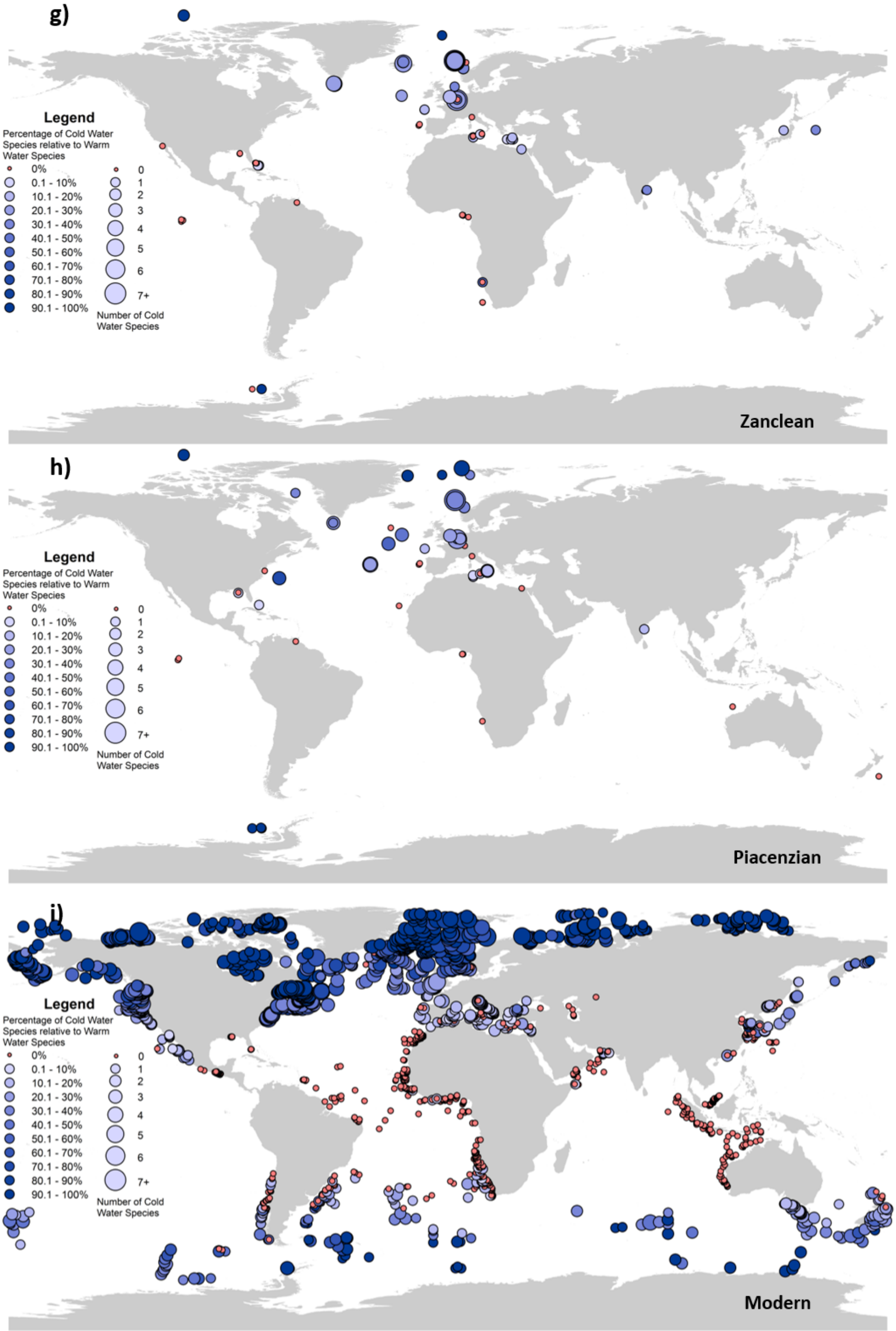
7+
Number of Cold Water Species
Messinian


g)
Legend
Percentage of Cold Water Species relative to Warm Water Species
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0.1 - 10%
10.1 - 20%
20.1 - 30%
30.1 - 40%
40.1 - 50%
50.1 - 60%
60.1 - 70%
70.1 - 80%
80.1 - 90%
90.1 - 100%
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1
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7+
Number of Cold Water Species
Zanclean
h)
Legend
Percentage of Cold Water Species relative to Warm Water Species
0%
0.1 - 10%
10.1 - 20%
20.1 - 30%
30.1 - 40%
40.1 - 50%
50.1 - 60%
60.1 - 70%
70.1 - 80%
80.1 - 90%
90.1 - 100%
0
1
2
3
4
5
6
7+
Number of Cold Water Species
Piacenzian
i)
Legend
Percentage of Cold Water Species relative to Warm Water Species
0%
0.1 - 10%
10.1 - 20%
20.1 - 30%
30.1 - 40%
40.1 - 50%
50.1 - 60%
60.1 - 70%
70.1 - 80%
80.1 - 90%
90.1 - 100%
0
1
2
3
4
5
6
7+
Number of Cold Water Species
Modern

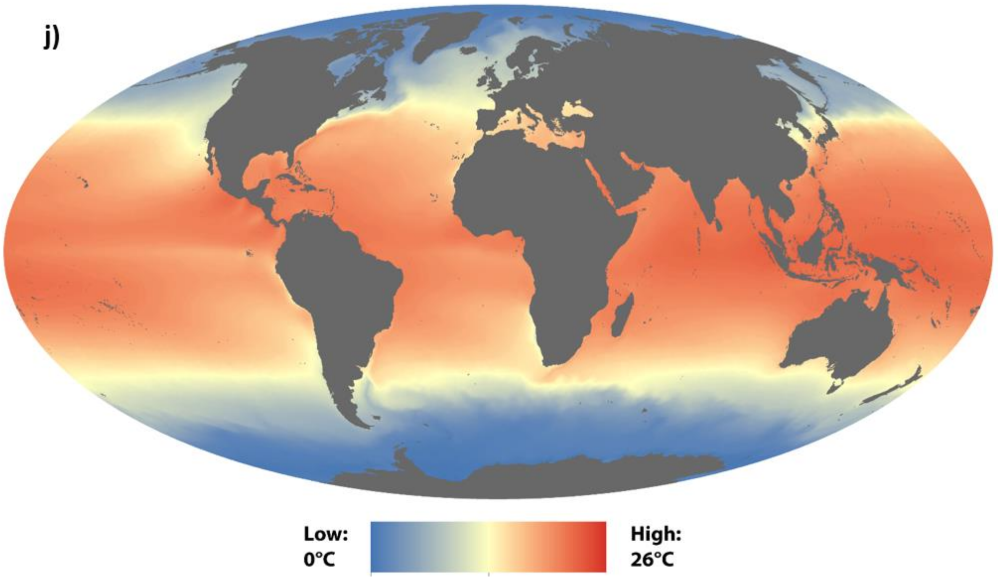
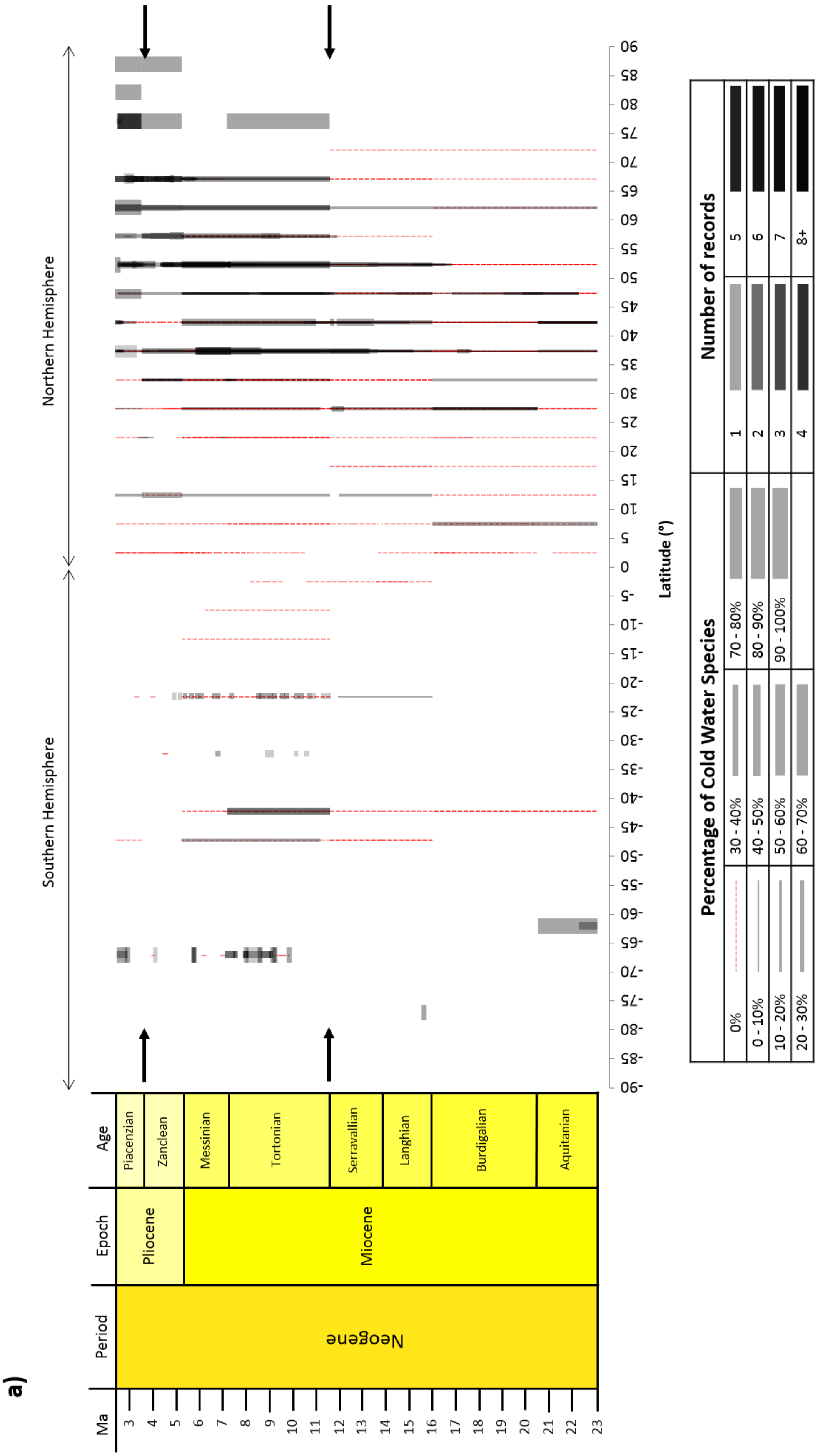


Figure 3-3: Distribution of records in (a) Aquitanian, (b) Burdigalian, (c) Langhian, (d) Serravallian, (e) Tortonian, (f) Messinian, (g) Zanclean, (h) Piacenzian and the (i) modern. Records are plotted at their palaeo latitude and longitudes. Size of the points represents the number of Cold Water Species (CWS) present in each record. The colour of the points represents the percentage of CWS relative to the total number of species with known temperature preferences present in each record. Darker shades represent higher percentages of CWS. Small red circles represent records that only contain Warm Water Species. Data for the modern (i) are from Zonneveld et al., 2013b. For comparison of the modern data (i), Figure 3.3j is included and represents actual Sea Surface Temperatures averaged from 2009 to 2013. The Figure was created using remotely-sensed images from NASA's Ocean Color database (http://oceancolor.gsfc.nasa.gov; NASA Ocean Biology OB.DAAC; 2014).

3.3.1 Overview of the Neogene (23.03–2.59 Ma)

3.3.1.1 Southern Hemisphere

Data in the Southern Hemisphere are much sparser than for the Northern Hemisphere. Only 10 of the 18 latitudinal bins in the Southern Hemisphere contain any data, and there is no latitudinal bin with data representing every stage (Figure 3.4). The Aquitanian has only two latitudinal bins that contain any data. These are between 40 and 45° S where no CWS are present, and between 60 and 65° S, where the maximum percentage of CWS is 100%. The Burdigalian has only one latitudinal bin with data and no CWS are present. The Southern Hemisphere in the Langhian, has a record where all the species with known temperature preferences are CWS between 75 and 80° S. Between 40 and 50° S there are no CWS present, and between 20 and 25° S eight percent of the species present with known temperature preferences are CWS. There is no data available for the remaining latitudinal bins. The Serravallian has the same values as the Langhian, but with no data between 75 and 80° S.


a)
Ma
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
Period
Neogene
Epoch
Pliocene
Miocene
Age
Piacenzian
Zanclean
Messinian
Tortonian
Serravallian
Langhian
Burdigalian
Aquitanian
Southern Hemisphere
Northern Hemisphere
-90
-85
-80
-75
-70
-65
-60
-55
-50
-45
-40
-35
-30
-25
-20
-15
-10
-5
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
Latitude (°)
Percentage of Cold Water Species
0%
0 - 10%
10 - 20%
20 - 30%
30 - 40%
40 - 50%
50 - 60%
60 - 70%
70 - 80%
80 - 90%
90 - 100%
Number of records
1
2
3
4
5
6
7
8+

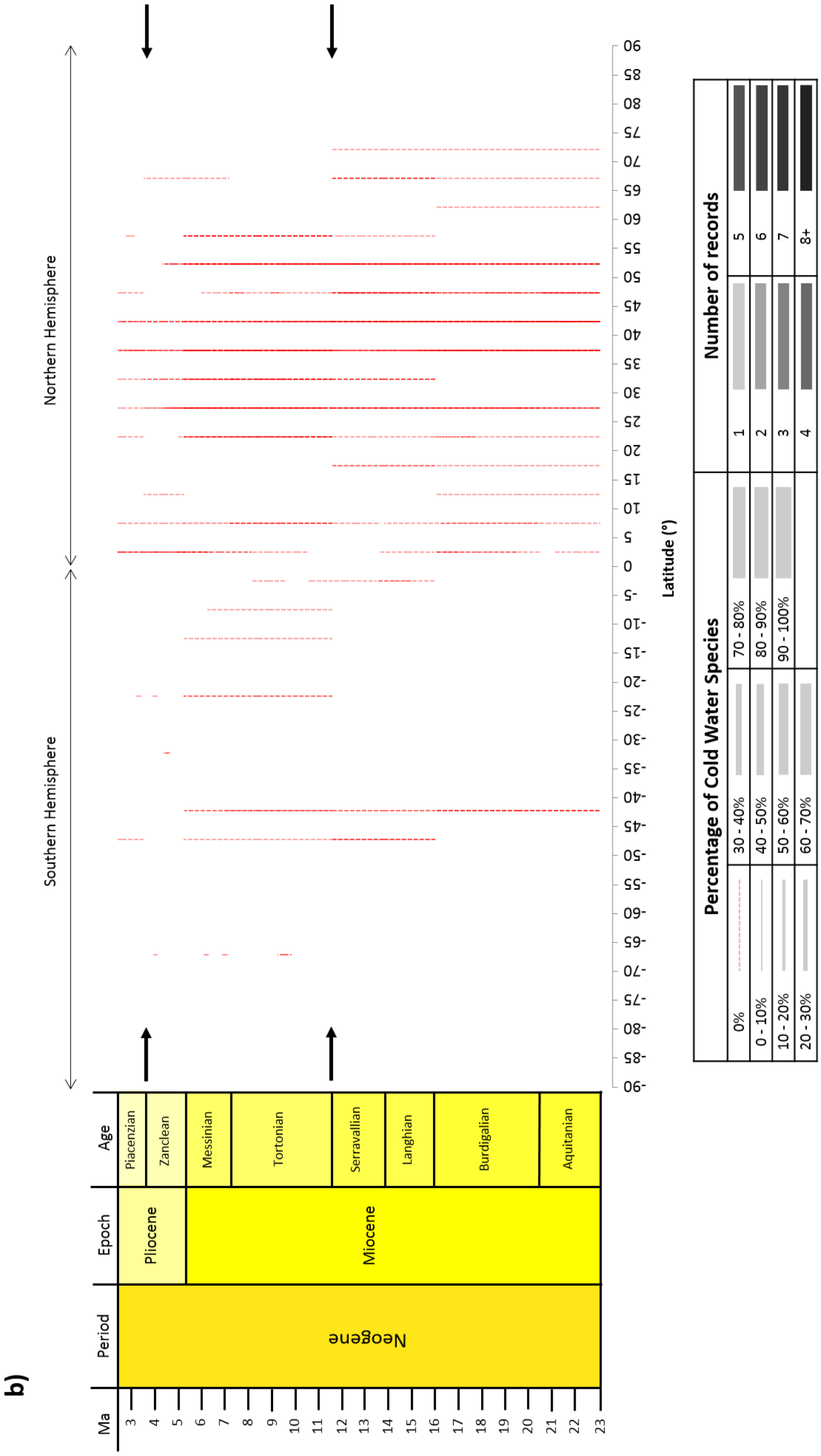


Figure 3-4: Data for the whole of the Neogene are split into latitudinal bins spanning five degrees. There is consistently more data for the Northern Hemisphere then in the Southern Hemisphere. For each record the percentage of CWS was calculated relative to the number of species with known temperature preferences. The percentage of CWS is displayed and is represented by the horizontal thickness of the line. The shading of the lines represents the number of records present within each latitudinal bin. Dashed red lines represent records with no CWS. Figure 3.4a represents all records and Figure 3.4b contains only those records with no CWS present. Arrows indicate the two main periods of cooling.

The stage with the most data is the Tortonian, which has data for eight of the latitudinal bins. Three of the eight, 0–5° S, 5–10° S and 15–15° S are represented by WWS only. Between 65 and 70° S the maximum percentage of CWS is 100%. The other three latitudinal bins in the Tortonian with data are between 45 and 50° S (17%), 40 and 45° S (33%) and between 30 and 35° S (50%). The Messinian has two records, between 65 and 70° S, where all the species present with known temperature preferences are CWS and has six records (20–25° S) with CWS percentages between 33 and 50%. Between 45 and 50° S there is a record with a CWS percentage of 14%. Between 5 and 10° S, 10 and 15° S, 30 and 35° S and between 40 and 45° S there are no CWS present, and there are no data available for the remaining latitudinal bins. In the Zanclean, the Southern Hemisphere has two records with CWS percentages of 50%. These are both between 20 and 25° S and there is one record with a CWS percentage of 100% (65–70° S). The remaining records present during the Zanclean, in the Southern Hemisphere, contain no CWS. In the Piacenzian there are four latitudinal bins with data present. The 45–50° S, 20–25° S and 15–20° S latitudinal bins all have no CWS present, but between 65 and 75° S there are records where all of the species with known temperature preferences are CWS.

3.3.1.2 Northern Hemisphere

Data from the Northern Hemisphere are much more continuous then for the Southern Hemisphere (Figure 3.4). For example, between 25 and 55° N there are data for all stages. The Aquitanian and Burdigalian show very similar results. In both stages, 13 latitudinal bins (out of the 14) have records where no CWS are present and the highest percentage of CWS (25%) occurs between 5 and 10° N. The next highest percentage of CWS is 11% in three latitudinal bands between 30 and 35° N, 40 and 45° N and 60 and 65° N. Cold Water Species are also present between 25 to 30° N, 35 to 40°, N and 45 to 50° N, where all CWS percentages are 10% or less. In the Langhian 13 out of the 15 latitudinal bins with data have records where no CWS are present. However, in seven of the latitudinal bins there are also records that do contain CWS. The highest percentage of CWS is 25% between 40 to 45° N and

50 to 55° N. The Serravallian also has seven latitudinal bins with CWS present (out of 14), but the highest CWS value in the Serravallian is 43%. In the Serravallian there are 12 latitudinal bins that have records with no CWS present.

In the Tortonian, there are 14 latitudinal bins with data and CWS are present in 11 of them. Only 10 of the latitudinal bins have records with no CWS present. The next highest percentage of CWS is 50% (40–45° N, 50–55° N and 55–60° N). In the Messinian, there are 13 latitudinal bins with data present and 11 of them contain CWS. The highest percentage of CWS is 50% (35–40° N, 40–45° N, 50–55° N and 55–60° N). Eleven of the latitudinal bins include records where no CWS are present. The Zanclean and Piacenzian both have records where no WWS are present. These records are found in the 75–80° N and the 85–90° N latitudinal bins in both stages and additionally between 80–85° N in the Piacenzian. Records where all the species with known temperature preferences are CWS are found between 50 to 55° N and between 60 to 65° N for the Piacenzian. In the Zanclean, there are 15 latitudinal bins with data present, nine of them have records with no CWS present and 11 of them contain records with CWS. In the Piacenzian, the number of latitudinal bins with data present is 16. Nine of them contain records with no CWS present and 13 of them contain records with CWS present.

From the Tortonian onwards, only one record that contains no CWS is found above 60° N and far fewer are found above 20° N in the Pliocene than in the older stages. There appears to be two main stages of increase in the percentage of CWS, these take place at the Serravallian to Tortonian boundary and then again at the Zanclean to Piacenzian boundary (Figure 3.4). Both steps are most evident in the mid to high latitudes (45–65° N).

3.3.2 Overview of the modern

There is a significantly higher number of sites in the modern than for the Neogene and a more or less global distribution is achieved (Figure 3.3i). As in the Neogene, there are fewer records for the Southern Hemisphere compared to the Northern Hemisphere and the Indian and Pacific oceans are also under represented. For the majority of ocean basins, most of the records come from coastal regions, and relatively few come from deeper and more oceanic regions. Sites that are composed only of CWS are common in higher latitudes in both the Southern and Northern Hemispheres. In the lower latitudes, species with known temperatures are nearly all WWS. Between 20° N and 20° S there are only four records (out of 377) that contain any CWS. Three of these are found off the west coast of Africa and the fourth is off the east coast of Africa, all have CWS percentages under 10%. Records composed entirely of CWS are common above and below 45° N and 45° S respectively. Asymmetry occurs either side of the North Atlantic. Records where all of the species with known temperature preferences are CWS reach as far south as 42° N on the western edge of the North Atlantic, but only as far south as 56° N on the eastern side. This suggests that the eastern North Atlantic is warmer than the western North Atlantic and can be related to the presence of the North Atlantic Current, which transports warm water to the higher latitudes of the northeast Atlantic Ocean.

For comparison between Neogene dinoflagellate cyst data (and the methodology) and known sea surface temperatures of the modern, Figure 3.3i can be compared to Figure 3.3j. This validates the methodology used, and demonstrates that surface waters that are known to be warm, have a lack of CWS species present.

3.3.3 Mean temperature changes (latitude)

The mean percentage of CWS was calculated for each latitudinal bin (Figure 3.5) to investigate if cooling occurred at all latitudes equally. The mean percentages of CWS for each latitudinal bin, for the Aquitanian and Burdigalian, are similar at all latitudes and range between 0 and 11% (Figure 3.5a and b). In the Langhian and Serravallian the highest mean percentage of CWS is between 60 and 65° N and is 18% (Figure 3.5c and d). The mean percentage of CWS for each latitudinal bin in the Tortonian and Messinian are more varied and range between 0 and 100%, although for all but one latitudinal bin (100%; 75–80° N;

Figure 3.5e) the values are between 0 and 27% (Figure 3.5e and f). The mean percentage of CWS between 0 and 35° N all remain low (five percent and under), with the exception of one latitudinal bin (15–20° N), where the mean percentage of CWS is 20%. In the Zanclean and Piacenzian (Figure 3.5g and h), the mean percentages of CWS, between 0 and 45° N are all under seven percent, with the exception of between 10 to 15° N, which has a mean CWS percentage of 17%. The mean percentages of CWS north of 55° N are all over 20% and above 75° N they are 87% and higher. In the modern (Figure 3.5i), between 0 and 35° N, the mean percentages of CWS relative to WWS are all under five percent, which quickly rises to 50% and above north of 45° N.

3.3.4 Mean temperature changes (stage)

Average percentages of CWS (for each stage) illustrate that the Aquitanian to Langhian stages all have CWS means of five percent or less (Figure 3.6a). The mean percentage of CWS increased from the Serravallian to the Tortonian (up to 19%) before dropping back to 12% in the Messinian. An increase followed and resulted in a peak in the modern of 38%. When just using data from the Northern Hemisphere (Figure 3.6b), there is no peak in the Tortonian.

To further investigate possible sampling biases, the mean percentages of CWS (for the Northern Hemisphere) were recalculated ignoring any data from latitudinal bins where the entire Neogene was not represented (Figure 3.6c). The mean percentage of CWS is low at the beginning of the Neogene (two percent; Aquitanian), which increases to six percent in the Serravallian. The mean percentage of CWS then increased to 10% for the Tortonian and Messinian, to 16% in the Zanclean, 23% in the Piacenzian and up to 34% for the modern.

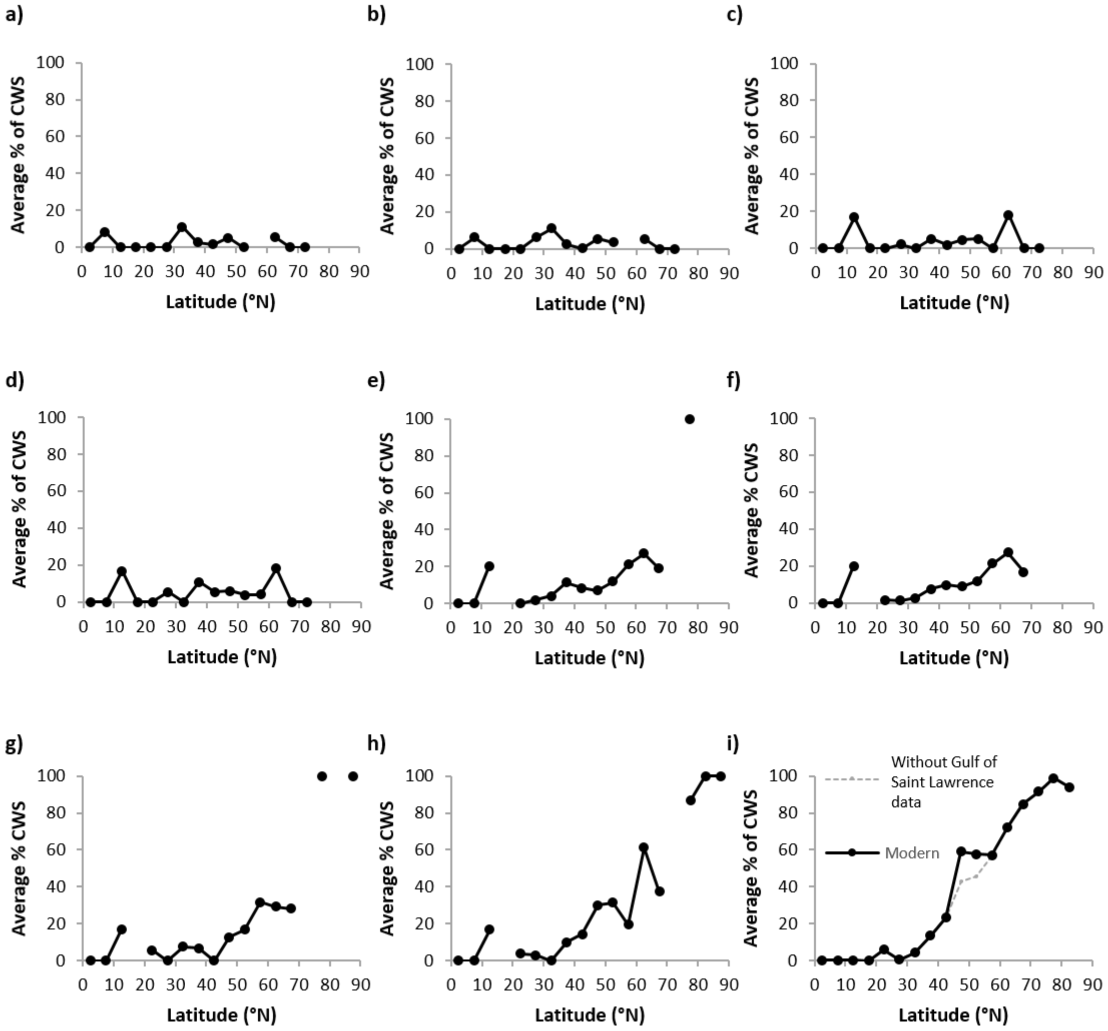


Figure 3-5: The mean percentage of Cold Water Species (CWS) relative to the total number of species present with known temperature preferences for each five degree latitudinal bin. (a) Aquitanian, (b) Burdigalian, (c) Langhian, (d) Serravallian, (e) Tortonian, (f) Messinian, (g) Zanclean, (h) Piacenzian and (i) the modern. For the modern (i) data were replotted without data points from the Gulf of St. Lawrence (grey dashed line), a densely sampled region, to investigate sampling bias (see Section 4.2.2).

The means of CWS for each stage, when only using data from Northern Hemisphere latitudes that have data for every stage (Figure 3.6c), are comparable to those where all the data for the Northern Hemisphere are used (Figure 3.6b). For example, in both cases mean percentages of CWS between the Aquitanian and the Messinian range between 2 and 10%. However, values are higher when all of the data are used (Figure 3.6b), due to the few records in the highest latitudes that are present only in the Pliocene and Modern (Figures 3.3g, h, i and 3.4).

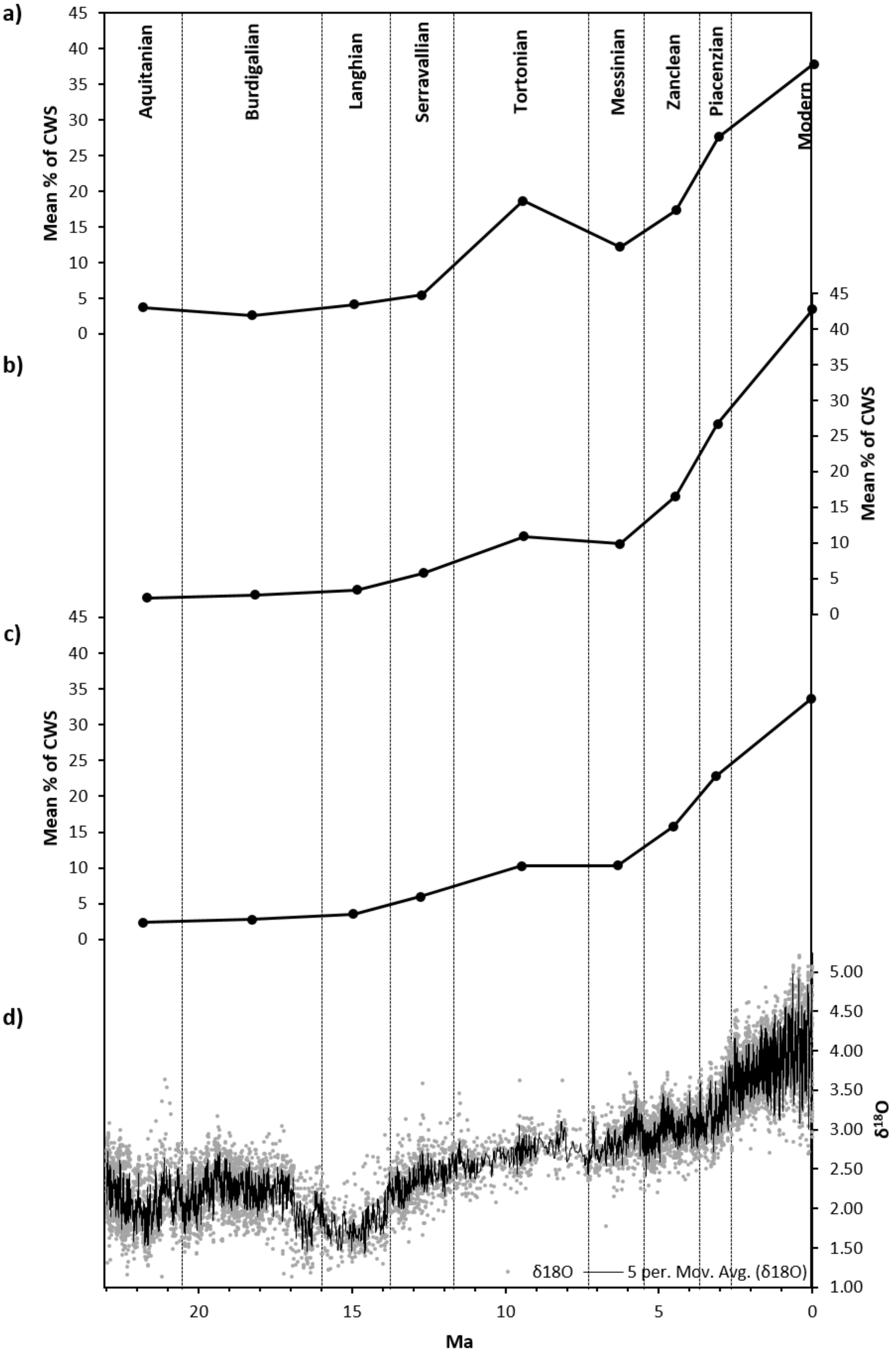


Figure 3-6: Mean percentages of Cold Water Species (CWS) for each stage for (a) all records, (b) just records in the Northern Hemisphere and (c) using only the latitudinal bins (in the Northern Hemisphere) where data are available for all stages. (d) Benthic $\delta^{18}O$ compilation (Zachos et al., 2001; 2008) demonstrating cooling through the Neogene to present for comparison with the mean percentage of Cold Water Species of dinoflagellate cysts.

3.4 Discussion

3.4.1 Neogene climate and dinoflagellate cysts

In this study, an increase in the percentage of CWS (relative to the total number of species present with known temperature preferences) is qualitatively indicative of sea surface temperatures, and the results presented here agree with the previously established cooling trend of the Neogene (Figure 3.6d; Zachos et al., 2001; 2008; Billups and Schrag, 2002; Ravelo et al., 2004; Shevenell et al., 2004; McKay et al., 2012; Miao et al., 2012; Pound et al., 2012a; Lear et al., 2015). An increase in the mean percentage of CWS for each stage correlates very well with cooling deep water (benthic $\delta^{18}O$ values) shown in Zachos et al. (2008; Figure 3.6a-d). The two main stages of cooling are noted and labelled on Figure 3.4. The first took place between the Serravallian and the Tortonian (~11.62 Ma) and the second between the Zanclean and the Piacenzian (~3.60 Ma).

The benefits of a global dataset means that different latitudes can be compared to see if the cooling trend occurred at all latitudes or was more localised. Global compilations also are useful to help understand large scale changes rather than potential local anomalies. Another benefit for the methodology used in this chapter is that, unlike benthic $\delta^{18}O$ values (e.g. as compiled by Zachos et al., 2001; 2008), the results presented here are not influenced by ice volume as the majority of dinoflagellate cyst live in ice free conditions. There are however, other limitations to using previously published data and dinoflagellate cysts as a temperature proxy, which will be discussed in Section 4.3. Preceding this, Neogene cooling will be discussed in terms of the rate and extent of cooling.

3.4.1.1 The early Miocene (23.03–15.97 Ma)

Prior to the Miocene, the earliest Oligocene saw the establishment of the predecessors of both the east and west Antarctic ice-sheets, with volumes comparable to or exceeding, by 25%, that of todays (Wilson et al., 2013). Just preceding the Oligocene-Miocene boundary (23.03 Ma) the Mi-1 glaciation occurred, accompanied by an increase of ice on Antarctica

(Zachos et al., 2001; Billups and Schrag, 2002; Wilson et al., 2013; Beddow et al., 2016). The records in this study have a mean CWS percentage of 2% for the Aquitanian and 3% for the Burdigalian, demonstrating very little temperature change between the two stages (Figure 3.6c). However, it has been shown from alkenones that Europe (the old Paratethys) cooled on average 2–3 °C in ~600 years between 18.4 and 17.8 Ma (Grunert et al., 2014). The lack of change in this study may be related to the resolution of the data as the average age range of the records is 4.7 Myr for the Aquitanian and 4.4 Myr for the Burdigalian (Figure 3.7). This means that many of the records must span the two stages, potentially blurring any temperature change, and are not sufficiently resolved to capture sub-millennial changes. Thus, the warming trend towards the end of the Burdigalian, due to the MMCO (Savin et al., 1975; Shackleton and Kennett, 1975; Zachos et al., 2001; Böhme, 2003; You et al., 2009), may have resulted in any cooling prior to the event being effectively counteracted (or smoothed out) in the record.

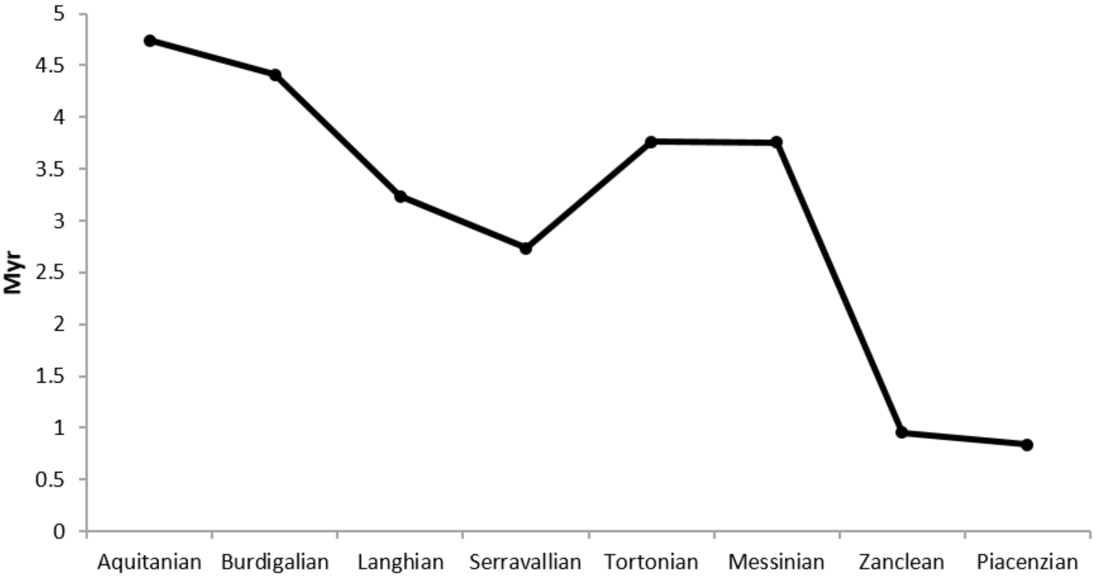


Figure 3-7: The mean age range (maximum minus minimum estimates for the age of each record) of records for each stage. Generally, temporal resolution of the data increases in stages of a shorter duration.

To understand more clearly how the temperature changed at different latitudes, analysis of the relationship between each latitudinal bin and the mean percentage of CWS was carried out for each stage (Figure 3.5). The different latitudinal bins for the Aquitanian and the Burdigalian show similarities for their mean percentage of CWS, and values for all latitudinal bins were under 11% (Figure 3.5a and b). This suggests that there was a shallower latitudinal temperature gradient in the early Miocene than at present, with the high latitudes having similar or slightly cooler water temperature to the lower latitudes (Nikolaev et al., 1998; Pound et al., 2012a).

3.4.1.2 The middle Miocene (15.97–7.25 Ma)

Towards the end of the early Miocene, benthic $\delta^{18}O$ values quickly dropped suggesting a warming event (Zachos et al., 2001; 2008). The warming event culminated in the MMCO, which was a period of global warmth occurring between 17 and 15 Ma (Zachos et al., 2001). It resulted in the tropical climate zone having a much greater latitudinal extent, abundant precipitation and increased seasonality (Böhme, 2003; Bojar et al., 2004; Kroh, 2007; Pound et al., 2012a). Even though global temperatures of the MMCO were 3 °C higher than today, with atmospheric CO_2 concentrations between 200 and 450 ppmv (Pagani et al., 1999; Kürschner et al., 2008; You et al., 2009; Foster et al., 2012), evidence for such warming is not obvious in this study, and the dinoflagellate cyst cooling trend does not follow that of Zachos et al. (2001; 2008; Figure 3.6a-d).

For example, the average percentage of CWS relative to WWS in the Burdigalian and Langhian is very similar (3% and 4% respectively, Figure 3.6c). This is not surprising due to a lack of high resolution data in the TOPIS database, which is unable to resolve the MMCO and preceding warming (Figure 3.7). For example, the average length of the records of the Langhian (Figure 3.7) is 3.2 Myr, which spans the entire MMCO event. In order to fully understand the effect that the MMCO had on dinoflagellate cysts, data points of higher resolution data are required. It may also be pertinent to calculate the averages of the MMCO event rather than the stages, but this would require more constrained dating than the publications contained in TOPIS allows. As the event spans the upper Burdigalian and the lower Langhian, any changes caused by the MMCO may have been smoothed out from the relatively cooler periods on either side. However, the lack of warming observed during the

MMCO in TOPIS might also be due to a lack of abundance counts. For example, Warny et al. (2009) observed the MMCO in Antarctica by a 2000-fold abundance increase of just two species. They associated the peak in productivity to increased ice runoff from the elevated temperatures of the MMCO. This demonstrates how improved literature reporting of abundance counts would enhance our ability to understand Neogene climate trends.

What is evident in the database is a cooling trend that took place between the Langhian and the Serravallian, which resulted in a slight increase in the percentage of CWS (4% and 6% respectively, Figure 3.6c). Whilst the slight increase in the percentage of CWS is apparent, it is not as distinguishable as the cooling event demonstrated by benthic $\delta^{18}O$ values (Figure 3.6d), which occurred as a result of the MMCT (Flower and Kennett, 1994; Zachos et al., 2001; 2008; Shevenell et al., 2004). The lack of a major cooling event (MMCT) displayed in the dinoflagellate cyst record may again be due to a sampling bias. However, when comparing the mean percentage of CWS at different latitudinal bands (25-50° N; Figure 3.5) the Serravallian consistently has higher percentages of CWS, suggesting that perhaps the dinoflagellate cysts did respond to the MMCT, but not uniformly in the surface waters at all latitudes.

While the benthic $\delta^{18}O$ values significantly increased in the Serravallian, and less in the Tortonian, the dinoflagellate cyst record (Figure 3.6a-d) demonstrates the opposite (i.e. a more significant cooling is indicated in the Tortonian than the Serravallian). This suggests a delayed response of the dinoflagellates reacting to the cooling during the MMCT, possibly due to surface water cooling at a different rate to the deep waters. Pollen records also demonstrate that the cooling was more pronounced between the Serravallian and the Tortonian than the Langhian and the Serravallian (Pound et al., 2012a), suggesting that deep water cooling did occur prior to surface water and terrestrial cooling. In addition, pollen records (Pound et al., 2012a) demonstrate that the Southern Hemispheres cooled prior to the Northern Hemisphere and as the majority of the records used in this study are from the

Northern Hemisphere, this could be a further explanation for the delayed response of the dinoflagellate cysts to the global cooling signal produced by the benthic δ^{18}O values (Zachos et al., 2001; 2008).

3.4.1.3 The late Miocene (11.62–5.33 Ma)

The Tortonian (11.62–7.25 Ma) is characterised by warmer and more humid conditions than today, particularly in continental Europe (Bruch et al., 2006). Mean annual temperatures were between 14 and 16 °C in northwest Europe (Donders et al., 2009; Pound et al., 2012b), and the global cooling trend, which began during the Langhian, continued (Zachos et al., 2001). However, the benthic δ^{18}O values from Zachos et al. (2008) demonstrate that the cooling was more gradual for the Tortonian compared to the Serravallian (Figure 3.6a-d). The cooling affected the presence of dinoflagellate cysts with cold water preferences, and the mean percentage of CWS reached 10% in the Tortonian (Figure 3.6c). However, when all of the data are included in the analysis (Figure 3.6a), the value for the Tortonian increases to 19%, a substantially higher value then for the stages either side. This discrepancy may be an artefact of sampling bias (see Section 4.2.2). However, it may reflect the asymmetrical cooling of the Northern and Southern hemispheres. For example, the Southern Hemisphere had a more modern-like latitudinal temperature gradient as early as the Serravallian (Pound et al., 2012a). Unfortunately a lack of Messinian and Serravallian Southern Hemisphere data means that this hypothesis cannot be tested with TOPIS.

On the other hand, the large amount of data in the Northern Hemisphere means that conclusions can reliably be drawn on Northern Hemisphere cooling. Like in the middle Miocene, cooling in the Tortonian was particularly prominent in the higher latitudes of the Northern Hemisphere (Flower and Kennett, 1994; Bojar et al., 2004). The percentage of CWS in the Tortonian mid to high latitudes increased while the percentage in the low latitudes remained similar to the values for the early and middle Miocene (Figure 3.5e). For example, throughout the early (Aquitanian and Burdigalian) and middle Miocene (Langhian and

Serravallian), the average proportion of CWS for each 5° latitudinal bin ranged from 0 to 11% and 0 to 18% respectively (Figures 3.5a-d). In the late Miocene (Figures 3.5e and f) this increased to between 0 and 27% with the exception of one latitudinal bin in the Tortonian (75–80° N), where all the species with known temperature preferences were CWS. This increase mostly occurred in the higher latitudes, from 55° N northwards, suggesting that the higher latitudes cooled more than the lower latitudes (Pagani et al., 2010). The increase in the percentage of CWS in the higher latitudes compared to the low latitudes reflects how the tropical regions in the Miocene remained at similar temperatures, but the high latitudes cooled (Williams et al., 2005; Steppuhn et al., 2006). This effect caused the latitudinal temperature gradient to steepen throughout the late Miocene and Pliocene in the Northern Hemisphere (Nikolaev et al., 1998; Crowley, 2000; Fauquette et al., 2007; Pound et al., 2012a). This decrease of temperature in the high latitudes is described by Nikolaev et al. (1998), who depicted a 4–6 °C increase in the latitudinal temperature gradient between 10 and 5 Ma.

Several important changes to marine gateways and ocean circulation occurred during the late Miocene, particularly in the Mediterranean region. One of these was the Messinian Salinity Crisis where the ocean gateways between the Atlantic Ocean and the Mediterranean Sea closed due to tectonic changes (Flecker et al., 2015). This resulted in the Mediterranean Sea nearly completely drying up, and the precipitation of several kilometres of evaporites (Hsü et al., 1973; 1977; Martín et al., 2001; Krijgsman et al., 2002). The event had profound effects on the Mediterranean biota, and diversities declined in groups such as calcareous nannofossils (Wade and Bown, 2006), foraminifera (Lozar et al., 2010) and patch reef organisms (Dornbos and Wilson, 1999), as well as dinoflagellate cysts (Section 3.6). It is perhaps for these reasons that the benthic δ^{18}O values of the Messinian are much more erratic (Figure 3.6d) than for the Tortonian (Zachos et al., 2001; 2008). Despite this, the Messinian had a similar percentage of CWS as the Tortonian (10%; Figure 3.6c). This suggests that global sea surface temperatures did not significantly change during the late Miocene. To investigate the effects that the gateway changes had on dinoflagellate cyst assemblages and diversity TOPIS is further utilised (Section 3.6).

3.4.1.4 The Pliocene (5.33–2.59 Ma)

Whilst the Pliocene was still a time of global warmth, compared to today, it saw a continuation of the previous cooling trend interrupted by short lived episodic glaciation events (De Schepper et al., 2014). Short lived glaciation periods were infrequent in the Zanclean, but became more common in the Piacenzian as the temperature continued to cool (Lisiecki and Raymo, 2005; Miller et al., 2005; 2012). The East and West Antarctic ice sheets were both well established by this time (Naish and Wilson, 2009; Dolan et al., 2011), but ice sheets in the Northern Hemisphere were significantly reduced, or absent, compared to the modern (De Schepper et al., 2014). Global climate started to significantly deteriorate (cooled) towards the end of the Piacenzian at 2.75 Ma, leading to the intensification of the Northern Hemisphere Glaciation (Ravelo et al., 2004; Mudelsee and Raymo, 2005; De Schepper et al., 2014). This agrees with the data presented in this study as the Pliocene has the highest percentage of CWS for the Neogene (Figure 3.6c), with values for the Zanclean and the Piacenzian of 16 and 23% respectively.

The rise in the percentage of CWS particularly increased in the high latitudes, from 45° N northwards (Figures 3.5e and f), further steepening the latitudinal temperature gradient. Nikolaev et al. (1998) found that during the late Pliocene, the latitudinal gradient increased by 4–5 °C. This cooling of the higher latitudes compared to the lower latitudes is a result seen in a variety of studies (Nikolaev et al., 1998; Pound et al., 2012a) and is associated with the development of ice due to the cooling temperature. For example, lower CO_2 levels allowed further ice to develop in high latitudes, causing local cooling. This results in a greater ice albedo and increased inception of ice sheets and so additional cooling (Lunt et al., 2008b).

3.4.1.5 Comparison to the modern

Zonneveld et al. (2013b) collated publications on dinoflagellate cysts from surface sediment, and by using the same method described above the Neogene can be compared to the modern. There is a considerably larger dataset for the modern (compared to the Neogene), with many more sites in the tropical regions and in the Southern Hemisphere. However, the Southern Hemisphere still has far fewer sites than for the Northern Hemisphere, and again the North Atlantic Ocean and Mediterranean Sea contain a high proportion of the data (Figure 3.3i). Compared to the Piacenzian, the modern has records with higher percentages of CWS at lower latitudes. For example, records where all the species with known temperature preferences are CWS can be found as far away from the poles as the 30–35° N and 35–40° S latitudinal bins (Figure 3.3i). In the Piacenzian the lowest latitudinal bin with a CWS percentage of 100% is 50–55° N and 65–70° S (Figure 3.3h). The results of the modern agree with the known sea surface temperatures of the modern, i.e. warm low latitudes and cold high latitudes (Figure 3.3j), and hence increases the reliability of the method used for the Neogene.

During the Neogene, the latitudinal temperature gradient in the Northern Hemisphere was always less steep than it is for the present (Nikolaev et al., 1998; Pound et al., 2012a). Today, the average water temperature difference ranges from on average 28 °C in the tropics to -2 °C in the polar regions (Levitus, 1982; Hay and DeConto, 1999). This TOPIS study demonstrates that the steepening latitudinal temperature gradient was due to cooling temperatures in the mid to high latitudes with little to no temperature change in the low latitudes (Figure 3.5).

3.4.1.6 The Cooling Neogene

There are several theories as to why the Neogene cooled, and the general consensus is that a combination of a variety of events caused the decreasing temperatures. These include: changes to the ocean circulation, surface albedo and the configuration of the continents (DeConto et al., 2007; Potter and Szatmari, 2009). Other events that took place included a

CO_2 decline, caused by enhanced silicate weathering due to the uplift of mountain chains, which also resulted in the reorganisation of both the atmospheric and oceanic circulation (Raymo et al., 1988; Raymo and Ruddiman, 1992; Mudelsee and Raymo, 2005; Ruddiman, 2013).

Increases in the mean percentage of CWS in the late Miocene were smaller than they were in the Pliocene (Figure 3.6c), suggesting less rapid cooling. Cooling in the late Miocene followed the establishment of ice on Antarctica after the most severe Mi-event at roughly 13.82 Ma (Abels et al., 2005). The cause of this cooling cannot be attributed to one event, and CO_2 reconstructions suggest that a drawdown of CO_2 and/or changes in ocean circulation was the cause (Shevenell et al., 2004; Kürschner et al., 2008; Pagani et al., 2009; Badger et al., 2013). However, minima nodes in eccentricity and obliquity may also have contributed (Shevenell et al., 2004; Abels et al., 2005).

Likewise, the more rapid cooling in the Pliocene, which specifically cooled the high latitudes (Figure 3.5), can be attributed to a variety of factors, although like for the middle and late Miocene, a decrease in atmospheric CO_2 (from modelling studies) is thought to have been the main driver (Lunt et al., 2008a), and has also been demonstrated by alkenones (Pagani et al., 2010). Other changes such as the closure of the Panama Seaway (Haug and Tiedemann, 1998) and tectonic uplift (Ruddiman and Kutzbach, 1989), whilst perhaps adding to the cooling, are not thought to have been the primary mechanism for the Neogene cooling that helped establish the Greenland ice sheet (Lunt et al., 2008a).

By comparing the dinoflagellate cyst record to previously published records of climate change, which use well established temperature proxies (e.g. Figure 3.6d; Zachos et al., 2001; 2008), it is possible to deduce that temperature is one of the main limiting factors causing the global changes to the assemblages. Whilst it is not possible to provide absolute values for temperature change (due to a lack of consistent abundance counts provided in TOPIS; see Sections 1.3.7 and 2.1.6), this study confirms that it is possible to use dinoflagellate cysts to determine that cooling took place on a global scale during the Neogene. They can be used to deduce when and where the cooling took place and the results demonstrate a similar cooling trend that is depicted by the deep-sea benthic foraminiferal oxygen-isotope curve (Figure 3.6d; Zachos et al., 2001; 2008).

3.5 Global summary

Changes to the distribution of dinoflagellate cysts during the Neogene reflect a general cooling trend. However, they demonstrate that cooling was not uniform at all latitudes and that the rate of cooling was not consistent. From the work presented in this chapter, the following conclusions can be drawn in relation to the research questions outlined in Section 3.1:

Can dinoflagellate cysts be used to determine global cooling in the Neogene?

- Dinoflagellate cysts are increasingly being used in palaeoclimate studies and this study corroborates their usefulness as a temperature proxy. Dinoflagellate cysts with known temperature preferences can be used to determine cooling on a global scale and the general cooling trend shown in this study broadly agrees with the benthic $\delta^{18}O$ curve of Zachos et al. (2008); see Figure 3.6a-d. The methodology is substantiated by applying it to the modern, where sea surface temperatures are known (Figure 3.3i and j). This corroborates the potential of dinoflagellate cysts as a qualitative temperature proxy over long timescales.

Was the cooling uniform at all latitudes?

- Increases in the percentage of CWS occurred most prominently in the mid to high latitudes, while the lower latitudes remained relatively low in CWS percentage throughout the Neogene, suggesting that the mid to high latitudes underwent more cooling than the lower latitudes, at least in the Northern Hemisphere (Figure 3.5). The lower latitudinal temperature gradient during the older portion of the Neogene, implied by smaller percentages of CWS in all latitudinal bins, agrees with terrestrial reconstructions from Pound et al. (2012a). They describe a steepening of the latitudinal temperature gradient as the high latitudes cooled in relation to the lower latitudes.

Can anything be said regarding the rate of cooling?

- Cooling of the Neogene did not always occur at a steady rate and the largest increase in the percentage of CWS took place in the Pliocene, between the Zanclean and the Piacenzian. There is a further decrease in temperature between the Piacenzian and the modern. The faster cooling rate from the Pliocene to the modern is in agreement with the benthic $\delta^{18}O$ curve of Zachos et al. (2008).

To improve this study it would be important to collect more data, particularly from the Indian and Pacific oceans and the Southern Hemisphere throughout the entire Neogene. This would enable further comparison between temperature changes between the Northern and Southern Hemispheres and permit analysis on the evolution of latitudinal temperature gradients. It would also be useful to gain more data with a higher temporal resolution to analyse shorter events, such as the MMCO, rather than solely the long term trends. It is equally important to add further records to the TOPIS database that contain abundance counts in order to facilitate the detection of more refined temperature changes. However, Chapter 3 does demonstrates that it is possible to use dinoflagellate cysts to determine large scale climate changes over the Neogene.

It is therefore clear that temperature affects the distribution of dinoflagellate cysts and that certain taxa are particularly useful warm or cold water indicators. With the use of these species with known temperature preferences it is demonstrated that dinoflagellate cysts can compete (at least qualitatively) with other previously established temperature proxies. However, temperature is not the only factor that influences the distribution and assemblage composition of dinoflagellate cysts and nutrient availability, salinity and ice cover are also known to affect dinoflagellate cysts. This means that regions (such as the low latitudes, e.g. the Mediterranean region), which did not substantially cool (Figure 3.5), can be investigated to determine what else influences the distribution and assemblage composition of dinoflagellate cyst over large regions. Gateway changes are one such geological phenomenon that alter oceanic circulation and conditions and because of this the following sections investigate the effects of previously established gateway changes on dinoflagellate cysts.

3.6 Mediterranean case study

During the Neogene (23.03–2.59 Ma) many changes took place that helped develop the Mediterranean Sea as it is known today (Figure 1.3). Some of the main changes that influenced the region were the opening and closing of ocean gateways, causing progressive isolation. Ocean gateways can have a significant influence on ocean circulation and consequently on climate (Raymo and Ruddiman, 1992; Sijp et al., 2014). Two major gateway changes occurred in the Mediterranean during the Neogene; the closing of the Eastern Gateway ~14 Ma, in the middle Miocene (Rögl, 1999; Popov et al., 2004; Harzhauser and Piller, 2007), and a brief closure of the Western Gateways in the late Miocene, between 5.97 and 5.33 Ma (Benson et al., 1991; Krijgsman et al., 2002; Ivanovic et al., 2013; Flecker et al., 2015). Both events are thought to have restricted or prevented the flow of water into and out of the Mediterranean, altering local conditions such as relative water depth, salinity and the presence of exotic species. The study of dinoflagellate cysts on a regional scale, in the Mediterranean, will provide a new perspective on how these changes affected marine life.

3.6.1 Climate and gateway changes

Gateway changes have often been linked to climate changes and the causes of the MMCT are still widely debated. Some authors (Woodruff and Savin, 1989; Wright et al., 1992; Flower and Kennett, 1994; 1995; Ramsay et al., 1998; Bartoli et al., 2005; Allen and Armstrong, 2008) suggest that the transition was due to the closure of the Eastern Mediterranean Gateway. For example, Allen and Armstrong (2008) posited that the closing of the gateway between the

Indian Ocean and the Mediterranean Sea changed the ocean circulation patterns, triggering the MMCT, with rapid cooling eventually resulting in the cooler Pleistocene (Woodruff and Savin, 1989; Flower and Kennett, 1993a; Krijgsman, 2002; Hüsing et al., 2009). Oceanic four-box models were used by Karami et al. (2011) to determine if the closure of the Eastern Mediterranean Gateway affected the temperature and salinity of the water bodies. The authors found that the closure caused cooling to the Paratethys and the Mediterranean Sea, and an increase in salinity in the Paratethys. Using fully coupled ocean-atmosphere General Circulation Models, Hamon et al. (2013) found that while the closure may have amplified the effects of cooling, it was not the initial cause for the global cooling of the MMCT. The initial cause of the MMCT is debated and has been attributed to a drawdown of CO_2 and/or changes in ocean circulation (Shevenell et al., 2004; Kürschner et al., 2008; Pagani et al., 2009; Badger et al., 2013). A drawdown of CO_2 during the MMCT was synchronous with glacial expansion and was caused by increased burial of organic carbon (Vincent and Berger, 1985; Flower and Kennett, 1993b). This has also been recorded by alkenones, boron isotopes and calcium isotopes (Tripati et al., 2009; Foster et al., 2012; Badger et al., 2013).

Consequences of the closures of the Western Mediterranean Gateway, and the MSC, on the climate are poorly understood (Flecker et al., 2015). Warny et al. (2003) use pollen studies to show that the MSC is not associated with any global or regional climate change and that the late Miocene remained stable and dry. However, modelling studies suggest that the MSC may have caused regional cooling (Murphy et al., 2009; Schneck et al., 2010; Ivanovic et al., 2014a). For example Murphy et al. (2009) saw strong cooling over the North Pacific, Schneck et al. (2010) saw cooling over central, northern and eastern Europe and Ivanovic et al. (2014a) saw cooling of up to 1 °C in the Barents Sea as well as cooling of 0.9 °C over central North America and the Greenland-Iceland-Norwegian seas. Even greater temperature changes were seen depending on the salinity fluctuations used in the model for Mediterranean outflow water (Ivanovic et al., 2014a).

Unlike previous studies, which have concentrated on just one or two sites, this chapter aims to investigate if changes to marine gateways influenced dinoflagellate cyst assemblages on a regional scale in the Mediterranean and Paratethys. Specific questions addressed are:

1. Are there any major changes to the diversity of Mediterranean dinoflagellate cysts through the Neogene?
2. Do Mediterranean dinoflagellate cysts assemblages change over time and space?
3. Are recorded changes in Mediterranean dinoflagellate cyst assemblages and species diversity directly related to marine gateway changes, or is there an alternative explanation?

3.6.2 Mediterranean methodology

TOPIS was once again utilised to investigate if dinoflagellate cysts can be used to determine changing conditions, potentially as a result of gateway closures. Sites/assemblages located within the once larger Western Tethys, Mediterranean and Paratethys regions were extracted from TOPIS. This resulted in 188 assemblages, from 92 sites, and 60 publications (Figure 3.8). References for publications used can be found in Appendix C. Reworked species were removed and any synonyms were combined, a full list of the species used, and their original publications can be found in Appendix D. To avoid using poorly dated data, any assemblage with an age range spanning more than two stages was removed. This is consistent with the methodology applied for the global study. This method (the two stage method) is discussed in this chapter, but additional analyses were carried out on the data that are dated to within one stage (the one stage method) and is discussed in Appendix E. The age range of each species used in this study is displayed in Figure 3.9, where the first and last appearance is given for the Neogene Mediterranean from TOPIS.

3.6.2.1 Diversity

The definition of biological diversity according to Magurran (2004, p. 8) is “the variety and abundance of species in a defined unit of study”. It can be split into three main components:

genetic diversity, species diversity and ecological diversity (Norse et al., 1986). There are an overwhelming number of different ways to study diversity. However, the majority of them require abundance counts. Unfortunately, the larger the scale of the investigation, the harder it is to measure abundance, and many of the publications synthesised by this study do not provide such data. This means that measurements of evenness, which measure the differences in the number of individuals of each species, cannot be studied, and only the number of different species can be calculated (species richness).

To investigate changes to the diversity of dinoflagellate cysts over the Neogene, the Neogene was split into 0.5 million year time bins. The method follows that of MacRae et al. (1996), but uses 0.5 Myr time bins, rather than stages to try and avoid biasing of longer stages versus shorter stages. For example, the significant diversity drop in the Coniacian (89.8–86.3 Ma) seen by MacRae et al. (1996) may be related to the relatively short duration of this stage. The 0.5 Myr time bin method also allows for a higher resolution study into how diversity changed over the Neogene. For each 0.5 Myr time bin, the number of species present was calculated alongside the number of species that originated or went extinct. Values for the extinction or origination of species are also displayed as a percentage of the diversity for each time bin.

This was repeated for all of the selected assemblages, both for the combined region and for separate basins individually. Four distinct basins are defined: the Western, Eastern and Central Mediterranean basins and the Paratethys Basin (Figure 3.8). The Western Mediterranean Basin has the fewest assemblages and includes those sites situated between the Strait of Gibraltar and the Strait of Sicily. Central Mediterranean Basin sites are located to the south of France and along the Italian coast line. Eastern Mediterranean Basin sites are to the east of Italy. Paratethys sites are located where the Paratethys Sea used to be, in what is now mainland Europe, in countries such as Austria, Hungary and Romania.

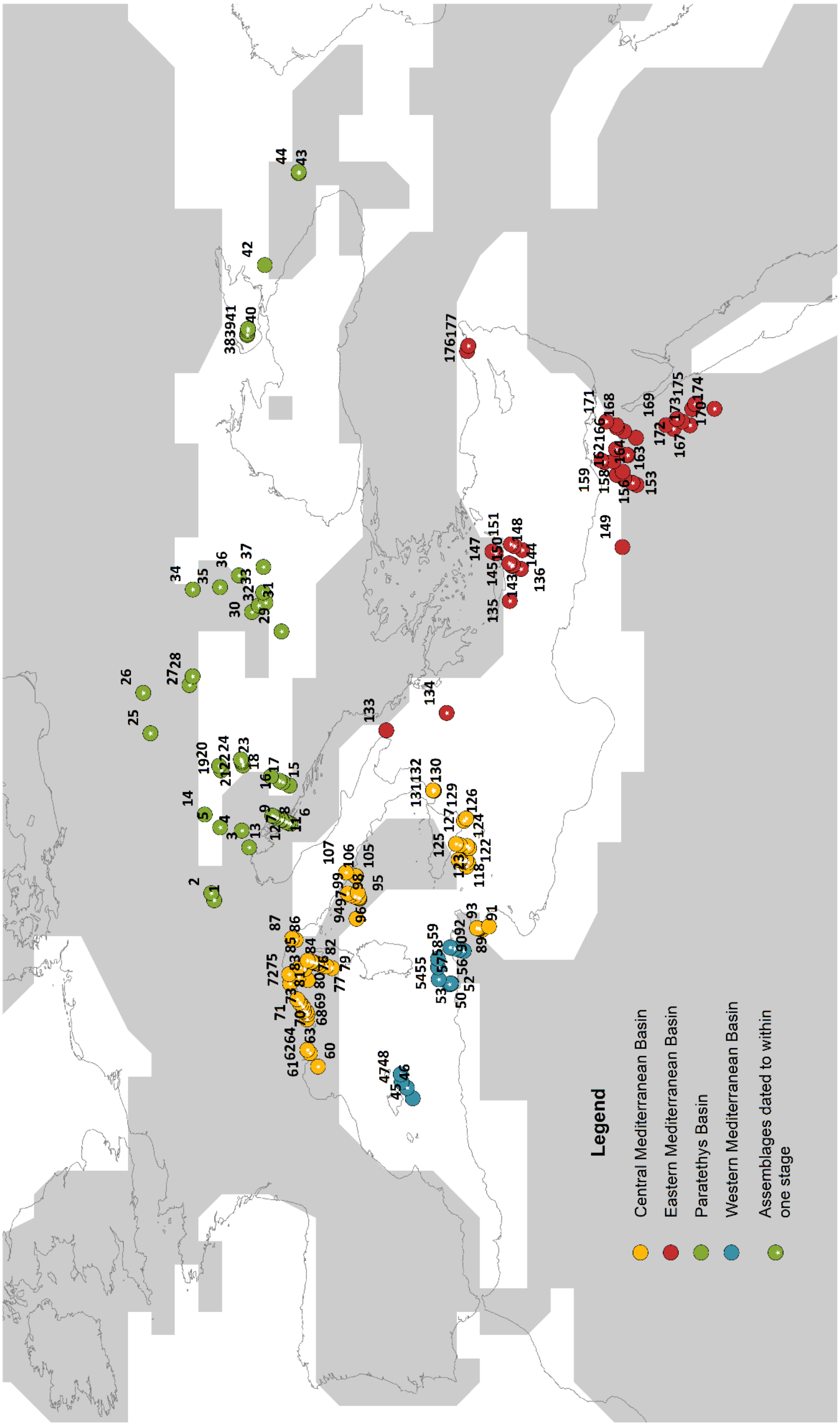
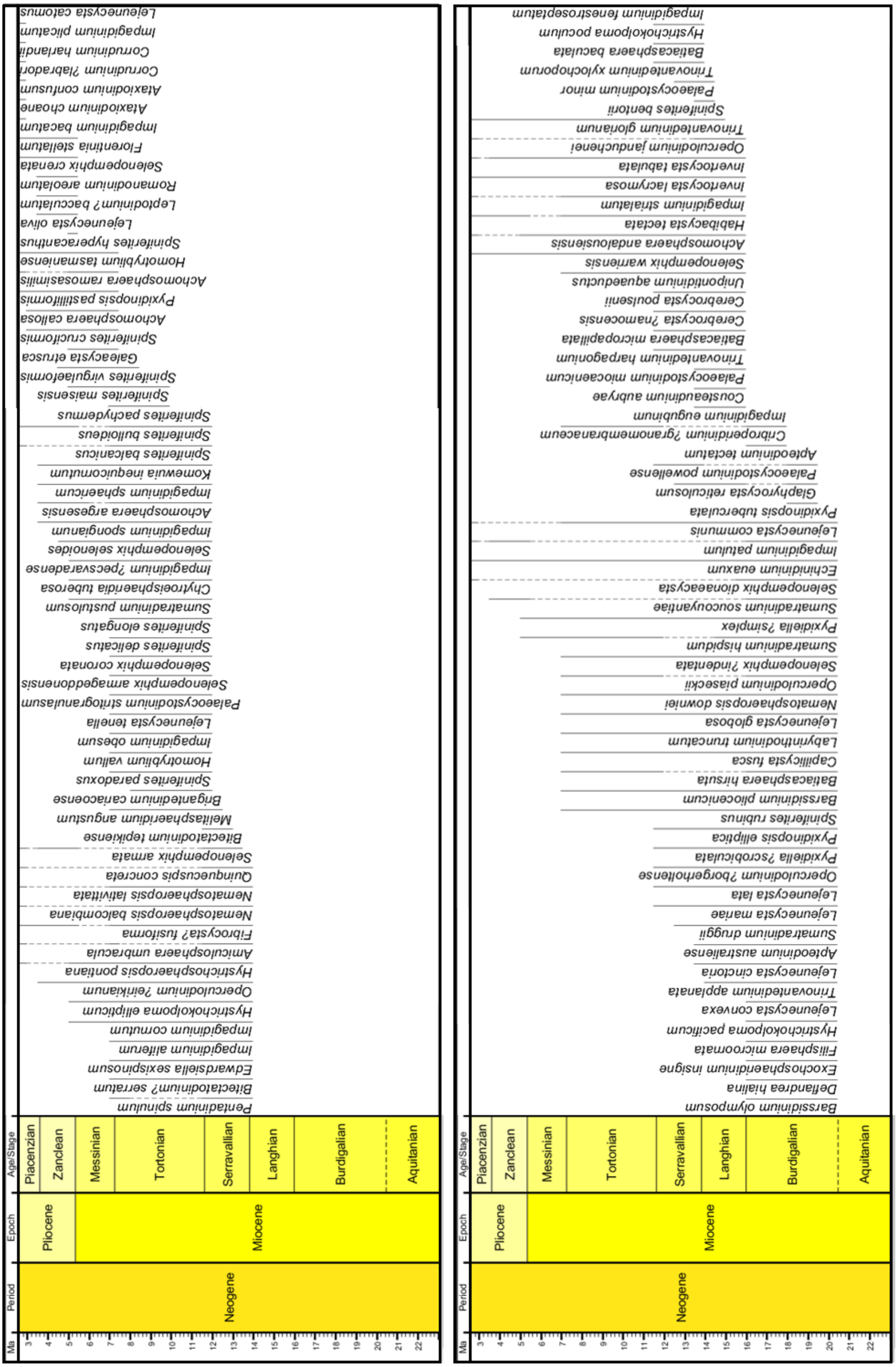


Figure 3-8: Location map of the assemblages used. Points with white stars indicate the assemblages dated to within one stage (the one stage method, see Appendix E). All of the data are used in the two stage dating method. References of the original publications for each site can be found in Appendix C. Rotated data (the palaeo latitudes and longitudes) are assigned according to palaeo rotation codes (Markwick et al., 2000) and the palaeogeography of the late Miocene is represented by grey shading.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Pliocene
Miocene
Age/Stage
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Zanclean
Messinian
Tortonian
Serravallian
Langhian
Burdigalian
Aquitanian
Pentadinium spinulum
Bitectatodinium? serratum
Edwardsiella sexispinosum
Impagidinium aliferum
Impagidinium cornutum
Hystrichokolpoma ellipticum
Operculodinium ?eirikianum
Hystrichosphaeropsis pontiana
Amiculosphaera umbracula
Fibrocysta? fusiforma
Nematosphaeropsis balcombiana
Nematosphaeropsis lativittata
Quinquecuspis concreta
Selenopemphix armata
Bitectatodinium tepikiense
Melitasphaeridium angustum
Brigantedinium cariacoense
Spiniferites paradoxus
Homotryblium vallum
Impagidinium obesum
Lejeunecysta tenella
Palaeocystodinium stritogranulasum
Selenopemphix armageddonensis
Selenopemphix coronata
Spiniferites delicatus
Spiniferites elongatus
Sumatradinium pustulosum
Chytroeisphaeridia tuberosa
Impagidinium ?pecsvaradense
Selenopemphix selenoides
Impagidinium spongianum
Achomosphaera argesensis
Impagidinium sphaericum
Komewuia inequicornutum
Spiniferites balcanicus
Spiniferites bulloideus
Spiniferites pachydermus
Spiniferites maisensis
Spiniferites virgulaeformis
Galeacysta etrusca
Spiniferites cruciformis
Achomosphaera callosa
Pyxidinopsis pastilliformis
Achomosphaera ramosasimilis
Homotryblium tasmaniense
Spiniferites hyperacanthus
Lejeunecysta oliva
Leptodinium? bacculatum
Romanodinium areolatum
Selenopemphix crenata
Florentinia stellatum
Impagidinium bacatum
Ataxiodinium choane
Ataxiodinium confusum
Corrudinium ?labradori
Corrudinium harlandii
Impagidinium plicatum
Lejeunecysta catomus
Barssidinium olymposum
Deflandrea hialina
Exochosphaeridinium insigne
Filisphaera microornata
Hystrichokolpoma pacificum
Lejeunecysta convexa
Trinovantedinium applanata
Lejeunecysta cinctoria
Apteodinium australiense
Sumatradinium druggii
Lejeunecysta mariae
Lejeunecysta lata
Operculodinium ?borgerholtense
Pyxidiella ?scrobiculata
Pyxidinopsis elliptica
Spiniferites rubinus
Barssidinium pliocenicum
Batiacasphaera hirsuta
Capillicysta fusca
Labyrinthodinium truncatum
Lejeunecysta globosa
Nematosphaeropsis downiei
Operculodinium piaseckii
Selenopemphix ?indentata
Sumatradinium hispidum
Pyxidiella ?simplex
Sumatradinium soucouyantiae
Selenopemphix dionaeacysta
Echinidinium euaxum
Impagidinium patulum
Lejeunecysta communis
Pyxidinopsis tuberculata
Glaphyrocysta reticulosum
Palaeocystodinium powellense
Apteodinium tectatum
Cribroperidinium ?granomembranaceum
Impagidinium eugubinum
Cousteaudinium aubryae
Palaeocystodinium miocaenicum
Trinovantedinium harpagonium
Batiacasphaera micropapillata
Cerebrocysta ?namocensis
Cerebrocysta poulsenii
Unipontidinium aquaeductus
Selenopemphix warriensis
Achomosphaera andalousiensis
Habibacysta tectata
Impagidinium strialatum
Invertocysta lacrymosa
Invertocysta tabulata
Operculodinium janduchenei
Trinovantedinium glorianum
Spiniferites bentorii
Palaeocystodinium minor
Trinovantedinium xylochoporum
Batiacasphaera baculata
Hystrichokolpoma poculum
Impagidinium fenestroseptatum

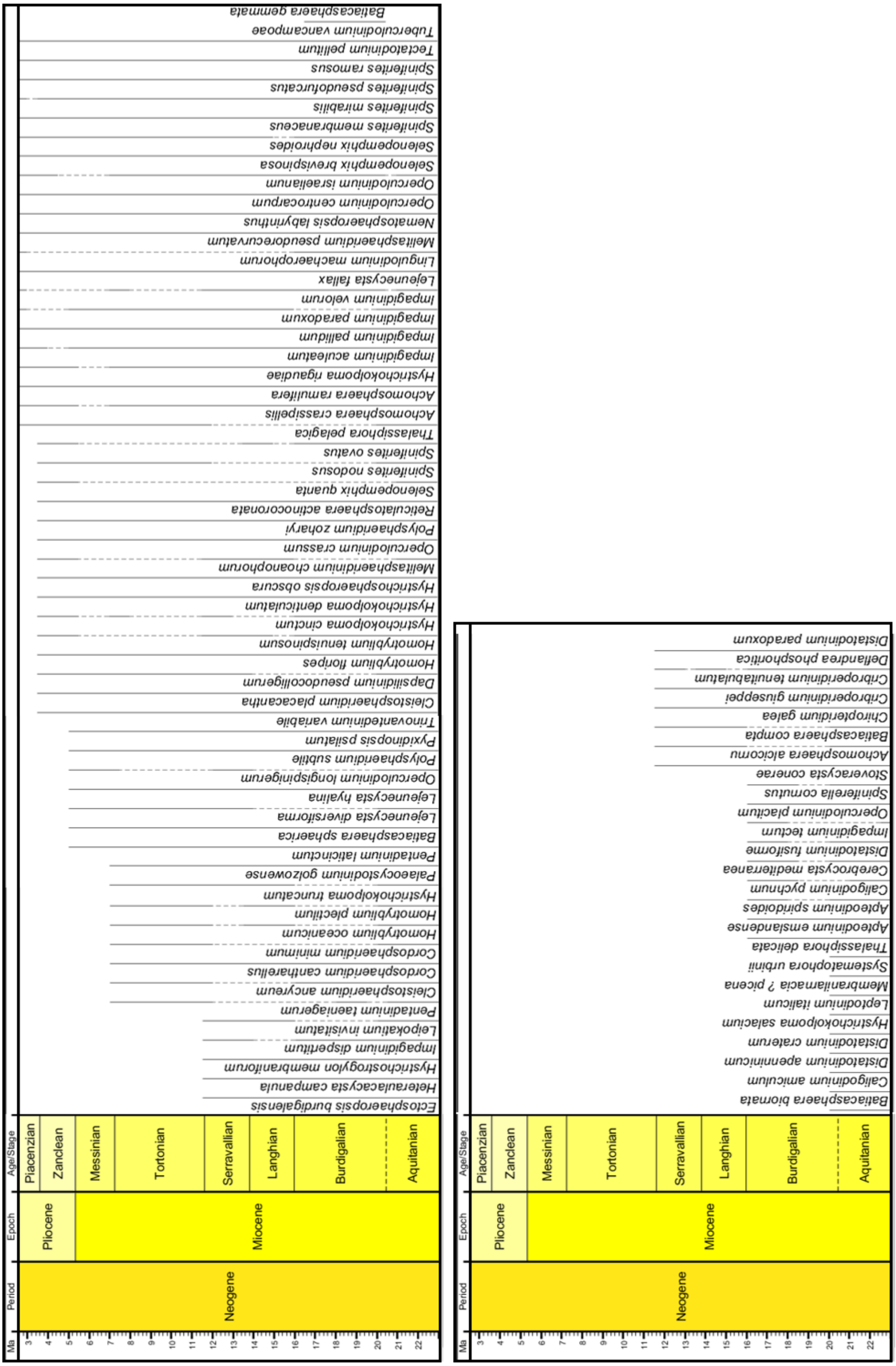


Figure 3-9: Range chart of the species used in this study. The first and last appearances are those that are provided from TOPIS for the Mediterranean. Dashed lines represent times when the species were not present in the Mediterranean literature within TOPIS for the Mediterranean. They may have locally gone extinct, but their reappearance in the younger stages suggests they survived elsewhere and migrated back into the region.

Using the 0.5 Myr time bin method means that the boundary between some of the stages runs through a time bin. These time bins have vastly greater diversities than the time bins either side because some authors date assemblages to within a stage. This means that the data within time bins spanning multiple stages have to be smoothed to get a more accurate understanding of the diversity. Smoothing is achieved by finding the diversity of the time bin before and after the boundary and dividing by the proportion of the 0.5 Myr that the boundary goes through (Figure 3.10). The diversity is not necessarily an integer because of this calculation (Figure 3.10).

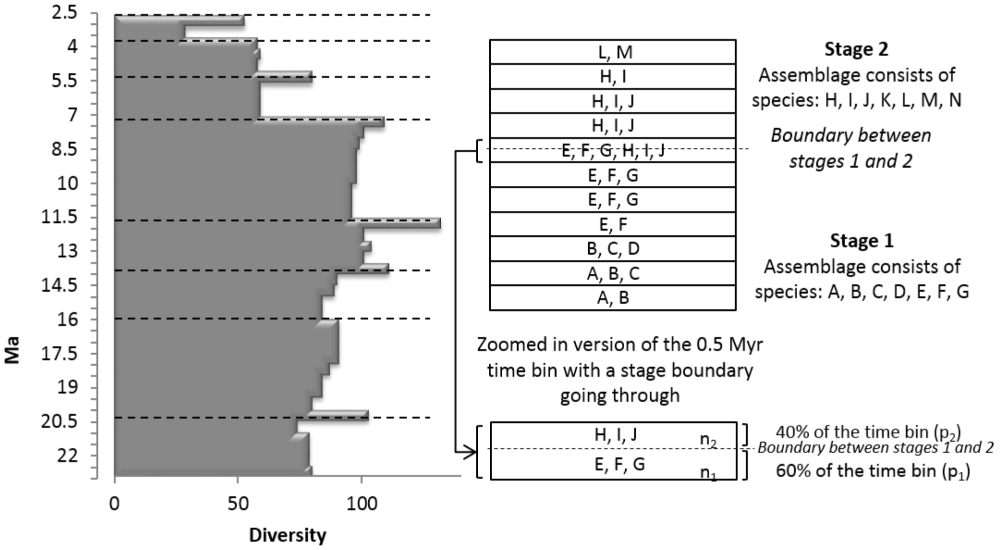


Figure 3-10: Example of how the smoothing of the diversity curves was carried out on the 0.5 Myr time bins with stage boundaries running through them. The smoothing was achieved by counting the number of species in the time bin both below (n_1) and above (n_2) the boundary. The proportion of the 0.5 Myr time bin below (p_1) and above (p_2) was also determined. Then the following calculation was used: smoothed diversity = ($n_1 * p_1$) + ($n_2 * p_2$).

This methodology was repeated for all the assemblages that had age ranges spanning two or fewer stages. The same 0.5 Myr time bin method was also used for calculating the number of publications to identify any potential biases. For example, could a higher diversity be related to a higher number of publications? To answer this question, the coefficient of determination (R^2) was calculated for the correlation between the number of species and the number of publications in each 0.5 Myr time bin; in this case R^2 is a measure of the dependence of the number of species in the database on the number of publications and so can be used to check for biases.

3.6.2.2 Quantifying change over time and space - Statistics

Statistical tools, including non-metric MultiDimensional Scaling (MDS) and ANalysis Of SIMilarity (ANOSIM), were used to quantify the amount of change in dinoflagellate cyst assemblages that took place through time and space. They were used to understand where/when the assemblages differed in order to identify the cause of the changes. To carry out these analyses on the Mediterranean data extracted from TOPIS, a presence and absence matrix was constructed. This involved noting which species were or were not present for every assemblage. Once this was complete, each assemblage was assigned a variety of factors such as age or location. Then, to avoid outliers skewing the results, any sites that contained only one species or any species that only appeared in one site were removed. Four age factors were assigned: the early, middle and late Miocene and the Pliocene. There were four assemblages that did not fit into any of these categories because their age range spanned two of the sub-epochs and so they were not included in the analysis. Factors used for the location were: the Western, Central and Eastern Mediterranean basins and the Paratethys Basin.

The presence and absence matrix was imported into the multivariate statistical software package PRIMER V6 (Plymouth Routines In Multivariate Ecological Research version six; Clarke and Gorley, 2006) and MDS and ANOSIM analyses were used to identify the possible influences on the assemblages with 999 permutations for both. The two factors used were the age and location of the assemblages (see below for a full description of MDS and ANOSIM). When using the age (sub-epochs) as the factor (i.e. testing if the species composition of the assemblages changed through time), species that had an age range spanning the entire Neogene were removed from the analysis because they are uninformative for temporal change analysis and interfere with temporal signals. However, when using the basin as the factor (i.e. testing if the species composition of the assemblages changed over a geographical region), the Neogene long ranging species were kept in the analysis because they were not necessarily present in every basin throughout the whole Neogene.

3.6.2.2.1 Non-metric MultiDimensional Scaling (MDS)

Non-metric MultiDimensional Scaling graphs, were made using the software PRIMER 6 with the Jaccard similarity coefficient (Clarke and Gorley, 2006), which represents the number of species shared by two assemblages divided by the total number of species for both assemblages. Thus, the similarity of species between different assemblages can be quantified; a useful analysis for presence and absence data (Magurran, 2004). Each point on an MDS plot represents a different assemblage and the colours of the points denote the factor; in this case, what age or basin the assemblage belongs to. The closer the points are together, the higher the similarity of the assemblages, i.e. the higher the number of shared species.

Non-metric MultiDimensional Scaling is an ordination technique, and differs to most other methods such as: principal component analysis, and correspondence analyses. One of the differences is that in MDS, data are fitted to a small number of axes that are chosen prior to the analysis and there are no hidden axes. Another difference is that unlike principle component analysis, where axis one explains the greatest amount of variance and axis two explains the second greatest, MDS is not an eigenvalue-eigenvector technique and so the data can be rotated, inverted or re-centred. However, the main difference is that MDS results do not have a unique solution. This is because it is a numerical technique that stops computation once it has found an acceptable solution or after a pre-specified number of attempts (Clarke and Warwick, 1994).

A ‘stress value’ is calculated during MDS analyses. Since there is no single answer for MDS plots, the acceptable solution (automatically computed) is reached when the stress value is at its lowest. The stress value represents how faithfully the relationship between the different samples (multidimensional relationships) is portrayed in a two dimensional space (Zuschin and Stanton, 2002). According to Clarke and Warwick (1994), if the stress value is less than 0.05 there is an excellent representation of the data with no prospect of misinterpretation. Less than 0.1 corresponds to a good ordination, less than 0.2 gives a potentially useful interpretation. However, for values close to 0.2 or above, alternative techniques should also be used to complete the analysis. More specifically, values between 0.2 and 0.3 should be treated with scepticism and if values are greater than 0.3, the points could have been placed at random.

3.6.2.2.2 ANalysis Of SIMilarity (ANOSIM)

Analysis of Similarity is also carried out using PRIMER (Clarke and Gorley, 2006). This is a relatively new technique that is being used increasingly for ecological studies (Clarke and Green, 1988; Clarke et al., 2008). It provides a way to statistically test if there is a significant difference between two or more factors (e.g. age or location) and gives the probability of any clustering (identified by MDS analysis) occurring due to chance.

To visualise the results, ANOSIM graphs consist of a histogram with a vertical line representing the global R value, which is a comparative measure for the degree of separation for the factor used (Clarke and Warwick, 1994). Values to look for when interpreting ANOSIM graphs are the global R value, the P value (the significance value) and whether the global R value overlaps with the histogram, i.e. do any of the 999 permutations not exceed the global R value. The higher the global R number, and the further it is away from the histogram, the greater the influence of the factor (e.g. age/basin). Global R values generally lie between zero and one. Negative values can occur, but are unusual. If global R values are high (i.e. close to one), and lie outside of the histogram (outside of the range of the 999 permutations), it is indicative of complete separation of groups. However, if they are close to zero, and the value falls within the histogram (within the 999 permutations), it implies little or no segregation between the factors, and assemblages are similar regardless of the factor used.

As an example of the statistical analyses used in this chapter, data have been fabricated to show the differences between data that show a high degree of separation (Figure 3.11a) and a low degree of separation (Figure 3.11b). A high degree of separation implies that the species found in the assemblages from one sub-epoch are very different to those found in a different sub-epoch (Figure 3.11a). A low degree of separation indicates that the species in assemblages from one stage are also found in the other sub-epochs (Figure 3.11b).

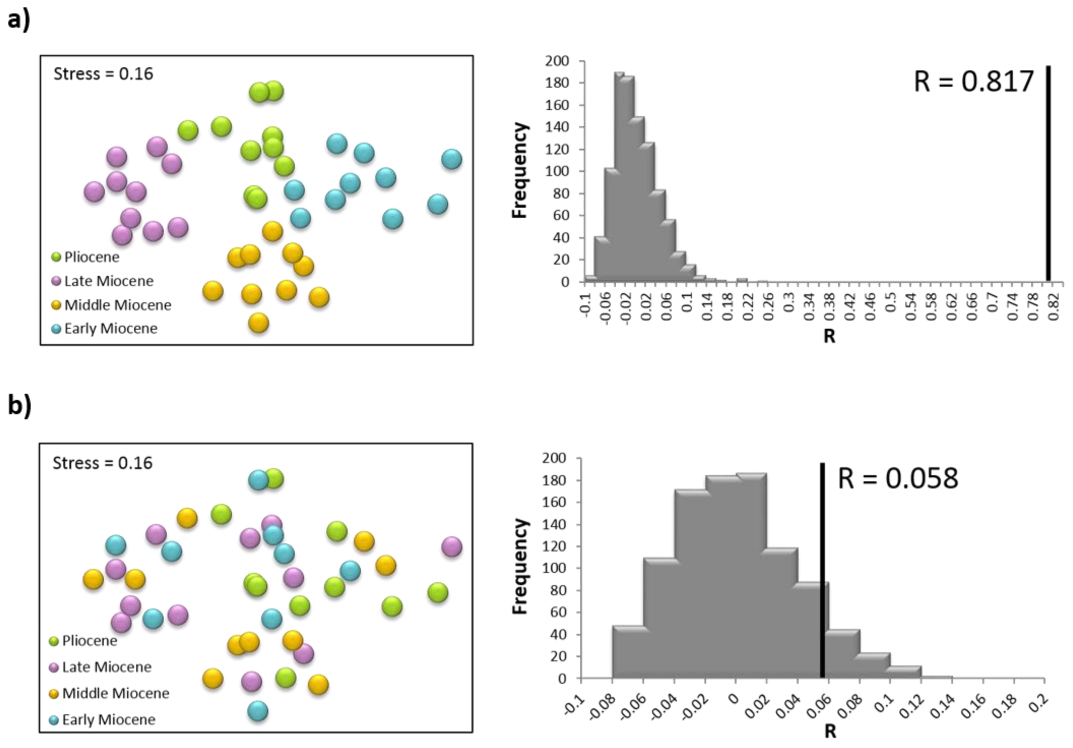


Figure 3-11: Examples of (a) high and (b) low degree of separation of the factors (age). MDS graphs are on the left and the graphs representing the ANOSIM are on the right.

3.6.3 Results

Data from the Mediterranean are extracted from the global analysis (Figure 3.4) and are presented below (Figure 3.12). Data are present at all latitudes but the Aquitanian to Serravallian have no data between 30 and 35° N. Records containing no CWS are present in all latitudes and where CWS are present, the percentage is never higher than 30% (Serravallian; 25-30° N). The percentage of CWS varies insignificantly, suggesting temperature was not the main control on the distribution and assemblage composition of dinoflagellate cysts during the Neogene in the Mediterranea/Paratethys. The following sections investigate other potential causes of the changes seen to the assemblage composition and diversity of dinoflagellate cysts.

The Western Mediterranean Basin has the fewest sites (8 sites, 15 assemblages) followed by the Eastern Mediterranean Basin (20 sites, 46 assemblages) and then the Paratethys Basin (27 sites and 44 assemblages), the Central Mediterranean Basin has the most (37 sites and 83 assemblages). This section is split into two parts. The first describes the changes to the diversity of the combined Mediterranean and Paratethys basins, as well as the Mediterranean basins separated out, and the second describes the differences/similarities between the assemblages through time and space. As mentioned in the methods (Section 3.6.2) all of the results described and interpreted in this chapter used the two stage method. For descriptions and comparisons between the one and two stage methods see Appendix E.

3.6.3.1 Diversity

3.6.3.1.1 All Mediterranean Basins

The Neogene started with 95 species (23–22.5 Ma; Figure 3.13a). This decreased to 91 species at the end of the Aquitanian between 21 and 21.5 Ma. The diversity in the Burdigalian (19 to 16 Ma) varied between 111 and 113 species and was also steady in the Langhian, increasing from 107 species (16–15.5 Ma) to 109 species (14.5–14 Ma). The number of species in the Serravallian peaked at 118 between 13 and 12.5 Ma. Diversity in the Tortonian was steady, increasing from 116 to 120 species, but in the Messinian it decreased to 92 species. It decreased further in the Zanclean where between 54 and 61 species were present. The two time bins in the Piacenzian, 3.5–3 Ma and 3–2.5 Ma, had 31 and 56 species respectively.

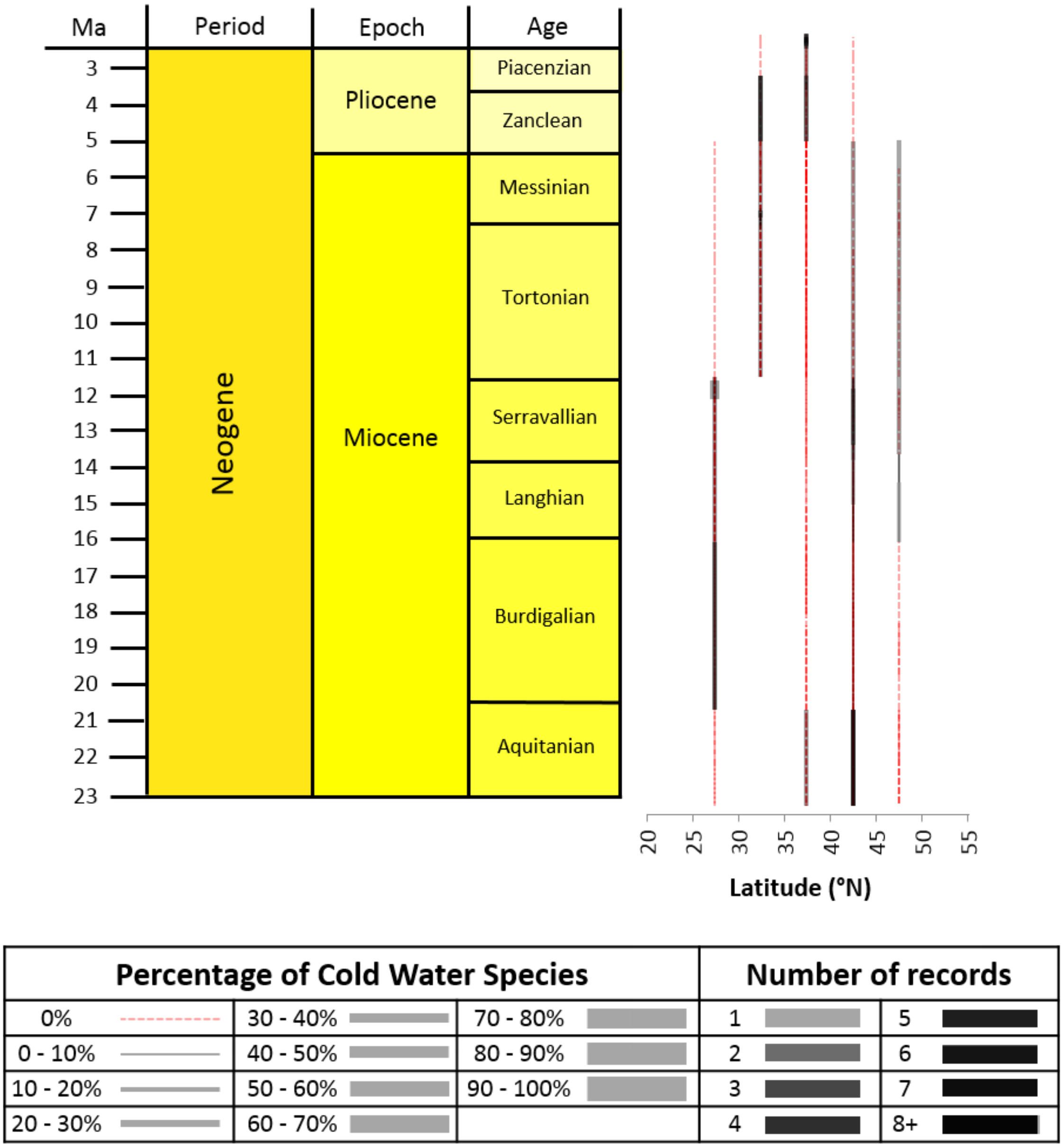


Figure 3-12: Percentage of Cold Water Species (CWS) relative to warm water species for each assemblage in the Mediterranean. For a full description see Section 3.2. Red dashed lines represent records with no CWS present. The thicker the grey/black line, the higher the percentage of CWS and the darker the line the more records there are.

3.6.3.1.2 Central Mediterranean Basin

At the start of the Neogene the diversity for the Central Mediterranean Basin was 74 species (Figure 3.13b). The diversity continued to have 74 species until 20.5 Ma. It dropped to 60.2 species between 20.5 and 20 Ma then remained between 73 and 78 species from 20 to 14 Ma. The diversity peaked at 95 species between 13.5 and 13 Ma. The diversity decreased from 64 species (between 7.5 and 7 Ma) to 52 species (between 7 and 5.5 Ma) and then again to 28 species until 3.5–3 Ma, before increasing to 56 species in the youngest time bin (3–2.5 Ma).

3.6.3.1.3 Eastern Mediterranean Basin

The diversity at the start of the Neogene, in the Eastern Mediterranean Basin (Figure 3.13c), was 43 species, and gradually increased to 56 species between 16.5 and 16 Ma. There were 52 species present between 16 and 14 Ma, the diversity then increased to a peak of 63 species between 12.5 and 12 Ma and then decreased to 46 species from 11.5 to 8 Ma. The diversity then increased to 57 species between 8 and 7 Ma. There was a large decrease in the number of species from 50 (7–5.5 Ma) to 39 species (5.5–4 Ma), and a further drop of 28 species from 32 species between 4 and 3.5 Ma to 4 species in the Piacenzian.

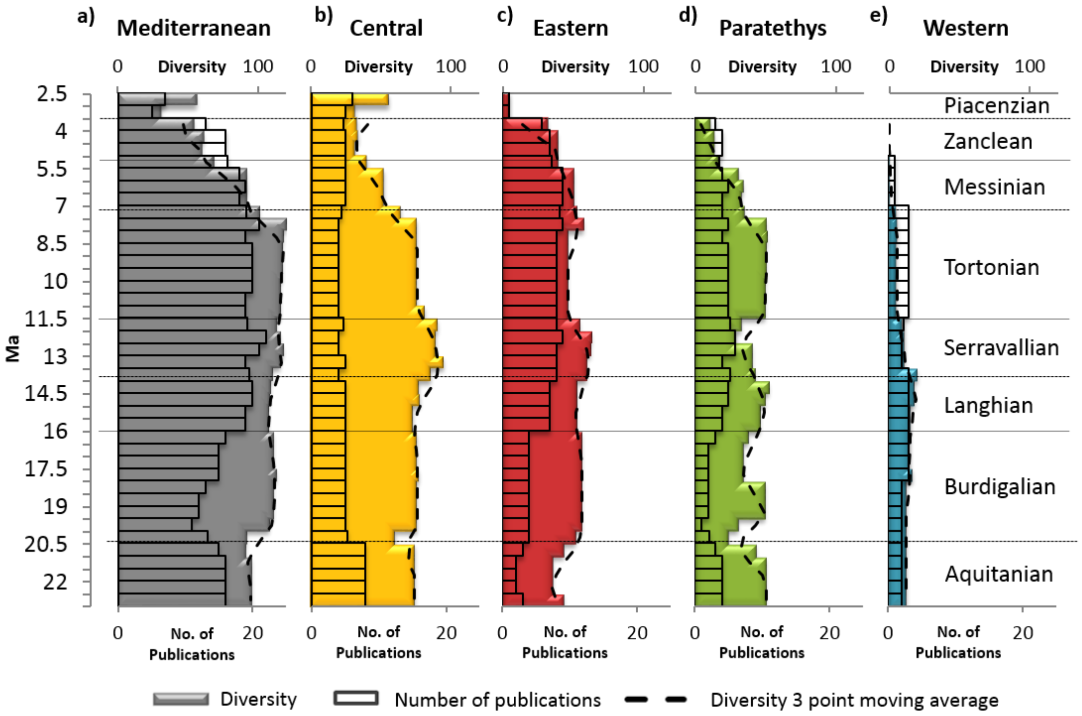


Figure 3-13: Diversity curve for (a) the whole Mediterranean, (b) the Central Mediterranean Basin, (c) the Eastern Mediterranean Basin, (d) the Paratethys Basin and (e) the Western Mediterranean Basin. The three point running mean for the diversity is represented by the dashed lines. The number of publications for each 0.5 Myr time bin is indicated by black outlined bars.

3.6.3.1.4 Paratethys Basin

In the Paratethys in the Aquitanian, 50 species were present between 23 and 21 Ma, which decreased to 22 between 20.5 and 20 Ma (Figure 3.13d). A second peak occurred between 19.5 and 18 Ma with 49 species, although the number of species then decreased to 34 between 18 and 16.5 Ma. During the Langhian the diversity increased from 46 to 52, but during the Serravallian it decreased to 28 species (12.5 to 12 Ma). Diversity during the Tortonian remained steady between 49 and 51 species, but in the Messinian it halved from 32 at the start of the stage, to just 16 species at the end. It decreased further in the Zanclean from 13 to 10 species, and no species were present in the Piacenzian.

3.6.3.1.5 Western Mediterranean Basin

The Western Mediterranean Basin had the lowest maximum diversity (20 species) of all the basins. The highest diversity took place between 14 and 13.5 Ma (Figure 3.13e). Prior to this, there were 12 species from 23 to 18 Ma. After the peak, the diversity nearly halved to 11 species for the 13.5–13 Ma time bin and halved again to five species from 11.5 to 8.5 Ma. It then decreased to just one species until the 5.5–5 Ma time bin, after which no species were present.

3.6.3.1.6 Extinctions/Originations

Absolute Values

The number of species that went extinct in the Neogene generally increased through the Neogene, whereas the number of species originating in each time bin generally decreased (Figure 3.14a). Generally, the largest origination and extinction events took place at the stage boundaries. Whilst this may be an artefact of the way that many of the assemblages are dated, stage boundaries are often placed at ‘geologically interesting’ points in time, which are easily recognisable, so it is plausible that the origination and extinction events did in fact occur at the boundaries.

At the Aquitanian to Burdigalian boundary 26 species appeared and 24 appeared at the Burdigalian to Langhian boundary. There were 23 species that appeared at the Serravallian to Tortonian boundary but after this the largest number of species that appeared was at the Messinian to Zanclean boundary (eight species). The number of species that went extinct shows the opposite pattern. For example at the Aquitanian-Burdigalian boundary just one species disappeared from the Mediterranean. A similarly low value of two species disappeared at the Langhian to Serravallian boundary. However, at the Serravallian to Tortonian boundary 31 species disappeared from the Mediterranean and a further 23 species disappeared at the Tortonian-Messinian boundary followed by 33 species at the Messinian-Zanclean boundary.

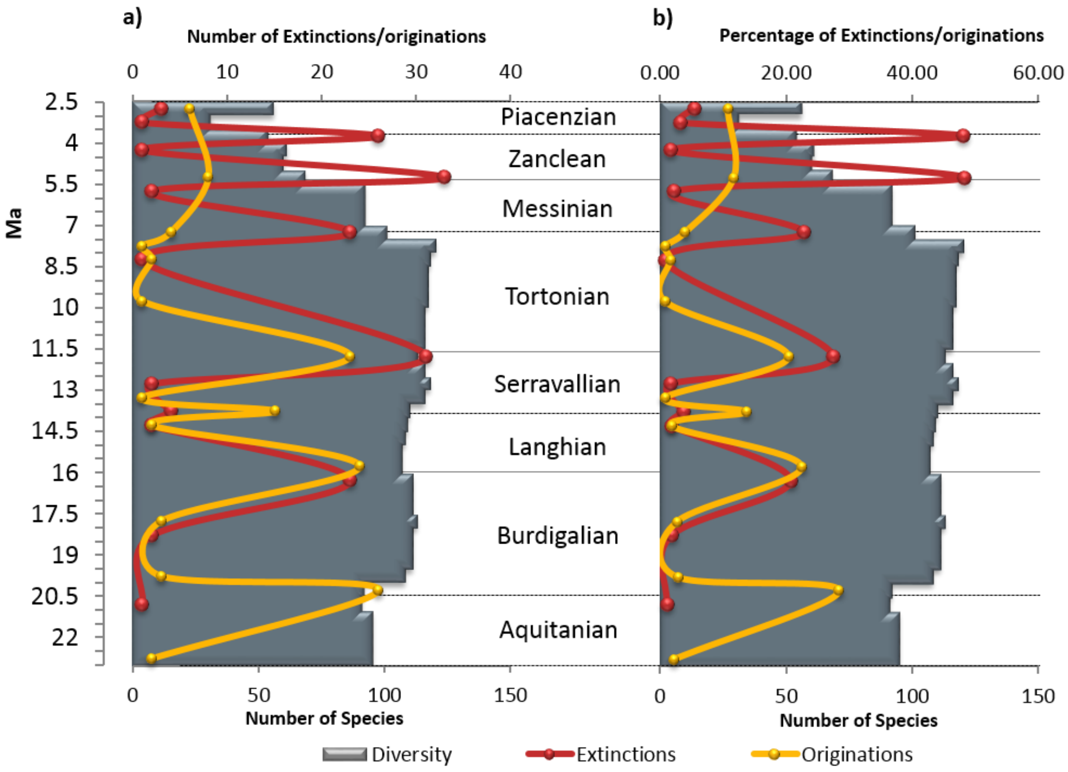


Figure 3-14: The diversity (grey) and (a) the number and (b) the percentage of species that disappeared (red) or appeared (yellow) in each 0.5 Myr time bin.

Relative Values

When looking at relative values, i.e. the percentage of species that either went extinct or originated in each time bin compared to the diversity, similar patterns are seen to the absolute number of species that went extinct or originated. Percentages of originations were higher in the older half of the Neogene and the percentages of extinctions were higher in the younger half (Figure 3.14b).

The highest percentage of species originating took place at the Aquitanian-Burdigalian boundary (28.3%). The percentage then decreased at each stage boundary to 13.6% at the Langhian-Serravallian boundary. At the Serravallian-Tortonian boundary the value increased to 20.3% but stayed low throughout the rest of the Neogene, peaking at 11.7% at the Messinian-Zanclean boundary. The percent of species going extinct at the Aquitanian-Burdigalian boundary was just 1.1%. This increased to 20.7% at the Burdigalian-Langhian boundary and again to 27.4% and the Serravallian-Tortonian boundary. The highest percentage of extinctions took place at the Messinian-Zanclean boundary (48.3%).

3.6.3.2 Quantifying assemblage change through the Neogene

3.6.3.2.1 The entire Neogene

Non-metric MultiDimensional Scaling and ANOSIM analyses of assemblages for the whole Neogene have been run with the age of the assemblage (sub-epoch) as the factor (Figure 3.15). The stress value is low (0.13), suggesting the data are well represented by the MDS graph (see Section 3.6.2.2.1). There is significant overlap of the different factors, especially in the early and middle Miocene, but the sub-epochs do tend to cluster (Figure 3.15). The late Miocene has the least similar assemblages, with the largest spread of points. The assemblages of the Pliocene, with the exception of three, plot closest together on the MDS graphs, suggesting that they share more common species than assemblages in the other stages. In the temporal domain, there is the least overlap of assemblages between the early Miocene and the Pliocene, suggesting that there are few shared species between these sub-epochs.

The fact that the assemblages from the different sub-epochs plot in clusters on the MDS implies that age is having a significant effect on what species are found in the assemblage, i.e. each sub-epoch had distinct assemblages. This is also confirmed by the ANOSIM for the full Neogene, which has global R values of 0.299 ($P = 0.1$), and none of the 999 permutations exceed the global R value (Figure 3.15).

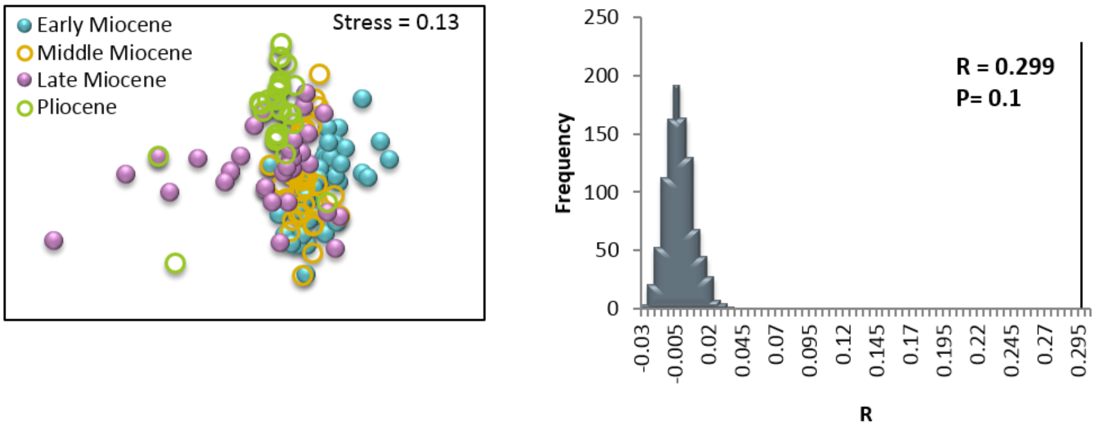


Figure 3-15: MDS (left) and ANOSIM (right) analyses of data distinguished by sub-epochs (early Miocene, middle Miocene, late Miocene and Pliocene).

3.6.3.2.2 Sub-epoch comparison

The early to middle Miocene has a global R value of 0.143 (P=0.1) and the stress value in the MDS is 0.17 (Figure 3.16a). The species structure of the middle Miocene is similar to many of the early Miocene assemblages, however there are additional early Miocene assemblages that plot separately, indicating that they do not share species. The middle and late Miocene sub-epochs also have some overlapping of their assemblages, representing assemblages compiled of similar species. However, the late Miocene assemblages are more spread out meaning the species composition is more varied (Figure 3.16b). The stress value is 0.13 and the global R value is 0.147 and none of the 999 permutations exceed the global R value. The global R value for the late Miocene and Pliocene is also outside of the histogram, but is higher than previous values (R=0.271, P = 0.1) and the MDS plot has a lower stress of 0.11 (Figure 3.16c). This implies that the Pliocene assemblages are more different to the late Miocene assemblages then the late Miocene assemblages are to the middle Miocene. The Pliocene assemblages are generally concentrated in one area, but four of them plot separately to the main concentration. This means that the assemblages in the Pliocene (with the exception of four) are all very similar.

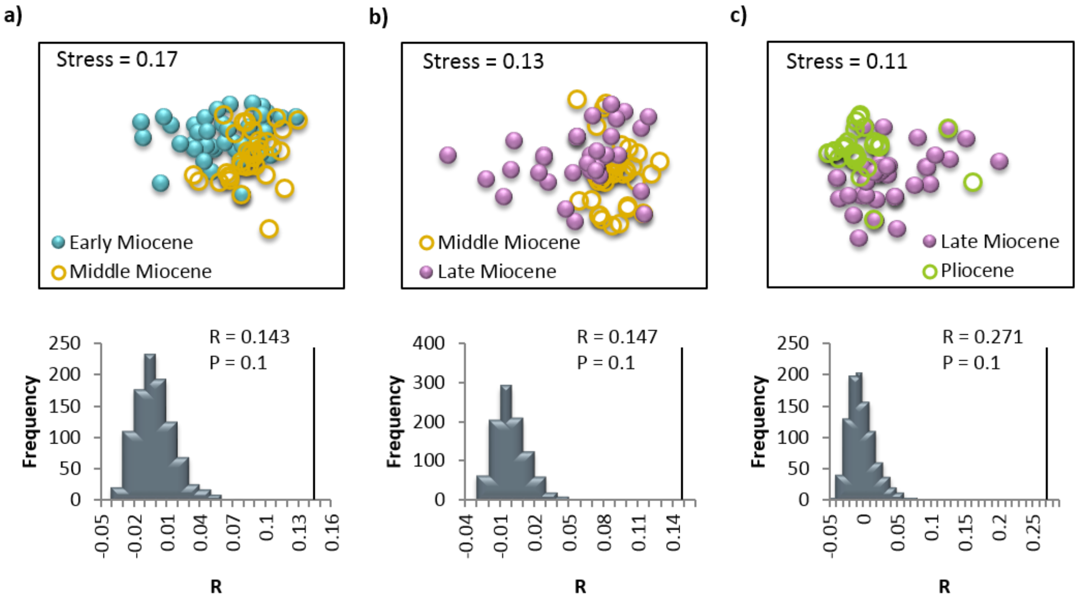


Figure 3-16: MDS and ANOSIM analyses using the two stage method, with two sub-epochs shown in each panel to indicate where the largest changes in assemblage took place. (a) Early to middle Miocene, (b) middle to late Miocene and (c) late Miocene to Pliocene.

3.6.3.3 Changes in assemblages over the Mediterranean and Paratethys basins

To understand how similar the assemblages from different basins are, the assemblages from each Mediterranean and Paratethys basin were analysed for the entire Neogene and for each subepoch using MDS and ANOSIM statistics.

3.6.3.3.1 The entire Neogene

There is little clustering by basin for the whole Neogene (Figure 3.17). The assemblages of the Western Mediterranean Basin cluster together more so than for the other basins, but there are too few sites to make any substantial conclusions. The assemblages of the Central and Eastern Mediterranean basins in particular occupy the same space on the MDS graph, demonstrating that the same species are common to both basins. The Paratethys Basin assemblages also overlap with the other basins. The stress value for the MDS is 0.15. The global R value provided by the ANOSIM is low at 0.164, P=0.01, and none of the 999 permutations exceed this, signifying that the basin does have a significant impact on how the assemblages cluster. However, with a smaller global R value than when age was investigated (Figure 3.15), it suggests that species that made up assemblages in the Mediterranean changed more over time than they did over geographical space, suggesting that the

Mediterranean dinoflagellate cyst assemblages were not as geographically distinct as they were in each sub-epoch.

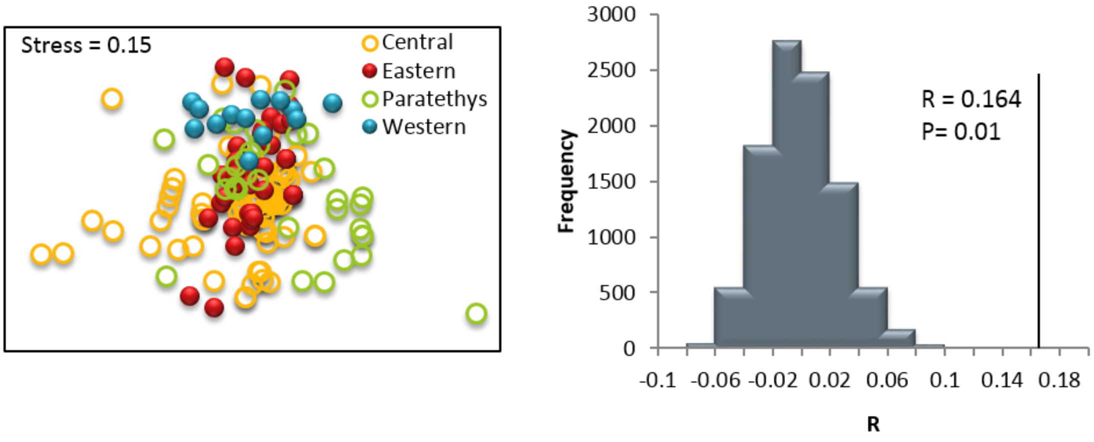


Figure 3-17: MDS (left) and ANOSIM (right) analyses for all the data with basins (Central, Eastern and Western Mediterranean basins and the Paratethys Basin) as the factor.

3.6.3.3.2 Individual sub-epochs – Basins

The location has no significant impact on how the assemblages cluster together for the early Miocene (Figure 3.18a) and so the assemblages are not location specific. This is demonstrated by the assemblages of the different basins overlapping with each other, suggesting similar species are found throughout. It is also shown by the global R value of 0.222, the P value of 0.4, and 3 of the 999 permutations exceeding the global R value. The stress value of 0.14 means that the two dimensional representation faithfully depicts the data (Figure 3.18a).This indicates that location has no significant control on how the assemblages cluster for the early Miocene. In the middle Miocene (Figure 3.18b), the Paratethys Basin assemblages cluster together but all four basins overlap with each other. However, none of the 999 permutations exceed the global R value (0.207; P=0.1), suggesting that the assemblages are geographically distinct in the middle Miocene.

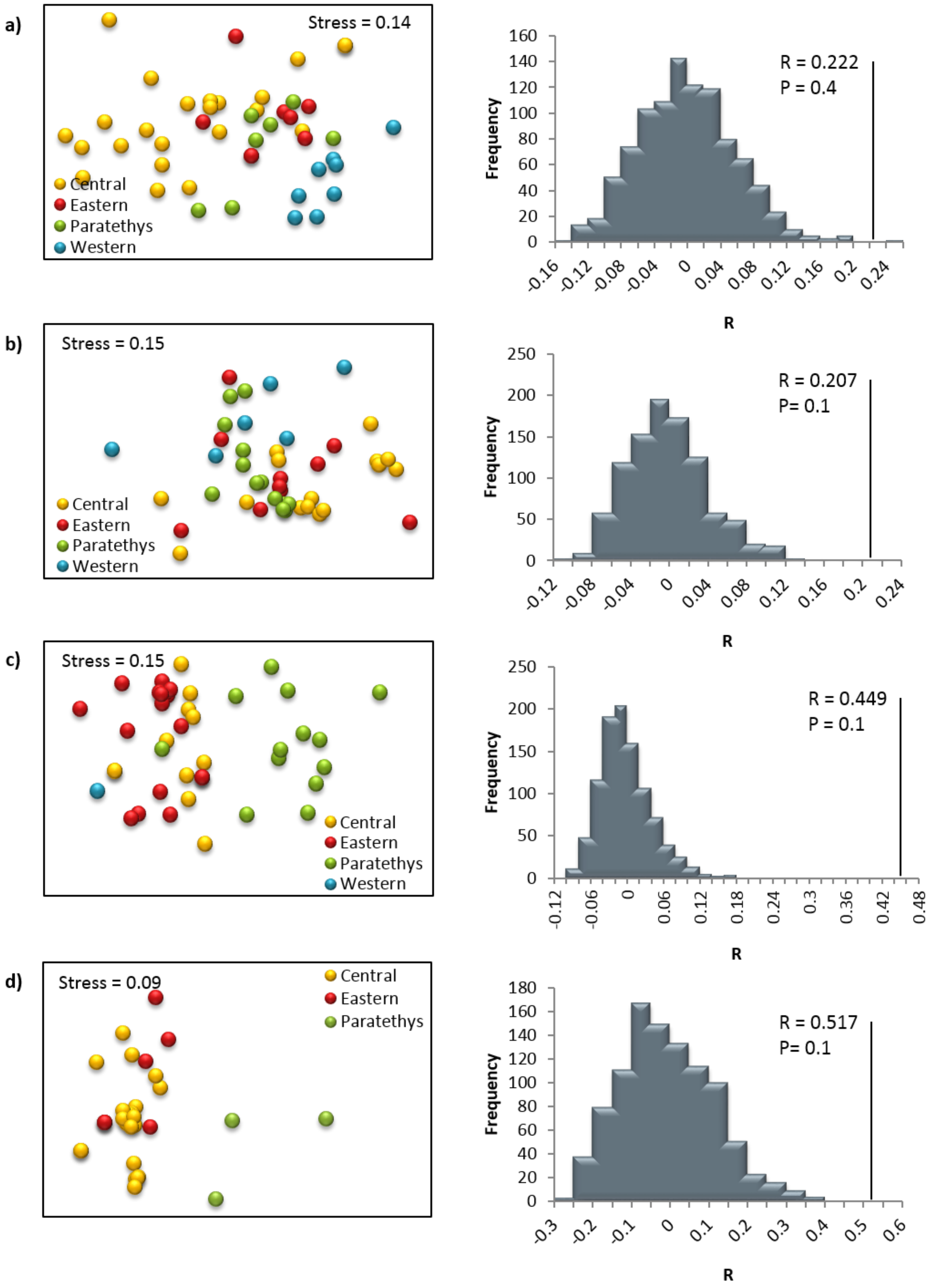


Figure 3-18: MDS and ANOSIM analyses for individual sub-epochs with location as the factor (Central, Eastern and Western Mediterranean basins and the Paratethys Basin). (a) Early Miocene, (b) middle Miocene, (c) late Miocene, (d) Pliocene.

In the late Miocene there is only one assemblage from the Western Mediterranean Basin and the Paratethys Basin assemblages of the late Miocene, with the exception of one, all cluster together away from the other basins. This increase in the influence of location on the assemblage is shown by none of the 999 permutations exceeding the global R value of 0.449 (P = 0.1). In the Pliocene (Figure 3.18d), there are no assemblages from the Western Mediterranean Basin and only three from the Paratethys Basin, which act as outliers to the assemblages of the other basins. The remaining Eastern and Central Mediterranean basins all cluster together. The global R value is high at 0.517 (P=0.1), but only just lies outside of the histogram, suggesting that the location is a significant factor, but not necessarily the most significant.

3.6.4 Discussion

3.6.4.1 Mediterranean diversity

Several global studies of dinoflagellate cyst diversity have been published that span the entire age range of dinoflagellate cysts from the Middle Triassic to the present, for example, Tappan and Loeblich (1972), Bujak and Williams (1979) and more recently MacRae et al. (1996). MacRae et al. (1996) show that the diversity of dinoflagellate cysts peaked in the Cretaceous and then decreased throughout the Paleogene and Neogene and into the present. They also show that dinoflagellate cyst diversity roughly correlates with sea level changes (Figure 1.11) produced by Haq et al. (1987).

Mediterranean diversity does not follow the same pattern as global diversity (Figure 3.20). MacRae et al. (1996) demonstrate that global diversity decreased throughout the Neogene, whereas the Mediterranean data shows a slight increase in the number of species present, peaking in the Langhian and the late Tortonian, before rapidly decreasing in diversity for the remainder of the Neogene (Figures 3.13a). The extinction and origination events in the Mediterranean (Figures 3.14a, b) are also not the same as the global pattern (Figure 3.19). In the Mediterranean, the percentage of extinctions is greatest in the Pliocene and the percentage of originations is greatest in the early and middle Miocene (Figure 3.14a, b). Globally (Figure 3.19; MacRae et al., 1996), the percentage of extinctions is greatest in the late Miocene and the percentage of originations is greatest in the early and late Miocene. This suggests that the alterations, which are seen in the Mediterranean Sea, are caused by a regional effect and not (solely) global changes. Unfortunately Neogene data in MacRae et al. (1996) have a very coarse temporal resolution, with only four data points, making it difficult to accurately compare them to the present study.

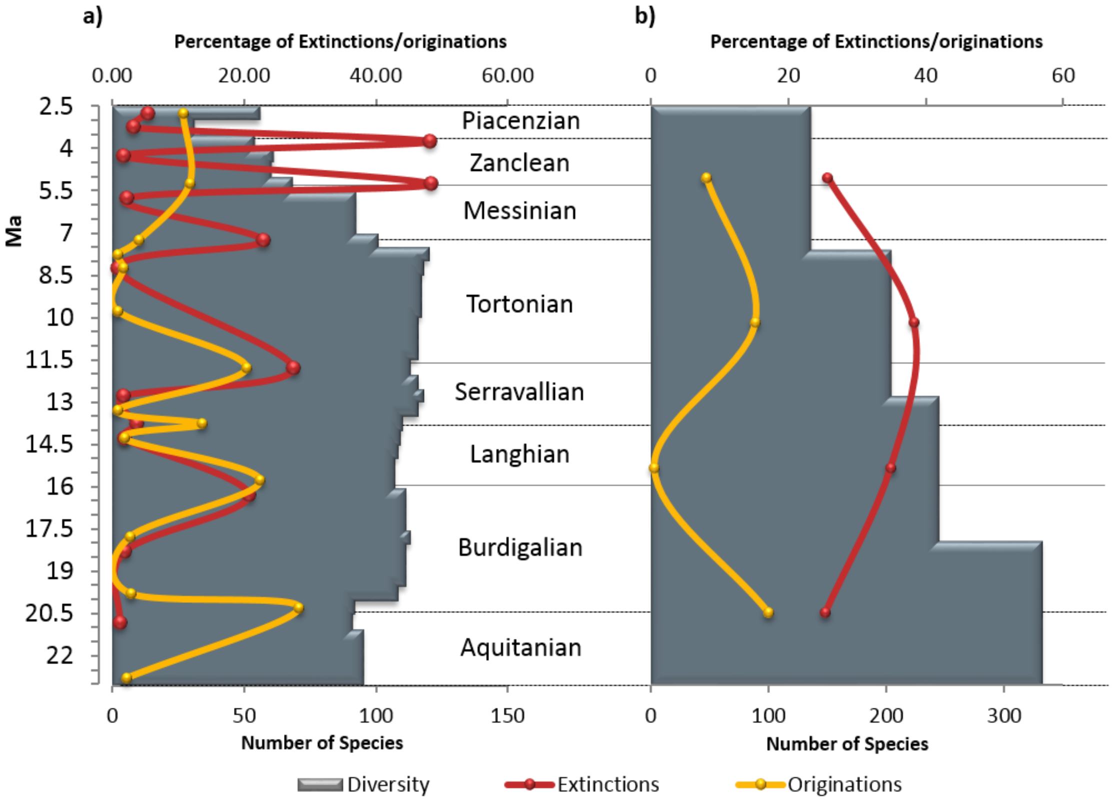


Figure 3-19: Diversity and the percentage of originations/extinctions from (a) the Mediterranean (this study (Figure 3.13a) and (b) global data (of a lower temporal resolution; MacRae et al., 1996).

3.6.4.1.1 The Aquitanian to Tortonian (23.03–7.25 Ma)

Many global-scale environmental changes took place during the early and middle Miocene (Figure 1.3) including the MMCO (Zachos et al., 2001; Böhme, 2003; You et al., 2009) and the MMCT (Flower and Kennett, 1994; Zachos et al., 2001; Shevenell et al., 2004). Events specific to the Mediterranean included: the closure of the Eastern Mediterranean Gateway (Rögl, 1999; Allen and Armstrong, 2008; Hüsing et al., 2009); changes to the gateways connecting the Paratethys and Mediterranean (Rögl, 1997; Harzhauser and Piller, 2007) and two washhouse events, where the hydrological cycle in Europe intensified and brought about several times more precipitation than present (Böhme et al., 2008). All of these events impacted the Mediterranean Sea, bringing about changes in climate, relative sea level and water exchange between the Mediterranean Sea, Paratethys Sea, Atlantic Ocean and Indian Ocean. Bearing this in mind, it is surprising how little variance there was to the dinoflagellate cyst diversity between 23 and 7.5 Ma. For example, the diversity increased by only 22 species over 15.5 My (Figures 3.13a), although short, small scale fluctuations within the general diversity pattern did occur.

Through the Burdigalian there was a small increase in the number of species (Figures 3.13a). This increase in diversity correlates with the rising temperatures that culminated in the MMCO (Zachos et al., 2001; 2008). Diversity increases have been seen in numerous groups during this time, such as gastropods, corals, molluscs and even toothed whales (Bianucci and Landini, 2002; Harzhauser et al., 2003; 2007; Harzhauser and Piller, 2007). The rising temperatures also resulted in raised sea levels (Zachos et al., 2008; Hansen et al., 2013), which reopened the Eastern Mediterranean Gateway, allowing species to migrate into the region, and explains the dinoflagellate cyst diversity increase. The elevated temperature and sea levels may also have provided new habitats and niches for new species to evolve (Harzhauser and Piller, 2007), which agrees with the high percentages of species originating in the early and middle Miocene (Figures 3.14a and b).

However, after the MMCO, when global temperatures cooled during the MMCT, these same authors found that diversity decreased once more. The diversity of the Paratethys Basin and the Western Mediterranean Basin also decreased during the Serravallian (Figures 3.13d and e); however, the diversity of the Central and Eastern basins increased (Figures 3.13b and c). The increase of dinoflagellate cyst species in the Langhian and Serravallian cannot be explained by climate changes and there must be a different controlling factor of the data that is so far unknown. One explanation could be a sampling bias but, particularly for the Central Mediterranean Basin, the number of publications shows no resemblance to the number of species, so this explanation seems unlikely. Therefore, the effect is either from an unidentified source of biasing or due to a localised event in the Central Mediterranean Basin. For example, changes to the palaeogeography in the southeast of France resulted in marine incursions during the Serravallian, locally increasing the diversity (Bialkowski et al., 2006).

Changes to the diversity and assemblages of dinoflagellate cysts (in the Mediterranean) during the early and middle Miocene cannot be correlated to the closing and opening Eastern Mediterranean Gateway or global climate changes. Not only does the diversity change very little during these events, but the species making up the assemblages are similar for both the early and middle Miocene (Figures 3.15 and 3.16a) a feature that is also seen in other marine fauna such as gastropods and bivalves (Harzhauser et al., 2002).

Another reason for the lack of change to dinoflagellate cyst diversities and assemblages at the time of the Eastern Mediterranean Gateway closure may arise from the low temporal resolution of the data, which could hide any short term effects that result from gateway changes, i.e. the gateways’ intermittent openings and closings. In addition, it is possible that other factors, such as local climate change, are overprinting any signal that may have otherwise been evident. Although the percentages of CWS that made up the assemblages in the Mediterranean during the Neogene varied very little (Figure 3.12). Primary data with higher resolution dating would be required to test this latter hypothesis. Nutrient availability also has an important influence on the Mediterranean. Much of the water that replenishes any evaporation in the Mediterranean comes from precipitation and rivers, the latter bringing nutrient rich waters into the basin.

3.6.4.1.2 Tortonian-Piacenzian (11.63–2.58 Ma)

From the end of the Tortonian to the end of the Neogene, the diversity of Mediterranean dinoflagellate cysts declined, and it did so at a faster pace than it increased in the older half of the Neogene (Figures 3.13a). For example, there were 120 species at the end of the Tortonian (8–7.5 Ma), which had halved to 56 species in ~5 Myr (3.5–3 Ma). This decrease in diversity, coincided with the closure of the Rifian and Betic corridors prior to the main MSC evaporite precipitation between 5.97 and 5.33 Ma (Benson et al., 1991; Krijgsman et al., 2000; Betzler et al., 2006; Corbí et al., 2012; Flecker et al., 2015).

In the lead up to and during the MSC, the Mediterranean underwent increased stratification, surface salinity and nutrient availability, as well as bottom water anoxia and shallowing of the water column (Lozar et al., 2010). These alterations are depicted by changes to the biodiversity, abundance and dominance of marine organisms as the basin became more isolated and increasingly stressed. For example, in the early Messinian, the diversity of calcareous nannoplankton in Cyprus became very low, between 3 and 11 species, and lacked open ocean taxa, indicating shoaling (Wade and Bown, 2006). Shoaling also took place near Cyprus, as indicated by the development of shallow water microbial carbonate communities (Krijgsman, 2002; Orszag-Sperber, 2006; 2009). The diversity of foraminifera also decreased in the early Messinian in the Sant’ Agata Foossili Marls in Italy (Lozar et al., 2010). Both these events show that deterioration of normal marine conditions occurred prior to the precipitation of evaporites. It had previously been argued that episodes of full desiccation took place, indicated by palaeosols, although Lugli et al. (2015) has since ruled this out.

If dinoflagellate cyst diversity is related to sea level change (MacRae et al., 1996), then the decrease in diversity seen in the Mediterranean from the late Tortonian (Figures 3.13a) is possibly related to the closure of the Western Gateways (primarily between 6.26 and 5.4 Ma), which caused sea levels to fall over one kilometre and the precipitation of several kilometres of salt (Warny et al., 2003; Gómez, 2006). As the sea level fell and salinity levels increased, many previously habitable areas where dinoflagellates once thrived became inhospitable. Only those species that could tolerate high salinities could have survived anywhere. For example, *Impagidinium strialatum*, an oceanic species, and *Spiniferites* *pachydermus*, a fully marine coastal species (Zonneveld et al., 2013a), both disappeared from any Mediterranean record in TOPIS between 7 and 5.5 Ma. They subsequently reappeared at the Zanclean boundary, once salinity levels returned to normal and the Mediterranean was reflooded with Atlantic water (probably bearing the species). Although it is also possible that species may have been able to survive in local refugias located in the Mediterranean (Montenat et al., 1980; Logan et al., 2004).

The assemblage composition of the late Miocene is the most varied (compared to the assemblages of the other sub-epochs), demonstrated by a large spread of data points in MDS analysis (Figure 3.15). The reason for this is likely related to the shallowing and increasingly hostile conditions brought about by the MSC. As mentioned above it is likely that there were local refugias where some marine species (including dinoflagellate cysts) could survive, and if the local refugias were all disconnected it may have resulted in taxonomic isolation, causing differing assemblages in each refugia. This means that while the diversity of each local refugia was low (Warny et al., 2003; Londeix et al., 2007), the regional diversity was higher. When the Western Mediterranean Gateway reopened, the refugias were able to reconnect, giving the local assemblages of the Pliocene a higher diversity, as is demonstrated in other studies such as Dornbos and Wilson (1999; coral reefs) and Bison et al. (2007; calcareous dinoflagellate cysts). However, regionally the diversity did not increase. Another reason for a lack of diversity recovering depicted by the dinoflagellate cysts might be because of the general decreasing diversity of dinoflagellate cysts globally (MacRae et al., 1996).

What the dinoflagellate cyst record does demonstrate, similar to Dornbos and Wilson (1999) and Bison et al. (2007), is that an increase in the percentage of originations took place in the Pliocene, relative to the late Miocene (Figures 3.15a and b), and that significantly different assemblages are found in each sub-epoch (Figures 3.15). This is also demonstrated in Figure 3.16c, where the largest global R value of consecutive sub-epochs is either side of the MSC (comparing assemblages of the late Miocene with those of the Pliocene). This shows that the largest change in assemblage composition through the Neogene took place either side of the MSC and confirms, with a basin-wide dataset the earlier more locally-derived suggestion, that this event (Ioakim et al., 1997; Kontopoulos et al., 1997), and the subsequent reflooding, caused a species turnover.

Due to the short lived nature of the MSC, from 5.97–5.33 Ma (Krijgsman et al., 1999a; Krijgsman et al., 2002; CIESM, 2008; Manzi et al., 2013; 2015), the event itself is likely not evident in the diversity curve due to the lack of high resolution dating. What is seen is a more progressive trend as the Western Mediterranean Gateways closed over the Tortonian and the Messinian. Likewise, the Zanclean flood event, which is thought to have occurred rapidly and introduced new species to the Mediterranean (Hsü et al., 1973; Blanc, 2002), is not recorded. However, there is a general increase in the percentage of originations in the Pliocene relative to the late Miocene (Figures 3.14a and b), and the analyses show that the species making up the assemblages in the Pliocene are different to those of the Messinian (Figure 3.16). This suggests that the closure and reopening of the Western Mediterranean Gateway did impact the diversity of the dinoflagellate cysts as well as the composition of the assemblages.

3.6.4.2 The Paratethys

The Paratethys Basin shows much greater fluctuations to its diversity in the early and middle Miocene (Figure 3.13d) than for the Mediterranean as a whole (Figures 3.13a). This is due to the very changeable conditions in the Paratethys during the early and middle Miocene. For example, the closure of the Paratethys Sea from the rest of the Mediterranean was progressive and complicated due to there being numerous gateways connecting the Paratethys to the different Mediterranean Basins, all of which had different final closure times. It was also sufficiently well connected to external water sources to be susceptible to the global sea-level fluctuations that took place during the MMCO, and the subsequent MMCT, further altering habitats and enabling the migration of marine species and resulting in diversity fluctuations (Harzhauser et al., 2003; Harzhauser and Piller, 2007; Karami et al., 2011).

In the early Miocene, the Paratethys had normal marine conditions and had gateways to the north connecting it to the North Sea via the Rhine Graben, but these connections were closed during the lower Aquitanian and fresh water environments developed in the western tip of the Paratethys (Reichenbacher, 2000). The changing environment explains the diversity fluctuations of the Paratethys Basin (Figures 3.13d) as diversity is partly controlled by abiotic changes (Benton, 2009). This means that dinoflagellates either had to adapt to their new surroundings, migrate elsewhere or go extinct. The diversity fluctuations presented here suggest that the dinoflagellates most likely migrated elsewhere, possibly into local refugias (although this is speculation), and returned when conditions were more favourable.

After the Rhine Graben closed, the Paratethys still had broad connections between the Paratethys and the Mediterranean, allowing mollusc, echinoid and bryozoa faunas to spread via the gateways during the late Aquitanian and early Burdigalian (Rögl, 1997; Harzhauser et al., 2003; Mandic and Steininger, 2003; Harzhauser and Piller, 2007; Kroh, 2007). The dinoflagellates must also have been able to pass through the gateways, as assemblages in the early Miocene are similar in all of the basins (Figure 3.18a).

Connections to the west of the Paratethys closed due to the uplift of the Alpine foreland (Berger, 1996; Harzhauser and Piller, 2007). The beginning of the isolation of the Paratethys was accentuated in the middle Burdigalian by a global sea level fall (Haq et al., 1988) and by the middle Miocene the trend towards more basin-isolated assemblages was first seen (Figures 3.18b). This suggests that due to the increasingly limited connectivity of the basins from the middle Miocene onwards, the assemblages became more geographically distinct. This is consistent with the beginning of the restriction of the connections between the Paratethys and the Mediterranean in the middle Serravallian, and by the end of the Serravallian stenohaline organisms were no longer found in the Paratethys (Rögl, 1999).

The increasing dissimilarity of Paratethys assemblages from those found in the other Mediterranean basins is particularly evident in the late Miocene, which has even greater global R values (Figure 3.18c). In the late Miocene all but one of the Paratethys assemblages are clustered together and are clearly separate from the assemblages of the other basins. This shows an increased taxonomic isolation and speciation due to the geographical isolation of the closing gateways. This can be explained by the strongly reduced salinities that were seen in the Paratethys (during the Tortonian) and the decrease of the aquatic realm as the Carpathian Foredeep became land and connections were lost during the MSC (Rögl, 1999; Popov et al., 2006; Harzhauser and Piller, 2007).

Towards the end of the Neogene, the Paratethys eventually turned into an intracontinental brackish basin (Popov et al., 2006), which explains the limited number of assemblages found within the Paratethys in the Pliocene. There are only three assemblages from the Zanclean and none from the Piacenzian. All of the Pliocene assemblage data demonstrate that the species composition of the Paratethys, in the Pliocene, is statistically significantly different to the species composition of the rest of the Mediterranean basins due to the increasing brackish nature of the Paratethys (Figures 3.18d). The Mediterranean Sea also saw brackish conditions towards the end of the MSC. The brackish conditions resulted in the Lago Mare facies, but due to its short duration (less than 200 Ka; Clauzon et al., 2005) any influences of it on dinoflagellate cysts are not detected in the course temporal resolution of the TOPIS database.

3.6.5 Mediterranean summary

Mediterranean dinoflagellate cyst assemblages from the TOPIS database demonstrate a response to Neogene tectonic changes, and were particularly affected by the closure of the Western Mediterranean and Paratethys Gateways. At the start of this chapter several questions were posed, and they are repeated below, followed by summarised answers:

1. Are there any major changes to the diversity of dinoflagellate cysts through the Neogene?
    - Diversity slightly increased from the Aquitanian to the end of the Tortonian with only minor fluctuations in the number of species present (Figures 3.13). However, at the end of the Tortonian/start of the Messinian, the diversity rapidly decreased before further decreasing into the Pliocene.
2. Do dinoflagellate cysts assemblages change over time and space?
    - In the early Miocene the species that made up each assemblage are similar across the whole Mediterranean-Paratethys basins.
    - From the middle Miocene onwards, the assemblages of the Mediterranean and Paratethys became more different to each other and in the late Miocene and Pliocene, the Paratethys assemblages plotted completely separately from the rest of the Mediterranean (Figures 3.18c and d).
    - Assemblage composition varied over the Mediterranean and assemblages from the same Mediterranean/Paratethys Basin shared more of the same species (Figure 3.17). While assemblages were significantly different in the different basins, they did not vary as much as they did in the different sub-epochs (Figure 3.15). This means that the species that made up the assemblages changed more through time than they did through space. Even so, the Mediterranean and Paratethys basins had significantly different species to each other from the middle Miocene to the Pliocene (Figures 3.18b-d).
    - The assemblages in the late Miocene were varied, shown by little temporal clustering of the data (Figure 3.15), and were significantly different to the assemblages of the middle Miocene (Figure 3.16b). The largest difference of species composition between two stages was between the late Miocene and the Pliocene (Figure 3.16c).

3. Are recorded changes in dinoflagellate cyst assemblages and species diversity directly related to marine gateway changes, or is there an alternative explanation?
    - There is no evidence of the dinoflagellate cyst assemblages from TOPIS being affected by the closure of the Eastern Mediterranean Gate. However, more primary data at a higher temporal resolution may help clarify the situation.
    - The closure of the gateways between the Paratethys and the Mediterranean resulted in Paratethys assemblages becoming progressively more taxonomically isolated as the basins became geographically isolated. This meant allopatric speciation occurred resulting in an increased number of endemic species in the Paratethys (Figures 3.18b-d).
    - The species turnover between the late Miocene and the Pliocene as well as the diversity decrease during the late Miocene can be attributed to the closure of the Western Mediterranean Gateways (Figures 3.13a and 3.16c). The closure resulted in the MSC, which lowered the sea level, increased the salinity basin-wide and meant the loss of marine areas as land emerged, resulting in a reduction in the habitable area for the dinoflagellates with few or no refugia.
    - The MSC came to an end at the Messinian-Zanclean boundary with the opening of the Strait of Gibraltar. The dinoflagellate cyst diversity did not immediately or fully recover at this time, but the number, and percentage of species, that appeared did gradually increase relative to the late Miocene, which had a high number of species becoming extinct, and a low number of species originating (Figure 3.14). The species that appeared in the Pliocene were different to those present in the late Miocene.

From the analyses discussed in this chapter it appears that the Western Mediterranean and Paratethys gateway closures affected the dinoflagellate cyst more so than the Eastern Mediterranean Gateway. However, if new primary data were collected (and added to TOPIS), particularly from the Eastern Mediterranean Basin, it may be possible to gain a deeper understanding of the effects (and timings) of the Eastern Mediterranean Gateway closure on dinoflagellate cyst assemblages. Also, if additional primary data were added to TOPIS that includes the environment of deposition, it would mean that other factors such as sea level changes could be taken into account, further constraining why the diversity and assemblage composition changed.

3.7 Final conclusions

This chapter demonstrates how dinoflagellate cysts can be used to determine if cooling took place over long periods of time (i.e. the Neogene). The findings can be broadly correlated to other established global temperature curves such as the Zachos benthic oxygen isotope curve (Zachos et al., 2001; 2008). However, small differences can be noted, for example cooling from the dinoflagellate cysts appears to occur more rapidly between the Serravallian and the Tortonian than between the Langhian and the Serravallian as is demonstrate by benthic foraminifera (Zachos et al., 2001; 2008). The dinoflagellate cyst record also does not depict short term climate changes such as the MMCO, although this is possibly due to the resolution of the dating (see Section 4.2.1).

However, as it is known that temperature is not the only limiting factor affecting the distribution of dinoflagellate cysts it is important to understand what other types of proxies dinoflagellate cysts can act as. The Mediterranean makes an excellent case study for further investigating their proxy potential as the temperature in the Mediterranean (Figure 3.12) record does not greatly vary throughout the Neogene. This means that other factors must be causing the changes to the distribution and assemblage composition. During the Neogene the Mediterranean and Paratethys regions were subjected to three major gateway changes that are thought to have resulted in changes to the both the diversity and assemblage composition of dinoflagellate cysts (see Section 3.6). Unfortunately further information on dinoflagellate cysts as a salinity proxy was not available due to a lack of abundance data (see

Section 4.3.2 for further details). It was, however, apparent that the Western Mediterranean Gateway, which resulted in sea level fall, coincided with a regional diversity decrease. It is therefore likely that the diversity decrease in the Mediterranean was being controlled by the loss of habitats as water levels decreased and salinity increased.

Comparing the differences between a global dataset and a regional dataset demonstrates the complex nature of climate proxies and the differing factors that take place on different scales. For example, with the data presented in this study, temperature is one of the controlling influences on dinoflagellate cyst distributions particularly in the higher latitudes where climate cooled the most, whereas regionally, the Mediterranean was subjected to very little temperature changes and the restriction of the exchange of water controlled the dinoflagellate cyst assemblages the most.

Chapter 4: Evaluation of databasing and dinoflagellate cysts

4.1 Introduction

When working with a fossil group is it important to understand both the advantages and limitations of the group. This insures that the methodologies applied are appropriate and enables a clearer understanding of the results obtained from any analyses. This means it is also important to investigate the effects of any sampling biases that might affect the group, particularly when working with a large dataset, as well as any other factors that should be taken into consideration. The following chapter discusses the considerations that have been taken into account when compiling and interpreting the analyses in Chapter 3.

4.2 Assessment of databasing

Global datasets compiling previously published data are becoming more prevalent and are increasingly being used in evaluating changes over longer time scales and over large regions (Salzmann et al., 2008; Masure and Vrielynck, 2009; Pound et al., 2012a; Masure et al., 2013; Woods et al., 2014). There are many strengths in databasing; such as examining sampling biases and locating literature deficient regions. However, the large amount of literature compiled in the TOPIS database addresses different research questions, meaning that information that is pertinent to one study may be absent in another and may bias the database. Examples of this include abundance counts versus presence or absence data, and information on the environment of deposition. For instance, if the environment of deposition was provided for all of the data, it would enable investigation into whether water depth was influencing the distribution of the dinoflagellates as well as temperature. If abundance data was consistently provided it would allow further investigations, such as producing quantitative temperature changes and would allow a more in depth evaluation of the functionality of TOPIS. It is for this reasons that it is suggested that abundance counts should be consistently included in all future publications.

4.2.1 Temporal spread of data and time bins

Many of the publications included in TOPIS (over half) are dated to within one or two stages, assemblages with estimated age ranges spanning more than two stages were not included in any analysis due to being too poorly constrained to be reliable (Figure 4.1). As the dating of so many assemblages is estimated to within a stage much of the analysis concentrates on comparing different stages. However, to utilise the data that is more temporally constrained (i.e. those assemblages dated to within 1 Myr) as well as to gain more detailed information, time bins of 0.5 Myrs were used to investigate changes to the diversity in the Mediterranean over the Neogene. This approach also avoids biases described in in MacRae et al. (1996) where the diversity decreased in the shorter stages (e.g. the Coniacian; 89.8–86.3 Ma).

However, this has limitations, as because many of the assemblages are dated to within a stage, it means that where the boundary between two stages goes through the middle of a 0.5 Myr time bin, there are large peaks in diversity. This bias was corrected by using the method described in Figure 3.10. Since many of the assemblages are dated to within a stage, it also results in the largest peaks of extinctions or originations occurring in the time bins containing stage boundaries (Figure 3.14a and b). However, as mentioned previously (Section 3.6.3.1.6), stage boundaries are often positioned at easily recognisable intervals such as biostratigraphic events (e.g. large extinctions/originations occurrences).This means that the large peaks of originations and extinctions at the stage boundaries may be representative of the changes that took place, and not merely a result of sampling biases.

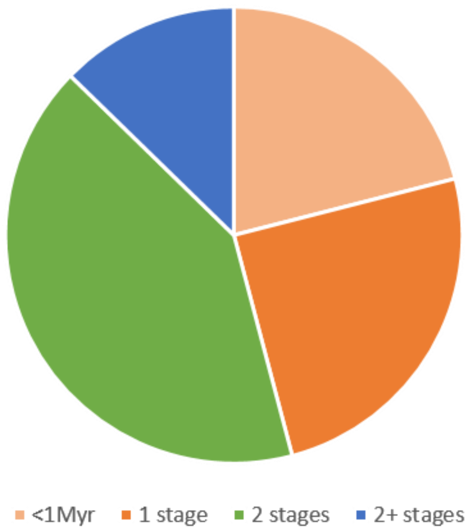


Figure 4-1: Representation of the number of assemblages with estimated age ranges spanning one and two stages, less than one million years and over two stages. Assemblages with age ranges spanning greater than two stages were not included in any analysis.

As mentioned above the majority of the assemblages have an estimated age spanning an entire stage with only ~20% of the assemblages dated to less than 1 Myrs. Unfortunately, this means that any evidence of short scale events affecting the dinoflagellate cysts, such as the MMCO and the MPWP, is lost. However, it is still possible to interpret long-term changes and to see the long-term effects of short-term events such as the MSC.

There are a greater number of records in the Northern Hemisphere than in the Southern Hemisphere. Because of this, the mean percentage of CWS for each stage (Figure 3.6a) was recalculated only using the records of the Northern Hemisphere (Figure 3.6b). The most obvious difference between the two methods (global versus Northern-only) was in the Tortonian. When all the data were used (Figure 3.6a), the mean percentage of CWS was higher for the Tortonian than for the stages either side. This difference for the Tortonian can be explained by the Southern Hemisphere Tortonian having substantially more records than in the other periods (Figure 3.4), the majority of which have CWS values of 33% or higher. These records, between 65 and 70° S and 20 to 25° S, are numerous, with tightly constrained ages, and result in a much larger percentage of CWS in the Tortonian (19%, Figure 3.6a) than in the stages either side (5% in the Serravallian and 12% in the Messinian). When only using data from the Northern Hemisphere, which has a more equal spatial distribution, the discrepancy between the Tortonian and the stages either side is less (Figure 3.6b). It is for this reason that the conclusions drawn from this study mainly concern the Northern Hemisphere. As the majority of data in the Northern Hemisphere is located in the North Atlantic and Arctic oceans and the Mediterranean region, it is likely that the signal produced is from those areas, rather than for the whole of the Northern Hemisphere.

This implies that care must also be taken in the Northern Hemisphere where there are latitudinal bins represented without data for every stage. For example, the three most northerly latitudinal bins only have data for the Pliocene, all of which have high percentages of CWS. To make sure that the data in the Pliocene was not skewing the results, further analysis of the data was carried out excluding latitudinal bins that did not have data for all stages (Figure 3.6c). Comparing results using all of the Northern Hemisphere data (Figure 3.6b), to those using just latitudinal bins with data present for every stages (Figure 3.6c), indicates that the cooling was more extreme when all the data for the Northern Hemisphere were used. However, the overall trend is the same and leads to the conclusion that the absence of data in the high latitudes for stages other than the Pliocene has not skewed the results.

4.2.2 Spatial spread of data

It is important to have a good spread of data both geographically and chronologically. TOPIS contains considerably more data for the Northern Hemisphere than for the Southern Hemisphere. This means that the signal produced is likely to be biased towards the changes that took place in the Northern Hemisphere rather than being representative of the whole globe. An example of where the spread of data influences the results can be seen in the modern map (Figure 3.3i) where there is a very high number of records in the Gulf of Saint Lawrence (85 records; east coast of Canada). In 72 of these records, all of the species with known temperature preferences are CWS (mostly *Spiniferites elongatus* and *Islandinium minutum*), the remaining 13 records have CWS percentages between 50 and 83%. These results indicate that the Gulf of Saint Lawrence is particularly cold. The Gulf of Saint Lawrence is a small, restricted basin with limited exchange with the open ocean (it is almost an inland sea in this regard) and it receives large quantities of freshwater from the continent (Long et al., 2015). The only open ocean water source is through the Belle Isle Strait, bringing cool Labrador Sea water into the Gulf. However, the majority of the cool waters form in situ during the winter season (Banks, 1966; Saucier et al., 2003). The plethora of sites reflecting the cool water Gulf of Saint Lawrence microclimate produces a noticeable feature in the modern, where in the 45–55° N latitudinal bins (Figure 3.5i) the mean percentage of CWS relative to WWS is significantly higher than it was in the 40–45° N latitudinal bin. If the 85 records in the Gulf of Saint Lawrence are removed from the analysis, the step like change seen at roughly 45° N is no longer there, providing a clear example of how a large quantity of records in a small region can alter the global signal, and demonstrating why it is preferable to have an even spatial coverage of data.

4.2.3 Edge effects

As TOPIS concentrates on the Neogene, it has an age cut off of 23.03–2.59 Ma, and outside of this age range the data are sparse. This could have resulted in edge effects when investigating diversity changes (Foote, 2000), where the number of originations and extinctions were much larger in the first and last time bins respectively. Species that would have crossed through to the Neogene from the Paleogene appeared to have originated in the Neogene along with any species that did actually originate at the boundary, giving false and unreliable counts of origination events. To avoid any edge-effects species with age ranges that stopped at the 'edges' of the Neogene were not included in the counts of originations and extinctions. One problem with this method is that species that did either appear or disappear at the start or end of the Neogene are not included. It would be necessary to collect data for a few million years either side of the Neogene to compensate for this potential effect.

4.2.4 Evaluation of diversity studies – sampling biases

Biodiversity influences the productivity and stability of ecosystems in both the marine and terrestrial realms across all trophic levels (Worm et al., 2006; Ptacnik et al., 2008). Higher species richness equates to increased ecosystem stability (Tilman et al., 1997; Yachi and Loreau, 1999). The controls of diversity are debated and ideas include the Red Queen (Van Valen, 1973) and the Court Jester models (Barnosky, 2001), i.e. biotic versus abiotic controls (Benton, 2009). Biotic diversity controls include competition, adaptability and body shape; whereas abiotic diversity controls are alterations to the physical environment, such as climate change, changes in food supply or landscape. All of which can occur due to gateway changes.

Diversity studies are extremely numerous in the literature (Sanders, 1968; Sepkoski, 1978; 1979; 1984; MacRae et al., 1996; Bambach et al., 2002; Rohde and Muller, 2005), but problems exist because it is difficult to determine if recorded changes are caused by real variability in the natural world or are an artefact of sampling biases. A further cause for concern regarding sampling biases is that it is feasible that when diversity is particularly high, it could be as a result of an increased number of publications/sites (and research) in a particular time period/region. However, this argument could be circular since it is also possible that a higher number of species resulted in a higher number of publications (MacRae et al., 1996). To investigate this effect, the number of species, publications, sites and assemblages in each time bin were compared (Figures 3.13). The R^2 values range from 0.656 to 0.001 (P values $1.44E^{-10}$ to 0.842 respectively; Western and Central Mediterranean basins, assemblages). As the same methods were used for each basin, but the statistics suggest varying levels as to whether the null hypothesis (that the number of publications does not control the number of species) should be rejected or not, it is difficult to untangle the cause from effect in this correlation, and it is considered overhasty to completely discount the results regardless of the R^2 or P values. However, the Central Mediterranean Basin has consistently low R^2 value for all the sampling proxies tested ranging from 0.001 to 0.010 and has high P values ranging from 0.537 to 0.842. This is interpreted as the data being consistent with the null hypothesis and is the basin least likely to have its dinoflagellate cyst diversity controlled by the number of publications.

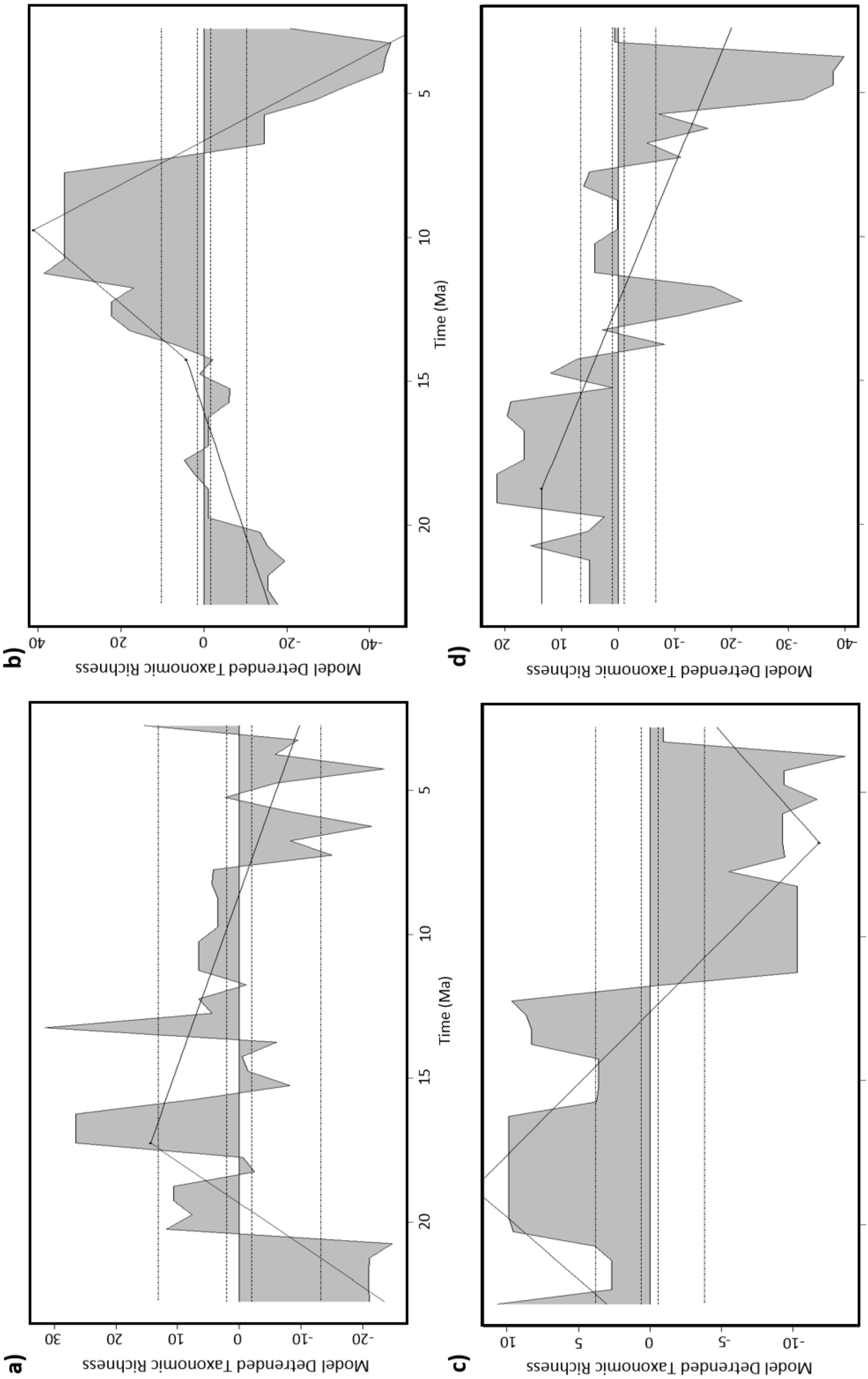
Two stages		**All Mediterranean**	**Central**	**Eastern**	**Paratethys**	**Western**
Publications	**R^2**	0.403	0.005	0.252	0.236	0.407
	P value	8.21E-06	0.651	0.001	0.001	7.19E-06
	Number	60	19	17	20	4
Sites	**R^2**	0.448	0.010	0.379	0.065	0.593
	P value	1.71E-06	0.537	1.81E-05	0.106	3.94E-09
	Number	92	37	20	27	8
Assemblages	**R^2**	0.384	0.001	0.297	0.063	0.656
	P value	1.54E-05	0.842	2.30E-04	0.114	1.44E-10
	Number	178	73	45	44	15

Table 4-1: Potential biases of diversity change for the whole of the Mediterranean, the Central Mediterranean Basin, the Eastern Mediterranean Basin, the Paratethys Basin and the Western Mediterranean Basin. The P and R^2 values are from the number of species present (diversity) versus the number of publications, sites and assemblages for each 0.5 million year time bin. The higher the R^2 value, and the lower the P value, the higher the correlation between the two, and the more likely that the diversity is controlled by a sampling bias. For example, the Central Mediterranean Basin has a low R^2 value and a high P value. This suggests that the number of publications and the number of species are unlikely to be causally related to each other. Both the R^2 and P values relate to the smoothed data (Figure 3.10). Figure 3.13 directly compares the number of publications and the number of species.

An alternative approach to determine if the diversity changes seen over the Neogene are 'real' rather than due to sampling biases is to use residual modelling (Smith and McGowen, 2007; Lloyd, 2012). This is a potentially more informative method as it demonstrates when during the Neogene diversity change is less (or more) likely to be influenced by sampling biases. Residual modelling assumes that diversity is constant and that any diversity changes displayed are due to sampling biases. It is then possible for the model to subtract the modelled estimate from the observed estimate, providing an unbiased diversity curve (represented by the grey polygon). However, whilst it represents data unbiased by the factor included in the model (in this case the number of assemblages) it is possible that an additional factor (such as the amount of available outcropping sediment) is still biasing the data. The significance of the test is displayed with 95% standard error and 95% standard deviation confidence intervals. Where data plot within the confidence intervals, the model is a good fit (i.e. sampling bias is likely to have affected the results) whereas if the residuals plot outside of the confidence intervals then the model is a poor fit and the diversity signal cannot be attributed to the number of assemblages, and is therefore more likely to represent true changes to the diversity.

The residual models depict that much of the diversity changes over the Neogene are not affected by sampling biases (Figure 4.2). The number of assemblages is likely to be controlling the number of species in a few cases, such as in the Central Mediterranean Basin (Figure 4.2b) between ~20 and 16 Ma and the Paratethys basin between ~7.5 and 11 Ma (Figure 4.2d). However, in the Eastern Mediterranean Basin, the number of assemblages appears to have very little control on the number of species present (Figure 4.2c). With the exception of the Western Mediterranean Basin (Figure 4.2e), which has no available data from 5 Ma to the end of the Neogene, the rest of the basins all have a ‘real’ diversity decrease in the late Miocene, coinciding with the closure of the Western Mediterranean gateways.

Whilst many publications have utilised this approach (Lloyd, 2012; Mannion et al., 2012; Benson and Upchurch, 2013; Near et al., 2014) the methodology has recently come under scrutiny. It is now suggested that residual modelling cannot be used to correct for sampling bias in palaeodiversity data due to the methods of independent sorting of the variables (Sakamoto et al., 2016). It is suggested that phylogenetic multiple regression models should be used instead, although Brocklehurst (2015) demonstrate that residual modelling still produces more reliable diversity curves then using raw data.


a)
b)
c)
d)
Model Detrended Taxonomic Richness
Time (Ma)
30
20
10
0
-10
-20
40
-40
5
-5
-30
20
15
10
5

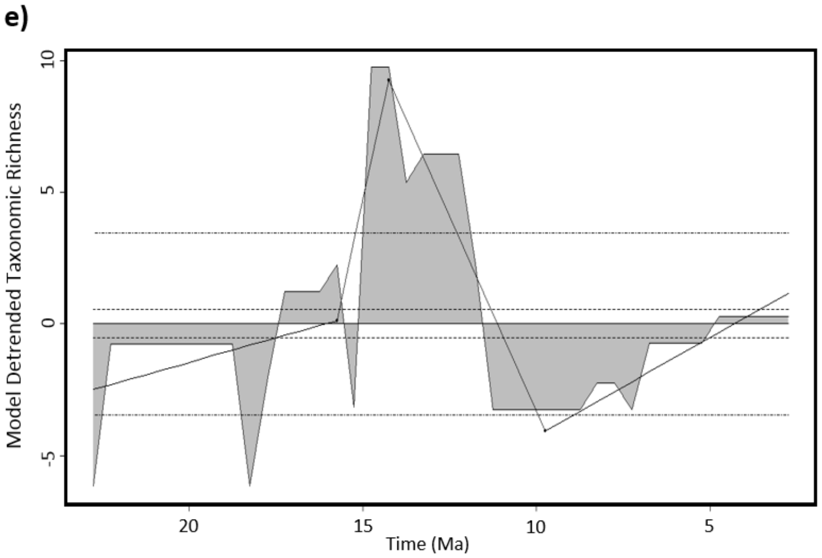


Figure 4-2: Residual models for (a) the whole Mediterranean, (b) the Central Mediterranean Basin, (c) the Eastern Mediterranean Basin, (d) the Paratethys Basin and (e) the Western Mediterranean Basin. Grey polygons represent the model-detrended diversity (sampling proxy is the number of assemblages). The horizontal lines represent the confidence interval. The dashed lines is the 95% standard error and the dashed-dot horizontal lines (outside) represent the 95% standard deviation of the model. The solid lines that move with the polygons represents the medium term diversity trends.

4.3 Dinoflagellate cysts as a climate proxy

Dinoflagellates can be limited by a range of environmental parameters, as discussed in Section 1.3.7, and it is because of this that they can be used to reconstruct palaeoenvironments. Examples include: de Vernal et al. (2005; Last Glacial Maximum); Head (1997; Pliocene); De Schepper et al. (2011; Pliocene); Londeix et al. (2007; Miocene) and Schrek and Matthiessen (2013; Miocene). They are also useful proxies for palaeoenvironments because they are globally abundant with a continuous fossil record from the Middle Triassic onwards, and are limited to a range of environmental parameters, which, if abundance data is provided, can be quantified. Unlike other palaeoenvironment proxies (such as foraminifera and calcareous nannoplankton, which are often restricted to oceanic environments), dinoflagellates are abundant nearshore, particularly in regions with varying salinity and seasonal temperature differences (de Vernal and Marret, 2007). This means nearshore palaeoenvironments can be reconstructed and inferences can be made to sea level fluctuations. Also unlike foraminifera, calcareous nannoplankton and siliceous microfossils, dinoflagellate cysts are made from the resistant material dinosporin, which is robust and not affected by dissolution (Dale, 1976), aiding their preservation through time. Furthermore their high latitude assemblages are relatively diverse (de Vernal and Marret, 2007), resulting in the potential for good global coverage of their data. Whilst it has been proved that they make an excellent climate proxy there are several complicating considerations to take into account, which are discussed below.

4.3.1 Taxonomy

A limitation of using previously published data is the fallible nature of dinoflagellate cyst identification and the peer review process. This, along with the changing nature of dinoflagellate cyst taxonomy, results in the necessity of a thorough evaluation of the data used prior to analysis. This was carried out with Dinoflaj2 (Fensome et al., 2008) to avoid/include any necessary synonyms. However, Woods et al. (2014) suggest that with an increase in the number of records included in the analysis comes a significant decrease in the chance of problematic taxonomy skewing the global signal.

4.3.2 Palaeoecology

Due to there being a finite number of species that have an absolute temperature range, and due to a lack of abundance data, this study is limited to presenting relative temperature change rather than quantifiable temperatures (Marret and Zonneveld, 2003; Zonneveld et al., 2013a).

Species that are constrained to certain temperatures often are regarded to be only prominent under those temperatures and rarely outside of them. An example from this study is *Batiacasphaera micropapillata* which is defined as a CWS. Due to complications with its identification is it often combined with *Batiacasphaera minuta* into the *B. micropapillata* complex (Schreck and Matthiessen, 2013). Species from the *B. micropapillata* complex are found in some records from low latitudes, for example, in the Aquitanian and Burdigalian off the northeast coast of South America (5–10° S) and off the east coast of India (10–15° N) in the middle Miocene to the Pliocene. The presence of species from the *B. micropapillata* complex in India are responsible for the higher latitudinal averages of CWS between 10 and 15° N (Figure 3.5c-h), where the mean percentage of CWS lies between 17 and 20%. These examples highlight the importance of providing abundance counts as without it, it is unclear whether the *B. micropapillata* complex made up a higher percentage of the assemblage (indicating cooler waters) or were present in low abundances. If they are present in low abundances it might be that the waters were not necessarily cool, as species of *Batiacasphaera* can be found in low quantities at lower latitudes (Schreck and Matthiessen, 2013).

Dinoflagellate cysts can not only be used as a proxy for sea surface temperature, but their distribution and assemblage composition can also respond to salinity, nutrient availability and sea ice cover (Marret and Zonneveld, 2003; Zonneveld et al., 2013a). This makes it problematic to determine what individual factor is causing any recorded changes. For example, changes in the Mediterranean are less likely to be related to global climate cooling, and more likely to be related to the gateway changes that altered the basin. The closure of the Western Mediterranean Gateway in particular, which resulted in lower sea level and increased salinity, is thought to have resulted in an assemblage turnover (Ioakim et al., 1997; Kontopoulos et al., 1997). However, it is particularly problematic to interpret the causes of any assemblage turnover or diversity changes when abundance counts are not consistently available, as in Chapter 3, although it is highly likely that the changes seen are due to the gateway closures.

4.3.2.1 Temperature

Dinoflagellate cysts have been shown to be a reliable proxy for temperature, as temperature affects where species preferring either warm or cold water will dwell (e.g. Marret and Zonneveld (2003), Zonneveld et al. (2013a) and Chapter 3). However, temperature has a secondary effect of dinoflagellate cysts as with cooling temperatures ice sheets develop in the high latitudes (see Section 1.2.4). As ice develops, sea level drops and results in less continental shelf space for the dinoflagellate cyst to live. This can result in a decrease in the diversity of dinoflagellate cyst diversity. Therefore sea level changes is postulated as one of the conditions affecting the number of dinoflagellate cyst species (MacRae et al., 1996; Figure 1.11). During the closure of the Western Mediterranean Gateway, towards the end of the Miocene, water depth in the Mediterranean Sea decreased as evaporation outpaced water inflow, possibly contributing to the decrease in the number of dinoflagellate cyst species present in the Messinian. It would be interesting to investigate the effect of depth and distance from land on the dinoflagellate cyst assemblages, but unfortunately, as with abundance counts, the literature synthesised by the TOPIS database does not consistently provide this information.

4.3.2.2 Nutrient availability

Temperature and nutrient availability (phosphate and nitrate concentrations) are thought to be one of the most important controlling variables for dinoflagellate cysts distribution (Marret and Zonneveld, 2003; Zonneveld et al., 2013a). For example, in areas of upwelling or river discharge, there is often an increase in the number of dinoflagellate cysts due to enhanced nutrient availability (Crouch et al., 2003). Without abundance counts, it is difficult to determine the location of upwelling systems and river outlets, and care must be taken to interpret results in light of local phenomenon such as the production of colder, nutrient rich waters. An example can be seen where CWS are present off the west coast of South Africa (Figures 3.3 e, f and g). The appearance of CWS, off the west coast of South Africa, during the late Miocene and in the modern may be related to the upwelling of the Benguela Current, which originated in the late Miocene (Siesser, 1980; Diester-Haass et al., 1990; Robert et al., 2005). The initiation of the Benguela upwelling produced cold nutrient rich waters at the surface and could be the reason for the appearance of CWS (*Bitectatodinium tepikiense* and *Ataxiodinium choane*) in that region (Heinrich et al., 2011).

Nutrient availability also has an important influence on the Mediterranean. Much of the water that replenishes any evaporation in the Mediterranean comes from precipitation and rivers, the latter bringing nutrient rich waters into the basin. In the Tortonian, between 10.2 to 9.8 Ma and 9.0 to 8.5 Ma, the Mediterranean experienced two washhouse events, which resulted in several times more precipitation than today (Böhme et al., 2008). This increase of rain over Europe caused river runoff to increase, bringing in more nutrients and changing dinoflagellate assemblage composition, including the dominant species. For example, increases in the abundance of *Lingulodinium machaeophorum* is thought to be a river discharge marker, particularly for the Nile (Elshanawany et al., 2010). If this study contained more records with abundance counts, it might be possible to examine the effects of river runoff in more detail. However, the present study only conveys that *Lingulodinium machaeophorum* were present in the majority of the assemblages. This again highlights the importance of obtaining abundance counts.

4.3.2.3 Salinity

The highly saline waters during the MSC may have been the cause of changes to the diversity and assemblages. Some species e.g. *Spiniferites cruciformis* and *Pyxidinopsis psilata* cannot tolerate high salinities and are found only in brackish waters (Kouli et al., 2001; Martín et al., 2009), while others thrive in areas of high salinity e.g. *Operculodinium israelianum* and *Polysphaeridium zoharyi* (Mudie et al., 2002; Marret and Zonneveld, 2003; Zonneveld et al., 2013a). Certain species, such as *Lingulodinium machaeophorum,* have been shown to increase the length of their processes when living in highly saline environments (Mertens et al., 2009a; 2012). Many species, such as *Operculodinium israelianum* and *Polysphaeridium zoharyi* mentioned above, can be found in areas of lower salinities, but are particularly abundant in highly saline waters. However, without abundance counts, this study cannot confirm if species with high salinity preferences became more abundant during the MSC or if they were persistently present in low quantities.

4.3.2.4 Ice cover

Ice cover is unlikely to affect Mediterranean dinoflagellates in the Neogene as even in the late Pliocene temperatures were 4–5 °C warmer than the present (Herbert et al., 2015) and sea ice was only seen at high latitudes, well outside of the Mediterranean's range (Knies et al., 2014a; Stein et al., 2016). There is a limited number of species preferring cold water temperatures that appeared in the Mediterranean region throughout the entire Neogene, and there is very little change to the percentage of CWS implying no significant temperature change. For example the percentage of CWS relative to the total number of species with known temperature preferences varies very little during the Neogene (Figure 3.12), meaning temperature change was not significantly influencing the dinoflagellate cyst assemblages.

4.3.3 Preservation/sample preparation technique

As mentioned in Chapter 1 (Section 1.3.7) the preservation of dinoflagellate cysts can be affected by oxidation, causing decay and poor preservation (de Vernal and Marret, 2007). Oxidation of dinoflagellate cysts can occur naturally, but also during sample preparation (particularly in older publications) when nitric acid or hydrogen peroxide is added to aid in the removal of residual fine organic material (Riding and Kyffin-Hughes, 2004). Oxidation particularly affects heterotrophic species (e.g. *Brigantedinium* spp.), which are less resistant, and often results in their removal from assemblages (Marret, 1993; Head, 1996; Zonneveld et al., 1997; 2001; Hopkins and McCarthy, 2002). Autotrophic species (G-cysts) such as *Impagidinium* spp. are less sensitive to oxidation (Marret and Zonneveld, 2003). This means that the method used for sample preparation must be carefully chosen as some techniques will selectively remove the more sensitive taxa from the assemblage (Marret, 1993; Mudie and McCarthy, 2006). The method of sample preparation should therefore always be provided in publications to inform the reader if there is a possibility that P-cysts/heterotrophs have been destroyed during the preparation process. It also means that the use of the P/G (peridinioid/gonyaulacoid) or A/H (autotrophic/heterotrophic) ratios must be used with extreme care (Zonneveld et al., 2008).

The distribution of heterotrophic species is controlled by the presence of nutrients, and therefore it is likely that both cold and warm water species will be equally affected by any biasing due to sample preparation methods. If nutrient availability and oxidation are the main controlling influences on the presence and distribution of heterotrophic taxa, rather than temperature (Bockelmann and Zonneveld, 2007), it explains the lack of heterotrophs included amongst the list of species with known temperature preferences (Figure 3.4 and Appendix B).

4.3.4 Transport

Dinoflagellate cysts are thought to behave as silt sized particles (Dale, 1983; Kawamura, 2004) and like other microfossil groups, can be transported both vertically through the water column and laterally with ocean currents. This means that there is a possibility that the location at which the fossil was found, may not represent their original environment. (Dale, 1996; de Vernal and Marret, 2007). Several studies have investigated the effects of vertical and lateral movements of dinoflagellate cysts through the water column by comparing cyst assemblages in the water column to the collection of cysts in the underlying sediments (Harland and Pudsey, 1999; Zonneveld and Brummer, 2000). These studies indicate that the transport of cysts is only a minor factor in the distribution of cysts and is likely to be a local influence only. Experiments in both laboratories and in the oceans demonstrate that dinoflagellate cysts sink through the water column relatively quickly by metres per day, which can increase to hundreds of metres per day if they are incorporated into faecal pellets or marine snow (Zonneveld and Brummer, 2000; Wefer and Fischer, 1993). In a large global study such as Chapter 3 each publication would need to be investigated separately as it is impossible to generalise the effects of ocean currents on the transportation dinoflagellate cysts (Marret and Zonneveld, 2003).

4.3.5 Incomplete fossil record

The percentage of dinoflagellates that produce preservable organic-walled cysts is thought to be between 15 and 20% (Fensome et al., 1996b). This low percentage, resulting in an incomplete record, is one of the main limitations of dinoflagellate cyst diversity studies. However, while the limitation is acknowledged, MacRae et al. (1996, p. 3) maintain that “patterns shown by the dinoflagellate fossil record reflect real evolutionary and palaeoenvironmental events and processes”.

4.3.6 Pull of the recent and the latitudinal diversity gradient

Temperature preferences of dinoflagellate cysts are better known for those species that are either extant or became extinct nearest to the present. Therefore, in a study such as this, it is important to be aware that the number of species with known temperature preferences is likely to increase through time (‘the pull of the recent’; Section 3.2). The lowest number of species with known temperature preferences is in the early Miocene, with five CWS and 30 WWS (Figure 4.3). However, the pull of the recent effect does not seem to influence the rest of the Neogene and the number of species found in each stage is highest in the Tortonian rather than the modern (Figure 4.3). It is also worth noting that when the percentage of CWS and WWS (present in each stage) is calculated relative to each other (Figure 4.3), the percentage of CWS in each stage increases through the Neogene with the cooling temperatures. As the pull of the recent assumedly effects CWS and WWS equally it suggests that the cooling climate outpaced any effects of the pull of the recent, resulting in a higher proportion of CWS (relative to WWS) in the cooler younger Neogene than in the warmer older half of the Neogene.

Throughout the Neogene, there is a significantly higher number of WWS than there is CWS (Figure 4.3). This is due to the latitudinal biodiversity gradient where the warmer, lower latitudes have a higher diversity than the cooler, higher latitudes; a phenomenon that has been in observed in the geological record for at least the last 30 Myr (Crame, 2001; Mittelbach et al., 2007; Mannion et al., 2014). This relatively low species richness of CWS is an enduring feature of the dinoflagellate cyst record and hence does not affect our interpretations.

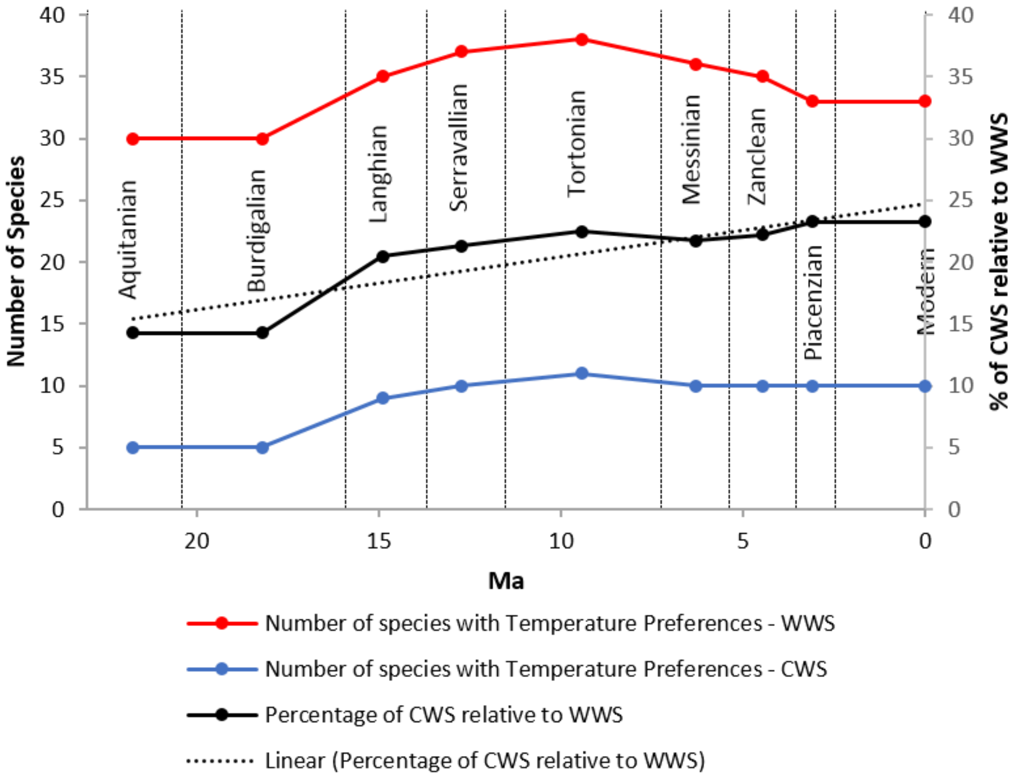


Figure 4-3: The number of species with warm or cold water preferences for each stage (plotted on the left axis) and the percentage of Cold Water Species (CWS) relative to the total number of species with known temperature preferences for each stage (plotted on the right axis). Data are obtained by counting the number of species in each stage from the range chart in Figure 3.1.

4.4 Conclusions and assumptions for the analysis in Chapter 3

Having discussed the various constraints and limitation of databasing and of using dinoflagellate cysts as a climate proxy, it is clear that there is still great value in their use. If the data included in TOPIS were more consistent (i.e. more abundance counts are provided as well as including data with a higher temporal resolution) then the potential of dinoflagellate cysts as a climate proxy potential would increase even more. It would allow more quantitative changes to be calculated and potentially provide more information on the shorter global/regional events.

Chapter 5: The effects of the Messinian Salinity Crisis on dinoflagellate cysts in Cyprus

5.1 Introduction

Cyprus is situated in the Eastern Mediterranean Sea and has a nearly continuous sequence of sedimentary rocks spanning from the Cretaceous to the present, which allows for the study of important palaeoenvironmental changes that took place during the Neogene. One such change was the closure of the Western Mediterranean Gateway, which briefly prevented the exchange of water between the Mediterranean and the North Atlantic (Weijermars, 1988; Duggen et al., 2003). As discussed in Chapter 3 (Section 3.6), this prevention of water exchange resulted in the Messinian Salinity Crisis (MSC), where vast quantities of evaporites were precipitated between 5.97 and 5.33 Ma, due to evaporation rates exceeding the influx of water from precipitation and continental runoff (Hsü et al., 1973; 1977). The MSC was of major consequence to Mediterranean marine organisms by reducing the amount of habitable space, and making for a hostile environment, which wiped out and diminished many taxa (Kouwenhoven et al., 2006; Bison et al., 2007).

Whilst numerous studies (e.g. Habib, 1971; Ediger et al., 1996; Ioakim et al., 1997; Londeix et al., 1999; 2007 and Section 3.6) have investigated the effects of the MSC on dinoflagellates cysts, the Eastern Mediterranean is one area that has been under sampled (~17 publications; Section 3.6), and no studies, to the best of the author's knowledge, have been carried out on organic-walled dinoflagellate cysts in Cyprus. This study aims to supplement the dinoflagellate cyst literature, and provide an insight into the consequences of the MSC on dinoflagellate cyst assemblages in the Eastern Mediterranean.

In the modern the distribution and relative abundance of modern dinoflagellate cysts have been revealed to be related to temperature, salinity and nutrient availability (Marret and Zonneveld, 2003; Zonneveld et al., 2013, see Chapter 1 for a more detailed discussion). This relationship has also been demonstrated to have existed in the geological past (e.g. de Vernal et al., 2005; Head, 1997; De Schepper et al., 2011; Londeix et al., 2007; Schrek and Matthiessen, 2013; Chapter 3). This means that they can be used to determine the palaeoenvironment of deposition including: distance to shore, temperature, sea surface salinity and productivity, during the study period. Section 3.6 presented a declining dinoflagellate cyst diversity and significantly different assemblage compositions between the late Miocene and the Pliocene. These changes were related to the MSC, but due to a lack of information on the environments of deposition and abundance counts, it was not possible to distinguish any differences to assemblages in deeper waters relative to shallow water assemblages. This is especially important because of the debate as to if the Messinian evaporites precipitated synchronously in shallow and deep waters (Roveri et al., 2014).

Therefore, this chapter specifically aims to investigate: what was the palaeoenvironment of deposition, do dinoflagellate cyst assemblages differ locally before and after the MSC (as they did regionally; Section 3.6), does the diversity change as a result of the MSC and do the Cyprus assemblages demonstrate a similar trend to the regional pattern depicted in Section 3.6? By answering these questions it is hoped it will be possible to infer the local and regional effects of the MSC on dinoflagellate cyst assemblages in the Eastern Mediterranean. This will aid in the understanding of the changes to the palaeoenvironment as a consequence of the closing Western Mediterranean Gateway.

5.1.1 Geological History of Cyprus

The island of Cyprus is located in the Eastern Mediterranean Sea and its position between two converging plates (the African and Eurasian plates) has resulted in a complex geological history (McKenzie, 1972; Papazachos and Comninakis, 1978; Jackson and McKenzie, 1984;

1988; Ben-Avraham et al., 1988; Follows, 1992; Payne and Robertson, 1995). The convergence of the plates resulted in an entire ophiolite sequence emerging above sea-level (as seen today). It first emerged at ~15 Ma and began to erode resulting in detrital material being deposited amongst the younger sediments (Robertson, 1977; Eaton and Robertson, 1993; Payne and Robertson, 1995; Robertson et al., 1995; Krijgsman, 2002; Lord et al., 2009). Uplift to the region is interpreted from the changing sedimentation of the Paleocene-early Miocene deepwater pelagic carbonate Lefkara Formation (Robertson, 1976), to the shallower mixed detrital carbonate sediment of the Nicosia Formation (McCallum and Robertson, 1995) and the eventual emergence of the entire ophiolite sequence seen today.

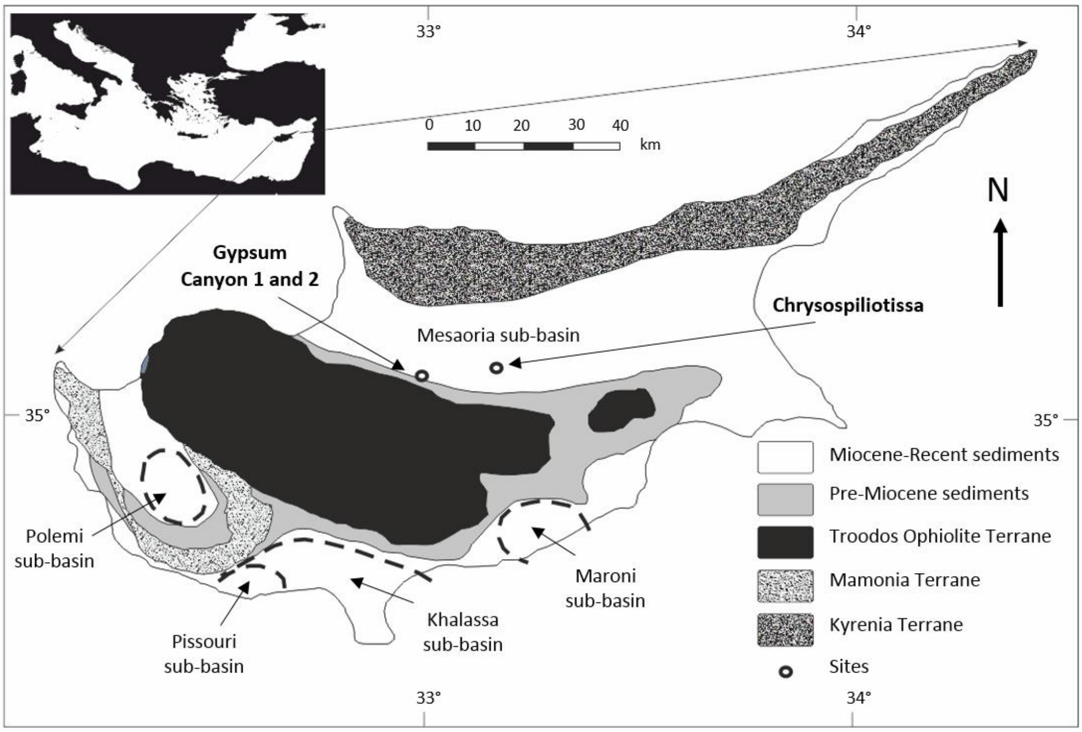


Figure 5-1: Location map with Cyprus's main basins, and the sites used in this study.

Due to the tectonic activity that took place during the formation of Cyprus, five distinct sub-basins formed (Figure 5.1). These are the Polemi sub-basin in the west, the Pissouri sub-basin in the southwest, the Khalassa sub-basin in the south, the Maroni sub-basin in the east and the Mesaoria sub-basin in the north (Payne and Robertson, 1995). Each basin has a slightly different sedimentary succession depending on where the basin was situated and when it formed. The duration of extensional periods leading to the formation of the basins were variable and occurred at different times. For example, the Mesaoria sub-basin formed during an extensional phase from the late Miocene to the early Pliocene, the Pissouri sub-basin formed during extension in the late Miocene but the Maroni and Khalassa formed in the early to middle Miocene (McCallum and Robertson, 1987; Orszag-Sperber et al., 1989; Robertson et al., 1991; Eaton and Robertson, 1993; Grand et al., 1993; Payne and Robertson, 1995).

5.1.1.1 Late Cretaceous (100.5–72.1 Ma)

The Troodos Ophiolite Complex formed during the Late Cretaceous (92–90 Ma; Mukasa and Ludden, 1987) in the Neotethyan Ocean at a subduction zone spreading axis (Pearce, 2003). It has been continually uplifting, due to the convergence and subduction of the African Plate under the Eurasian Plate, and today reaches a maximum height of 2000 metres above sea level (Robertson, 1977). Today the Troodos Ophiolite Complex outcrops in a band across the middle of Cyprus, and forms one of the three main terrains of Cyprus (Follows, 1992; McCallum and Robertson, 1995). The other terrains are the Mamoni and the Kyrenia (Payne and Robertson, 1995). Due to their continual uplift, the ophiolites have a broad anticlinal structure with harzbergites and dunites in the centre (at the highest elevation), radiating outwards to gabbros, sheeted dykes and pillow lavas, at lower elevations (Moores and Vine, 1971).

Before the Ophiolite sequence became exposed above the water, the Perapedi Formation was deposited directly on top of the pillow lavas of the Troodos Ophiolite. Today the Perapedi Formation is found on the edge of the Troodos, marking the start of the sedimentary succession. Sediments of the Perapedi Formation are deep water sediments, deposited below the carbon compensation depth and are primarily siliceous. The succession is not continuous and can be split into two main units. The base of the Perapedi Formation is made up of very fine grained brown umbers, which are a product of hydrothermal vents on the seafloor, and the upper part is a lighter pink colour composed of radiolarians dated 92–84 Ma (Bragina and Bragin, 2006; Bragina, 2013).

5.1.1.2 Maastrichtian – Aquitanian (72.1–20.44 Ma)

The oldest sediments found on Cyprus are from the Lefkara Formation. The Lefkara Formation was deposited from the Late Cretaceous to the early Miocene (~72–21 Ma; Kähler and Stow, 1998) and consists of massive, chert free, white chalks in its lower portion, which grade upwards into more thinly bedded chalk as shallowing occurred. Lefkara sediments occur in bands across southern Cyprus and reach thousands of metres thick in the southern basins (Follows, 1992). It was deposited in a small closing ocean basin, in water depths between 2000 and 3000 m, where the setting changed from a basin plain to a distal slope-apron (Robertson et al., 1991; Kähler, 1994; Kähler and Stow, 1998; Stow et al., 2002). Sedimentation was strongly controlled by tectonic activity including the continued uplift of the Troodos Ophiolite Complex, the subduction of the Kyrenia Range to the North of Cyprus and the onset of subduction to the south of the island (Stow et al., 2002).

The formation can be subdivided into four lithological units (Kähler and Stow, 1998). The oldest unit is made up of pinkish marls, white chalky marls and cherts. Bioturbation is present throughout and turbiditic structures are common in the upper section of this oldest unit (Kähler and Stow, 1998). Above this lies chalk, chert and marly chalks in which turbidite structures are less common, and above this is a more continuous subunit of massive chalks. The youngest subunit (late Oligocene-early Miocene) is composed of marls and chalky marls that become increasingly calcarenitic towards the top.

A generalised succession of events begins with pelagic deposition followed by turbidites, a return to pelagic deposition and then evidence of contourites formed by a bottom current (Stow et al., 2002). The contourites were thought to have developed due to an intensification of bottom current flow caused by the closing Tethys Seaway, i.e. the closure of the Eastern Mediterranean Gateway as well as the other tectonic events, which increased the slope gradient (Stow et al., 2002; Allen and Armstrong, 2008).

5.1.1.3 Aquitanian – Tortonian (23.03–7.25 Ma)

The Lefkara Formation grades into the Pakhna Formation and represents a shallower environment, which allowed the development of coral reefs in some regions (the Terra and Koronia members; Payne and Robertson, 1995). Its hemipelagic deposition is interpreted as relating to the continued uplift of the Troodos Ophiolite Complex, increasing the amount of terrigenous deposits (Eaton and Robertson, 1993; Lord et al., 2009). The Lefkara Formation's thickness ranges between 407 and 609 m (Bear, 1960; Robertson, 1977) and it is mostly composed of pelagic calcarenites and marls, which contain five main facies: lime mudstone, marlstone, laminated calcilutite, calcarenite and rudites (Eaton and Robertson, 1993).

The lime mudstone is dominant in the lower part of the Pakhna and is most often found deposited directly on top of the Lefkara formation, near the ophiolites (Eaton and Robertson, 1993). It was deposited in an outer shelf to bathyal setting and contains deep water trace fossils such as planolites, chondrites and zoophycos (Eaton and Robertson, 1993). The proportion of benthic to planktic foraminifera provide palaeo water depths between 700 and 1100 m (Parker, 1958; Eaton and Robertson, 1993). Calcarenites are found throughout the Pakhna Formation, but are more common higher up the section. They are formed from sediments deposited by dilute to high density turbidity currents, and contain shallow water carbonates that have been reworked into deeper waters. Marlstones are also found throughout the section and become more abundant towards the top of the Pakhna Formation. They include dark organic rich mudstones and were deposited in the deep sea (Eaton and Robertson, 1993). The laminated calcilutites and the rudite facies are both restricted to the uppermost sequences of the Pakhna Formation. The laminated calcilutite depicts a quiet marine environment of deposition that shallows upwards as it transitions into the Messinian Kalavasos Formation (Eaton and Robertson, 1993). The rudite facies represents two types of channel fill deposits. One is clast supported and the other is matrix supported. The first forms largely channelised or laterally extensive sheets with planar bases, whereas the second is found in channel-fill sequences and often cuts into the marls and chalks (Eaton and Robertson, 1993).

The Pakhna Formation includes two stages of reef growth, which are the Terra and the Koronia members. The Terra Member is the older (Aquitanian and Burdigalian) and lies between pelagic carbonates, and is a frame stone type reef (Follows, 1992), whereas the younger Koronia Member (Tortonian) formed in depocentres and is a bind stone type reef (Follows, 1992). Both the Terra and the Koronia members are not continuous and grade into the more prominent sediments, the hemipelagic calcarenites and chalks (Payne and Robertson, 1995). The environment of deposition is thought to be shallower than for the Lefkara, allowing the reefs to form (Robertson et al., 1991), and consists of hemipelagic sediments that generally shallow throughout the formation (Lord et al., 2009).

The conditions of deposition towards the top of the Pakhna Formation became more restricted, which can be seen in the assemblages of a variety of fossil groups. For example, the diversity of diatoms decreased and their assemblages switched from being dominated by marine species to being dominated by shallow water benthic species (Merle et al., 2002) a pattern that was also recorded in the molluscs (Pestrea et al., 2002). Similar patterns were seen in the Pissouri motorway section, where the diversity of plankton and benthic foraminifera, and calcareous nannoplankton decreased from just after the Tortonian/Messinian boundary at ~7.167 Ma (Kouwenhoven et al., 2006). These changes are thought to have been caused by regional factors and a similar decrease in the diversity can be seen throughout the Mediterranean Sea at this time (Seidenkrantz et al., 2000; Orszag-Sperber et al., 2009), with increasingly unfavourable and more restricted palaeoenvironments from the early Messinian (Kouwenhoven et al., 2006).

5.1.1.4 Messinian (7.25–5.33 Ma)

During the late Miocene, the Western Mediterranean Gateways began to close, restricting the throughflow of water between the North Atlantic and the Mediterranean Sea. This resulted in the amount of evaporation exceeding the replenishment of water, and led to the precipitation of vast quantities of evaporites (Martín et al., 2001; Manzi et al., 2015; also see discussion in Chapter 1, Section 1.2.6). The evaporites on Cyprus (the Kalavasos Formation) are composed of a variety of different types of gypsum including: banded-stacked (layered) selenite, swallow tail selenite, botryoidal selenite and sugary bedded selenite (Robertson et al., 1995). They are thought to have formed in semi-isolated and structurally variable basins such as the Polemi, Psematismenos and Pissouri basins (Orszag-Sperber et al., 1989; Robertson et al., 1995; Krijgsman, 2002; Bison et al., 2007), although the gypsum then precipitated widely and has been found reworked as deep as 70 m below the surface (Robertson et al., 1995). The evaporites are both under and overlain by shallow water sediments, the Pakhna (below) and the Nicosia (above), which provides evidence that the MSC occurred due to rapid evaporation and sudden reflooding events, allowing conditions to change and change back so abruptly (Hsü et al., 1977; Kastens et al., 1988). Some authors have argued that there is evidence of a complete drying up in certain regions; for example at Psematismenos, where desiccation cracks and palaeosols can be found (Krijgsman, 2002; Orszag-Sperber, 2006). However, new evidence suggests that there is no indication of desiccation, and that precipitation occurred under permanent subaqueous conditions (Lugli et al., 2015; Manzi et al., 2015). Pelagic oozes can be found within the Messinian evaporites, providing evidence of intermittent flooding of marine waters into the Mediterranean Basin, also contradicting any complete desiccation theories (Hsü et al., 1973; Rio et al., 1976; Di Stefano and Catalano, 1978). The Kalavasos Formation records the salinity crisis and the three stage model (Section 1.2.6; Figure 1.4), which is used in the Western Mediterranean, can be depicted in the Eastern Mediterranean, at least for the margins of the basins. This suggests that the salinity crisis affected the whole of the Mediterranean synchronously (Manzi et al., 2015).

The formation can be subdivided into three main subunits, which are: the lower gypsum, the intermediate breccia and the Lago Mare deposits/the Upper Gypsum (Rouchy, 1982; Robertson et al., 1995; Orszag-Sperber et al., 2009; Manzi et al., 2015). At the base is a carbonate breccia layer with stromatolitic deposits (Rouchy, 1982; Orszag-Sperber et al., 2009; Manzi et al., 2015). This is followed by the first subunit, the lower gypsum, which at its thickest is 70 m (Robertson et al., 1995; Manzi et al., 2015). It is composed of a variety of gypsums; including selenitic, laminar, clastic and nodular (Rouchy, 1982; Manzi et al., 2015). The intermediate unit is up to 20 m thick and is made up of gypsum clasts and blocks in a carbonate/gypsarenite matrix (Rouchy, 1982; Manzi et al., 2015). The upper gypsum unit is 60 m thick and has a very variable lithology, which has been subdivided into six beds (Rouchy, 1982; Manzi et al., 2015). The bottom three beds are dominated by selenitic gypsum, and the top three by laminar gypsum with clastic and nodular selenitic gypsum. The beds are separated by marl horizons, which include typical Lago Mare (a chain of shallow lakes) fauna of Paratethyan affinity (Roveri et al., 2008b).

Diversity in the Kalavasos Formation is thought to be very low. For example only 3 to 11 species of calcareous nannofossils were found in samples by Wade and Bown (2006), who noted that the assemblages were uneven with one of five species dominating in every sample, displaying opportunistic behaviour. A similar pattern is seen in the planktonic and benthic foraminifera where the diversity decreased through the Messinian (Kouwenhoven et al., 2006).

5.1.1.5 Pliocene – Pleistocene (5.33–1.8 Ma)

At the start of the Pliocene, the Western Mediterranean Gateway reopened and brought normal marine conditions back to the Mediterranean (Hsü et al., 1977). In Cyprus, the Nicosia Formation was deposited on top of the evaporites of the Kalavasos Formation, and four distinct facies have been recognised, representing 900 m of sediment (McCallum and Robertson, 1995). Facies one represents the bulk of the Nicosia Formation, and is composed of grey-brown homogeneous calcareous clayey siltstones. The fine grained sediments are thought to have been deposited through background sedimentation in shallow palaeo water depths ranging from tens to hundreds of metres deep. The water depths are inferred from the presence of a large number of bivalves and gastropods, such as *Turritella communis*, which today lives in water depths between 30 and 150 m (Pérès, 1967). Facies two and three are coarser and the sediments range from sandstone to conglomerates. Whilst facies two and three are distinct from each other, both are thought to have resulted from turbidites/mass flow deposits that cut into the background sedimentation of facies one. Facies four is composed of lenticular sandstones and siltstones and is thought to be the result of channel fill, but unlike facies two and three, the channel fill from facies four is thought to have been deposited further out into the basin (McCallum and Robertson, 1995).

The Nicosia Formation generally shallows from palaeo water depths of hundreds of metres to depths of tens of metres. This is as a result of the continued uplift of the Troodos Ophiolite Complex, which was by this point exposed above sea level, and is the reason for the increasing quantity of detrital and plant material moving up through the section (McCallum and Robertson, 1995).

The environments of deposition before and after the MSC were similar, and because of this Dornbos and Wilson (1999) were able to compare a patch reef in the Nicosia Formation (after the MSC) to one in the Koronia Member (before the MSC). They found that the structure of both patch reefs were similar. Epifaunal niches were dominated by suspension feeding bivalves and infaunal niches were dominated by shallow active suspension feeders, mostly burrowing bivalves with some *Turritellid* gastropods. The Nicosia reef was not as diverse and only 13% of the species found in the Koronia Member (Cowper Reed, 1935a) were also found in the Nicosia reefs. This suggests that the effects of the MSC were severe with relatively few reef forming species surviving. However, because of the similarity of the guild structures, it is thought that a near full and rapid recovery was made, but with new species appearing. Bison et al. (2007) saw similar patterns in the calcareous dinoflagellates of the Pissouri motorway sections, where diversities were roughly the same before and after the MSC, but the assemblages were composed of different species.

5.1.2 Previous dinoflagellate cyst studies

Previous dinoflagellate cyst work undertaken in the Mediterranean spans from the Cretaceous-Paleogene boundary (Brinkhuis and Zachariasse, 1988; Eshet et al., 1994) to studies on recent sediments (Montresor et al., 1998; Meier and Willems, 2003). Regarding the Neogene, ~230 individual dinoflagellate cyst species have been found in the Mediterranean/Paratethys (TOPIS; Section 3.6), and the late Miocene to the early Pliocene in particular have been researched. This is because much of the literature investigated the effects of the MSC on dinoflagellate cysts (Kontopoulos et al., 1997; Warny et al., 2003; Londeix et al., 2007; Melinte-Dobrinescu et al., 2009; Popescu et al., 2009; Do Couto et al., 2014).

There are several publications (Versteegh, 1994; 1997; Versteegh and Zevenboom, 1995) investigating cores south of Italy with ages ranging between the Miocene to recent. However, dinoflagellate cyst studies relating to Cyprus are limited to just two, both on calcareous dinoflagellates, one covering the Zanclean (Bison et al., 2009) and the other spanning the MSC (Bison et al., 2007). Further publications that concentrate on sites found in the eastern Mediterranean include, but are not limited to: Zonneveld (1995) and Sangiorgi et al. (2002) on the last deglaciation, Santarelli et al. (1998) on the late Miocene of Crete and Sancay et al. (2006) on the Oligocene-Miocene boundary in Turkey.

Literature focussing on dinoflagellate cysts from the Neogene have concentrated on a variety of aspects, such as: reconstructing palaeogeography and environments (Santarelli et al., 1998; Warny et al., 2003; Londeix et al., 2007; Popescu et al., 2009), effects of the MSC on (calcareous) dinoflagellate assemblages (Bison et al., 2007; Melinte-Dobrinescu et al., 2009), and marine incursions of the Paratethys/Mediterranean (Do Couto et al., 2014). Londeix et al.

(2007) focusses on dinoflagellate cysts in Sicily from before and after the MSC. Their oldest samples are from the end of the Tortonian, where assemblages have evidence for a marine environment of deposition, but with significant terrestrial input, which made it favourable for eutrophic species. At the start of the Messinian, shallowing occurred and meso-hyperhaline assemblages dominated. The basin became more confined, however, there was evidence of nearby normal marine sea surface waters that periodically infilled the basin. In the upper evaporites, the infilling of periodic marine waters reduced, as did any input from rivers, suggesting a drier climate. This was also observed from the pollen found in Messinian evaporites from Zakynthos (Kontopoulos et al., 1997). Bison et al. (2007) compare calcareous dinoflagellate cyst assemblages from before and after the MSC in Cyprus. They found that the assemblages of the lower Tortonian were rich, with a low diversity, and species preferred open ocean waters. In the upper Messinian, there were fewer cysts, although the diversity was higher. By the lower Pliocene normal marine conditions returned, as did rich assemblages, but with a low diversity. There was a shift in the dominant species and they conclude that there must have been marine refuges.

Palynology studies are also used to research the climate, and an example on the Greek island of Zakynthos (Kontopoulos et al., 1997) uses both dinoflagellate cysts and pollen to show that the area transitioned from being warm and wet prior to the MSC, to an arid environment during the MSC, and then to a moist temperate environment in the earliest Pliocene. Ioakim et al. (1997) looked at the Sita region in Eastern Crete (Greece) and concentrated on the upper Miocene and lower Pliocene. They demonstrate that the Tortonian had a diversified vegetation with dominantly tropical-subtropical elements and some temperate elements. Pollen of the Messinian exhibited a drier climate with open vegetation at low altitudes. Ioakim et al. (1997) found that the Messinian beds alternated between marls and selenite gypsum, and they equated this to alternations between warmer and drier conditions (gypsums) and cooler and shallow water (marls). By the early Pliocene, the flora was once again well-diversified, which was associated with the new water exchange with the Atlantic Ocean (Ioakim et al., 1997).

Dinoflagellate cyst studies that have focused on the older sediments of the early and middle Miocene include: Balteş (1967; 1969); Jimenez-Moreno et al. (2006) and Soliman and Piller (2007). Soliman and Piller (2007) found that the early Miocene of the Central Paratethys (now Austria) had a low diversity of species (36), which then decreased further at the Burdigalian-Langhian Boundary. They attributed this decrease to a shallowing shown by an increase in shallow water taxa. Jimenez-Moreno et al. (2006) also looked at dinoflagellate cysts in the early and middle Miocene, in the central Paratethys of what is now Austria, and published the first Miocene dinoflagellate cyst zonation for the Paratethys. The authors found strong similarities with assemblages from the Mediterranean Sea and North Atlantic Ocean for the early and middle Miocene, demonstrating that there was a strong connection between the Central Paratethys and the Mediterranean Sea. In the Eastern Paratethys, work undertaken by Clauzon et al. (2005) challenged the concept of Paratethys isolation since the Serravallian/Tortonian due to two brief influxes of both dinoflagellate cysts and calcareous nannofossils, one immediately before and one immediately after the MSC. Both of these events were correlated to two successive global sea level high stands (Shackleton, 1995; Clauzon et al., 2005).

5.2 Material and methods

The new dinoflagellate cyst data come from two land sections in the Mesaoria Basin, to the north of the Troodos Mountains in Cyprus (Gypsum Canyon and Chrysospiliotissa; Figure 5.1). The older of the sections (late Miocene) is from two closely located sites that are situated close to an abandoned gypsum quarry (Gypsum Canyon). Gypsum Canyon 1 and 2 are located unconformably below the quarry, at 35°03’54.6’’N, 33°06’07.5’’E and 35°03’56.1’’N, 33°06’01.3’’E respectively, both are at ~350 metres above sea level and are ~1 km northwest of Kato Moni (Figure 5.2 and Table 5.1). Seven samples were collected and processed, five from Gypsum Canyon 1 and two from Gypsum Canyon 2 (Figures 5.3a and b). The sediments are from the Pakhna Formation (Wood, 1996) and the evaporites of the Kalavasos Formation lie unconformably on top of the section (Robertson et al., 1991; 1995; Manzi et al., 2015). The samples were collected from every accessible marl layer, which ranged from a couple of centimetres to 1 m thick, resulting in a collection of five samples (Figures 5.2, 5.3a and b). Dating (late Miocene) of the site comes from a previous study on foraminifera (Wood, 1996) and the evaporites that lie unconformably ontop of the section (from facies analogies) are dated to the Messinian (Manzi et al., 2015).

The younger section (Chrysospiliotissa; Pliocene) is located at 35°05’27.452’’N, 33°16’48.269’’E and is ~260 metres above sea level. The section is 11 m in height and 14 samples were collected. The sediment, for all except the top most sample, is composed of faintly laminated marlstone and comes from the Nicosia Formation (Figures 5.3c and 5.4). The top most sample is a conglomerate with a marlstone matrix. The site is roughly 0.3 km north-northeast of the village Kato Deftera, and just 0.2 km west of the church Chrysospiliotissa. Dating of the samples stems from the sedimentology, which indicates the Nicosia Formation, and the age of the Nicosia Formation has been dated using foraminifera (Bellamy and Jukes-Browne, 1905), nannofossils (Follows, 1996) and macrofossils such as molluscs and brachiopods (Cowper Reed, 1935b).

Site	Age	Formation	Latitude	Longitude	MASL	Dating	Dating Method
Gypsum Canyon 1	Late Miocene	Pakhna	35°03'54.6''N	33°06'07.5''E	360	Wood (1996) and Manzi et al. (2015)	Biostratigraphy (planktonic foraminifera and calcareous nannofossils) and petrographic analyses
Gypsum Canyon 2	Late Miocene	Pakhna	35°03'56.1''N	33°06'01.3''E	348	Wood (1996) and Manzi et al. (2015)	Biostratigraphy (planktonic foraminifera and calcareous nannofossils) and petrographic analyses
Chrysospiliotissa	Pliocene	Nicosia	35°05'27.452''N	33°16'48.269''E	260	Bellamy and Juke-Browne (1905); Follows (1996); Cowper Reed (1935b)	Biostratigraphy (foraminifera, nannofossils, molluscs and brachiopods

Table 5-1: Site locations and dating methods

The presence of high organic silty marls suggests low energy conditions, and the indurated carbonate beds of the Pakhna Formation at Gypsum Canyon are possibly the result of the outer most limit of debris flows (Eaton and Robertson, 1993). This places the environment of deposition in middle-outer neritic waters for the late Miocene at Gypsum Canyon. The presence of turbidites/debris flows complicates the interpretation as it means that the dinoflagellate cysts may have been transported downslope in the currents, and therefore might not represent their original environment of deposition. The uppermost fine grained beds were preferentially sampled as they should be more representative of background sedimentation, and contain less transported material. There is less evidence of turbidites/debris flows in the Pliocene Chrysospiliotissa and the environment of deposition was low energy inner neritic (McCallum and Robertson, 1995). Every marl bed of sufficient size was sampled (collecting non-weathered material), and where a marl bed was especially thick, samples were collected every ~25 cm.

5.2.1 Sample processing

Fresh and unweathered sediment was collected from the various sites described above and brought back to the UK for processing at the British Geological Survey, Keyworth. Owing to the high carbonate content, where possible ~100 g of each sample was processed. However, due to weathering and the thinness of some of the marl layers, it was not always possible to collect so much fresh material. The cleaned and weighed samples were crushed into pea-sized fragments and a *Lycopodium* tablet (batch number 3862) was added. Once prepared, each sample was processed using the standard palynology technique described by Wood et al. (1996).

The processing technique is split into two main stages: chemical and mechanical separation. The aim of both stages is to separate and isolate the palynomorphs from the sediments, concentrating them in the process. Chemical separation was carried out using hydrofluoric (HF) and hydrochloric acid (HCl) and mechanical separation comprised of sieving and heavy liquid separation; the full process is described in more detail below.

HCl (36%) was added to the samples, to dissolve and break up the carbonates, and left until the reaction ceased (roughly two hours at room temperature). This process was then repeated but with HF (40%) to remove any silicates and left for roughly one week in a fume hood. The acid was decant-washed away and, when neutral, the residue was sieved with a >10 µm mesh to remove the finer debris. At this stage, amorphous debris can be removed from post-acid residue by brief oxidation using nitric acid. However, this was not necessary for the samples discussed in this chapter since there was no, to very little, amorphous debris in the samples.

Figure 5-2: Field Photos of Gypsum Canyon. (Top) Gypsum unconformably on top of the Pakhna Formation. (Middle) Gypsum Canyon 1. (Bottom) Gypsum Canyon 2. Dashed lines represent the boundary between the gypsum and the underlying sediments.

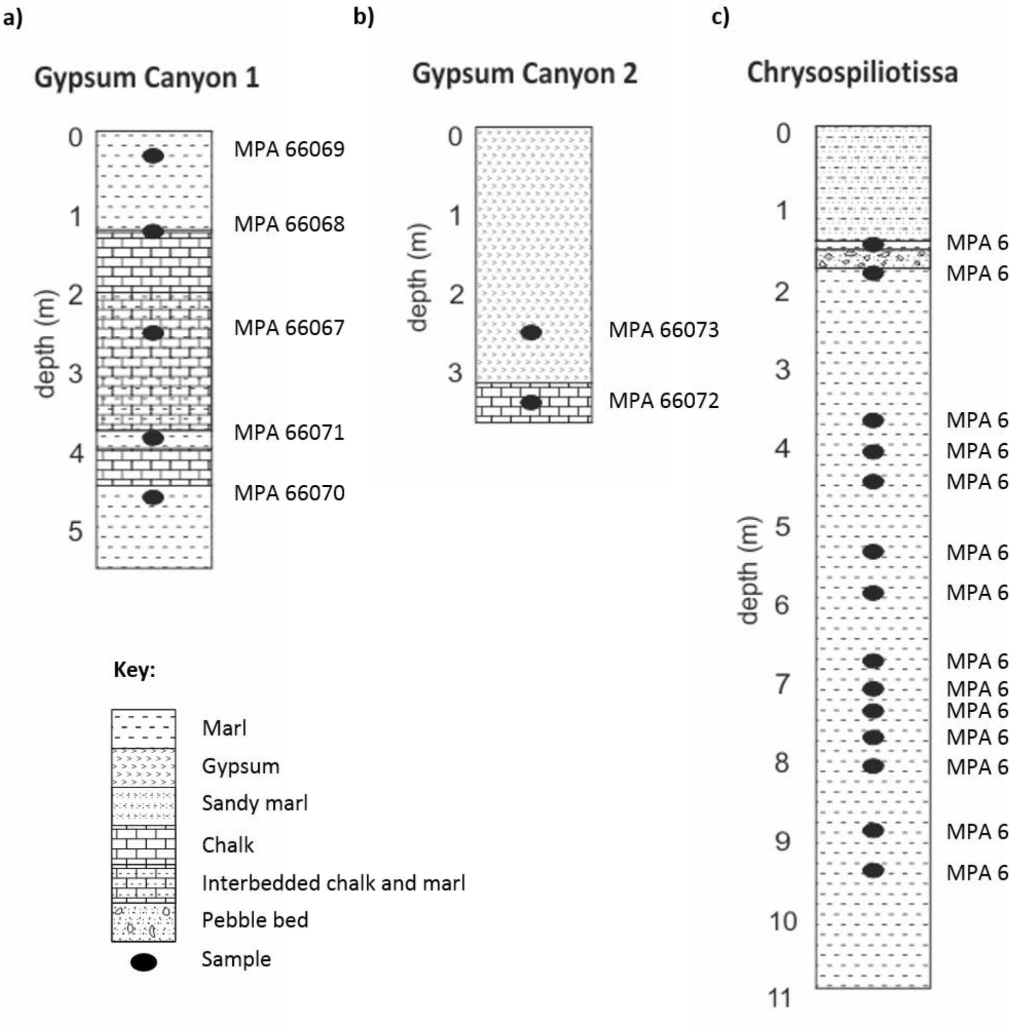


Figure 5-3: Sedimentary log of (a) Gypsum Canyon 1, (b) Gypsum Canyon 2 and (c) Chrysospiliotissa.

The material was then concentrated and centrifuged in water, which resulted in the palynomorphs having sunk to the bottom of the tube. The water was then decanted and acidified zinc bromide solution was added and centrifuged. This time, the palynomorphs floated on the surface and were pipetted out of the solution and added to a separate empty container. The acidified zinc bromide solution was then washed out and in some cases stain was added. In the final stage, dispersant was added and then the residue was mounted on a cover slip and left to dry. It was then mounted on a microscope slide using elvacite. Where possible, 300 palynomorphs were counted from each sample. However, two of the samples from Gypsum Canyon 1 (MPA 66068 and 66069; Table 5.2) and both of the samples from Gypsum Canyon 2 contained no dinoflagellate cysts.

Figure 5-4: Field photos of Chrysospiliotissa (top) conglomerate layer at the top of the section (indicated by the arrows). (Bottom) view of the full section.

5.3 Palynology results

The sites sampled and processed were Chrysospiliotissa (Pliocene) and Gypsum Canyon (late Miocene). All of the 14 samples from Chrysospiliotissa contained both dinoflagellate cysts and pollen, but only three of the seven samples from Gypsum Canyon contained both dinoflagellate cysts and pollen (MPA 66067, 66070, 66071). There was one sample (MPA 66073) that was completely barren and the other three (MPA 66068, 66069, 66072) only contained pollen. In both sites, the majority of the dinoflagellate cysts were *Spiniferites/Achomosphaera* spp. (Table 5.2).

5.3.1 Gypsum Canyon – late Miocene

Dinoflagellate cysts are present in three of the five samples at Gypsum Canyon 1 (MPA 66067, 66070 and 66071), and in all cases make up less than 40% of the total palynomorphs (terrestrial + marine) assemblage (Table 5.2 and Figure 5.5). The diversity in each sample ranges from five to seven species (in total there are 10 species) and the concentration ranges from 21 to 1395 dinoflagellate cysts per gram of dried sediment. The most abundant species are *Spiniferites/Achomosphaera* spp. (21.4–58.4%) followed by *Operculodinium* spp., which make a maximum of 57.1% of each assemblage. Also present are *Lingulodinium machaerophorum*, *Nematosphaeropsis labyrinthus/lemniscata*, the acritarch *Nannobarbophora sp.*, *Impagidinium patulum, Hystrichokolpoma rigaudiae* and *Tectatodinium pellitum*. A reworked species is *Hystrichokolpoma cinctum* (MPA 66071).The percentage of pollen in the assemblages ranges from 61 to 100% of the overall palynoflora.

	Gypsum Canyon 1					Chrysospiliotissa													
Age	Late Miocene					Pliocene													
Formation	Pakhna					Nicosia													
depth (cm)	455	385	255	118	15	950	900	816	785	741	715	688	592	548	452	412	377	184	160
Sample number	MPA 66070	MPA 66071	MPA 66067	MPA 66068	MPA 66069	MPA 66053	MPA 66054	MPA 66055	MPA 66056	MPA 66057	MPA 66058	MPA 66059	MPA 66060	MPA 66061	MPA 66062	MPA 66063	MPA 66064	MPA 66065	MPA 66066
Dinoflagellate cysts (raw counts)																			
Achomosphaera sp.	0	0	0	0	0	0	5	4	2	0	3	0	0	7	0	1	4	3	0
Dinocyst sp. A	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dinocyst sp.B	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Dinocyst sp.C	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
*Hystrichokolpoma cinctum**	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
*Hystrichokolpoma pusilla**	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Hystrichokolpoma rigaudiae	0	2	1	0	0	0	1	0	1	2	0	1	0	1	0	0	0	0	0
Hystrichokolpoma sp.	0	0	2	0	0	0	0	1	0	0	1	4	0	9	0	0	0	1	0
Hystrichokolpoma sp?	1	0	1	0	0	3	0	0	3	1	0	0	0	0	0	0	0	0	0
Impagidinium paradoxum	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Impagidinium patulum	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	4	0	0
Invertocysta lacrymosa	0	0	0	0	0	0	1	0	0	0	2	1	0	0	0	0	0	0	0
Lingulodinium machaerophorum	1	4	10	0	0	7	52	0	46	46	6	33	2	49	23	16	18	28	1
Lingulodinium machaerophorum?	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Nematosphaeropsis labyrinthus/lemniscata	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Operculodinium spp. indent	16	15	24	0	0	0	10	1	12	5	1	8	3	10	10	1	3	2	0
Operculodinium? sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Selenopemphix quanta	0	0	0	0	0	0	3	0	0	1	0	0	0	0	5	0	0	0	0
Spiniferites membranaceus	0	0	0	0	0	0	3	0	0	1	0	1	0	1	0	0	0	3	0
Spiniferites mirabilis	0	0	0	0	0	1	5	0	3	5	0	3	0	2	2	2	1	4	0
Spiniferites s p. A of Louwye and De Schepper (2010)	0	0	0	0	0	0	2	0	2	2	0	0	2	2	0	4	0	1	0
Spiniferites/Achomosphaera spp. indent	6	69	32	0	0	26	94	3	106	123	54	112	33	94	77	55	77	83	3
Spiniferites/Achomosphaera? spp. indent	0	5	4	0	0	5	4	1	1	4	1	0	0	1	1	1	0	3	0
Tectatodinium pellitum	0	2	0	0	0	5	1	4	2	2	0	1	2	0	2	3	1	0	0
Tuberculodinium vancampoae	0	0	0	0	0	4	10	11	3	6	9	5	4	8	8	3	6	1	0
Indeterminate	2	2	2	0	0	3	5	1	4	3	2	2	2	0	2	6	0	2	0

Sample number	MPA 66070	MPA 66071	MPA 66067	MPA 66068	MPA 66069	MPA 66053	MPA 66054	MPA 66055	MPA 66056	MPA 66057	MPA 66058	MPA 66059	MPA 66060	MPA 66061	MPA 66062	MPA 66063	MPA 66064	MPA 66065	MPA 66066
Total Dinoflagellate cysts	27	107	78	0	0	56	192	23	184	201	77	173	48	177	131	92	111	129	4
Dinoflagellate cyst concentration	21.3	1394.8	465.1	0	0	210.5	4186.9	40	932.9	1983.5	351.3	1314.4	376.7	1005.8	1062.6	209.2	203.7	849.1	16.7
Marine algae incertae sedis																			
Nannobarbophora sp.	1	11	0	0	0	1	0	0	1	0	5	2	2	2	1	0	1	5	1
Pollen																			
Pollen spp.	273	184	224	46	76	244	119	279	115	110	216	133	252	118	168	207	187	163	325
Total Palynomorphs	301	302	302	46	76	301	311	302	300	311	298	307	302	297	300	299	299	297	330
Indices																			
IN/ON = IN/(IN+ON)	0.14	0.07	0.23	N/A	N/A	0.33	0.36	0.65	0.31	0.29	0.20	0.25	0.19	0.35	0.30	0.26	0.24	0.24	0.25
N/O = (IN+ON)/(IN+ON+O)	0.88	1.00	1.00	N/A	N/A	0.98	1.00	1.00	0.99	1.00	1.00	0.99	1.00	1.00	1.00	0.99	0.96	1.00	1.00
P/D = P/(P+D)	0.91	0.63	0.74	1.00	1.00	0.81	0.38	0.92	0.38	0.35	0.74	0.43	0.84	0.40	0.56	0.69	0.63	0.56	0.99
P/G = P/(P+G)	0.00	0.00	0.00	N/A	N/A	0.00	0.02	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00
Dinoflagellate cyst richness (=number of species)	5	7	6	0	0	8	13	6	11	11	8	12	6	10	7	9	8	9	2
Shannon–Wiener Index	1.01	1.03	1.24	N/A	N/A	1.39	1.48	1.55	1.25	1.14	1.08	1.18	1.04	1.42	1.24	1.21	1.13	1.07	0.56
Evenness (Shannon)	0.55	0.40	0.58	N/A	N/A	0.50	0.34	0.79	0.32	0.28	0.37	0.27	0.47	0.41	0.50	0.37	0.39	0.32	0.88

Table 5-2: Raw counts of the palynomorphs at the two sites. Gypsum Canyon 2 was not include as it was barren. Species marked by an asterisk are reworked. Palynological indices are described in section 5.3.3.

5.3.2 Chrysospiliotissa – Pliocene

Chrysospiliotissa is a Pliocene site made up entirely of marls, of which 14 samples were processed (Figures 5.3c and 5.6). In five samples (MPA 66054, 66056, 66057, 66059, and 66061), dinoflagellate cysts make up more than half of the total palynomorph assemblage and in four samples (MPA 66053, 66055, 66060 and 66066) they make up less than 20% of the assemblages, pollen makes up the rest of the assemblages (Table 5.2 and Figure 5.6). Chrysospiliotissa has a higher diversity than Gypsum Canyon (18 species compared to 10 species) although the diversity of individual samples ranges from six to 13 species in all but one sample (MPA 66066), which only had three species present. The dinoflagellate cyst concentration per gram of dried sediment is also very varied and ranges from 17 to 4187. Overall, the dinoflagellate cyst concentration values decrease upwards in the section.

The most abundant species in samples from Chrysospiliotissa are *Spiniferites/Achomospharea* species with percentages ranging from 11.1 to 66.4% and the second most abundant is *Lingulodinium machaerophorum* with values between 0 and 26.4%. Also present are *Tuberculodinium vancampoae,* the acritarch *Nannobarbophora* sp.*, Tectatodinium pellitum, Spiniferites mirabilis, Hystrichokolpoma rigaudiae, Spiniferites membranaceus, Impagidinium patulum, Impagidinium paradoxum, Selenopemphix quanta* and *Invertocysta lacrymosa.* The sample at the top of the section (MPA 66066) is a conglomerate, possibly produced by a storm event or a debris flow, and contains only four individual dinoflagellate cysts (two different species). Pollen makes up the rest of the count. Sample MPA 66055 also has a very low count of 27 dinoflagellate cysts, but in this case the sedimentology appears no different to the other samples. The percentage of pollen that makes up each assemblages varies from 35% to 99% and there are several spikes of pollen (MPA samples 66055, 66058, 66060, 66063 and in 66066). The presence of one specimen of *Hystrichokolpoma pusilla* in sample MPA 66056*,* is likely reworked.

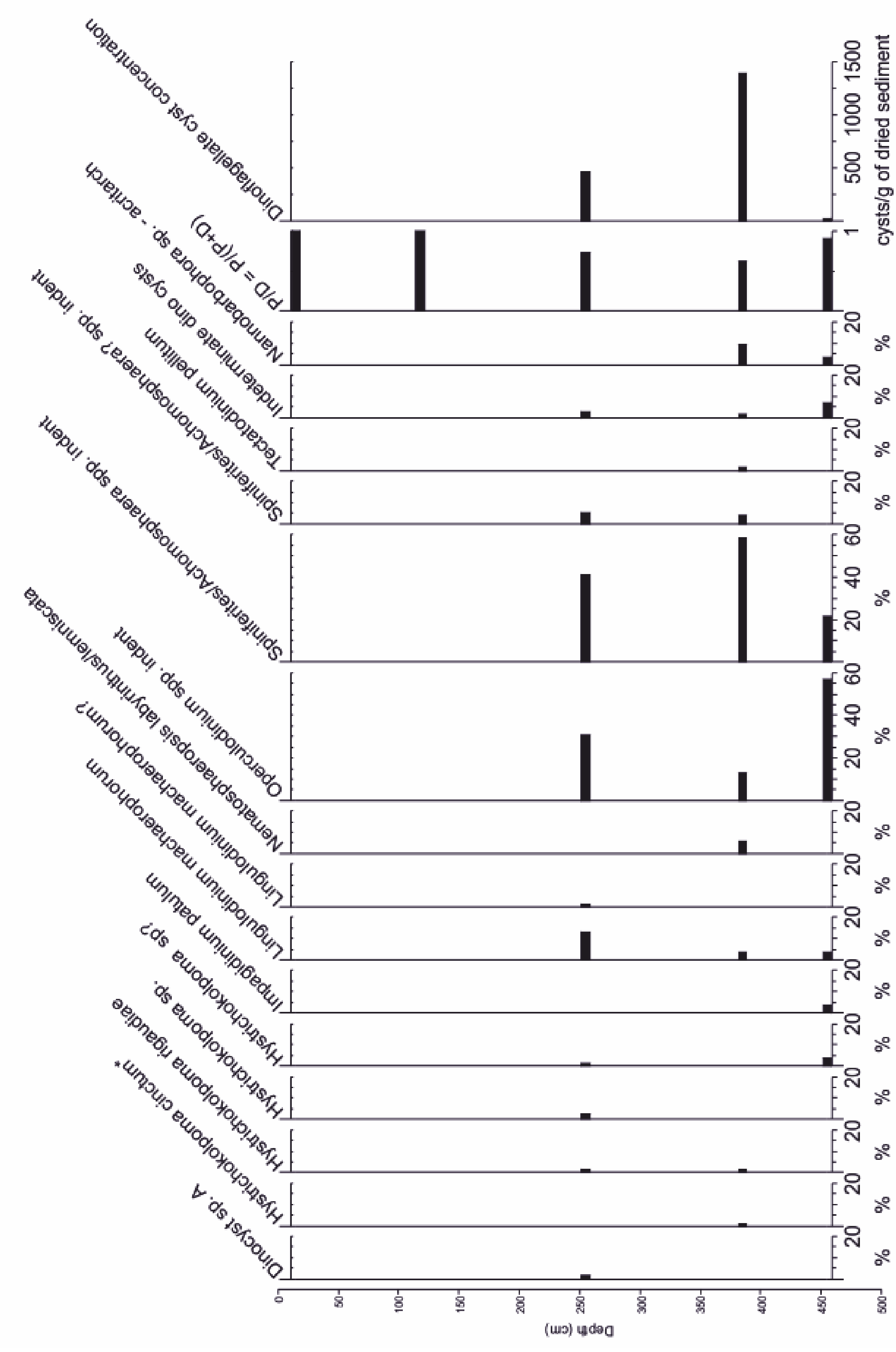


Figure 5-5: The palynology of Gypsum Canyon 1. Dinoflagellate cyst percentages are calculated as a percentage of the total dinoflagellate cyst assemblage.

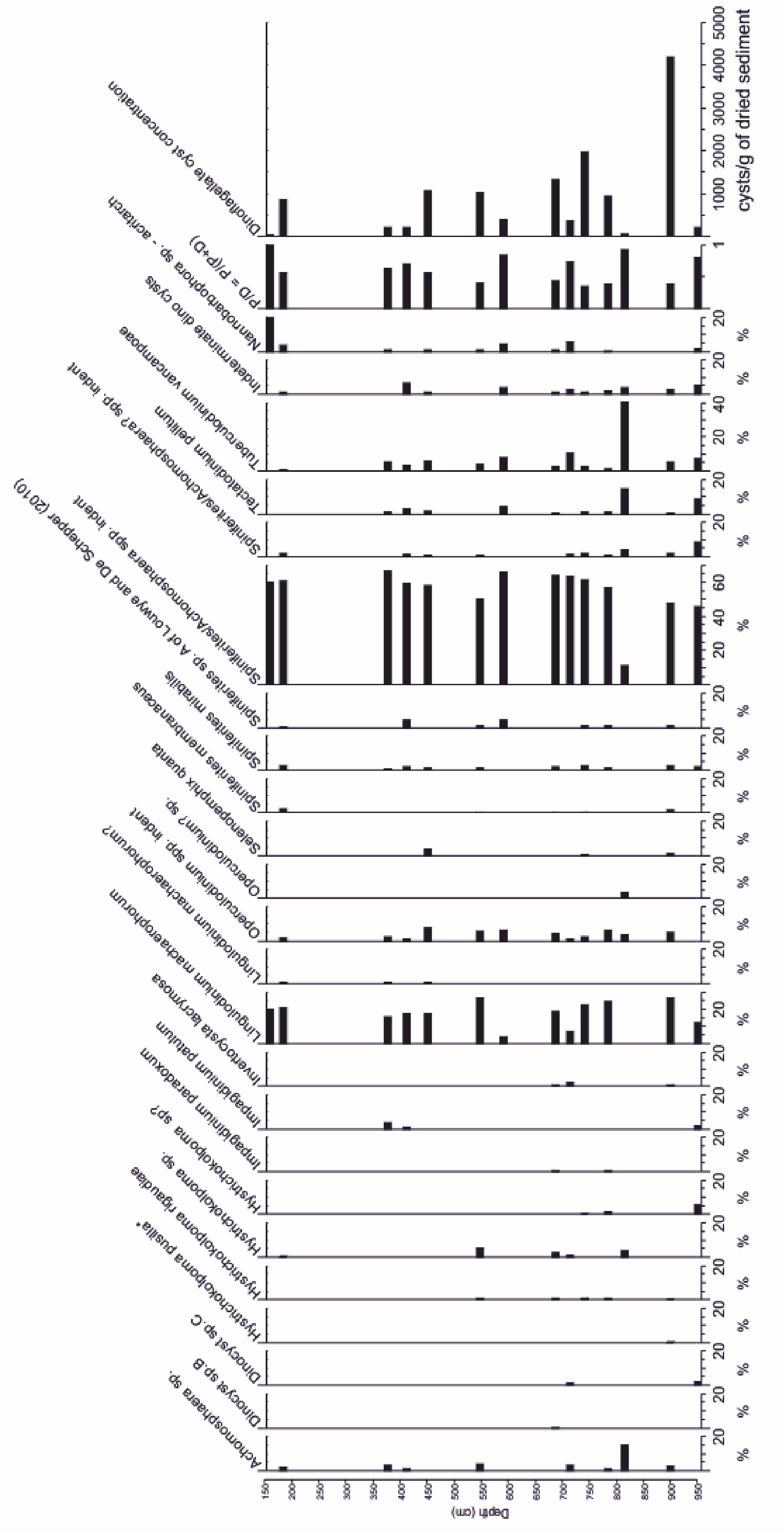


Figure 5-6: The palynology of Chrysospiliotissa. Dinoflagellate cyst percentages are calculated as a percentage of the total dinoflagellate cyst assemblage.

Plate 1

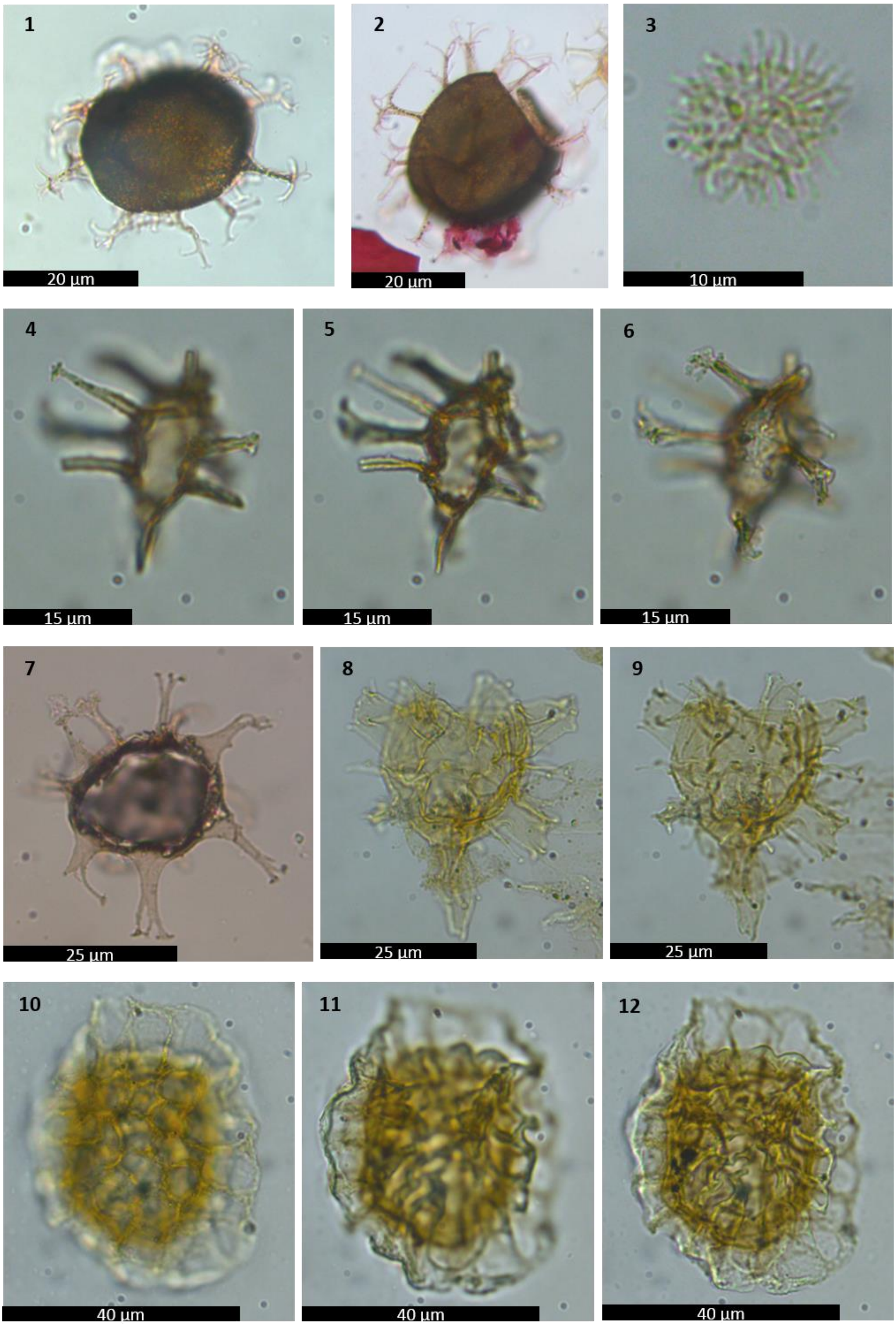

1
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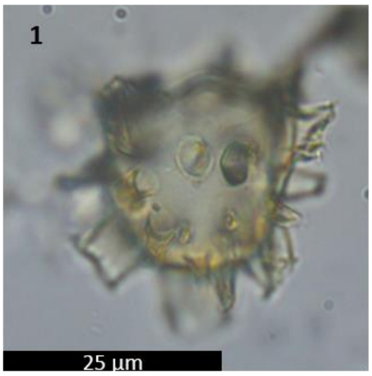
Plate 2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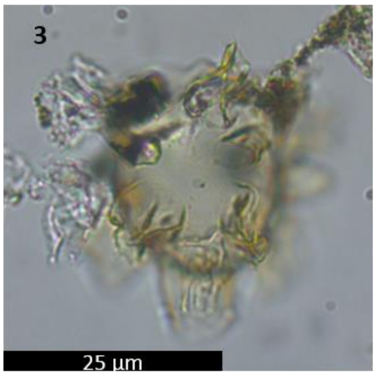
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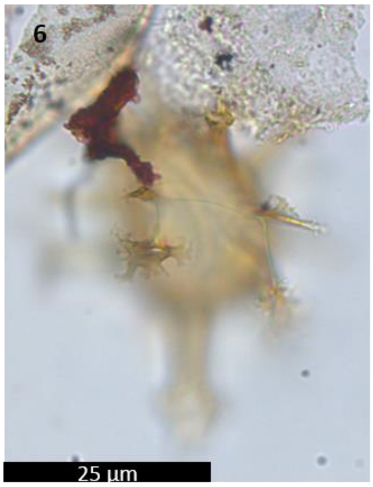
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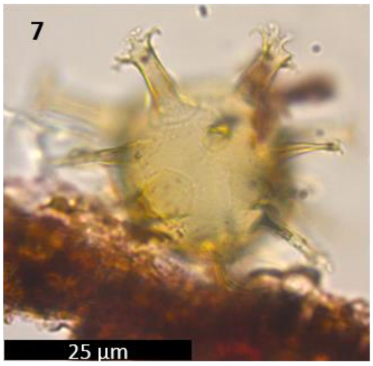
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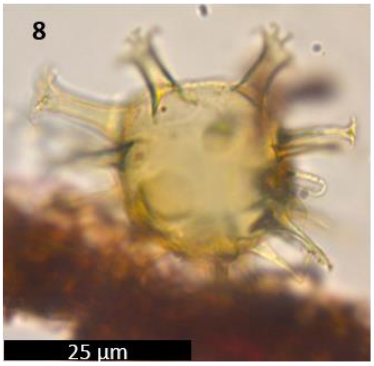
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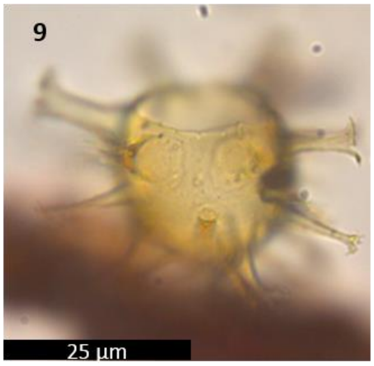
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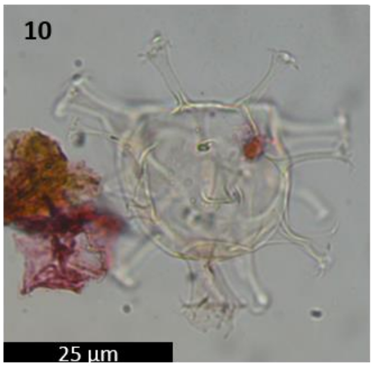
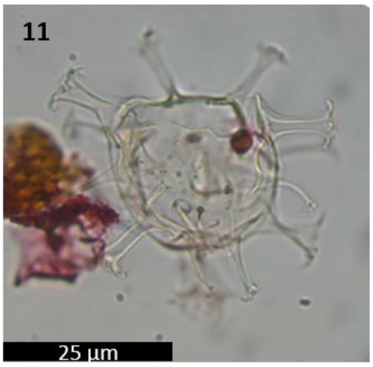

10
25 µm


11
25 µm

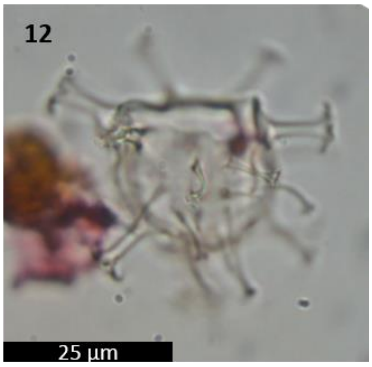

12
25 µm

Plate 3

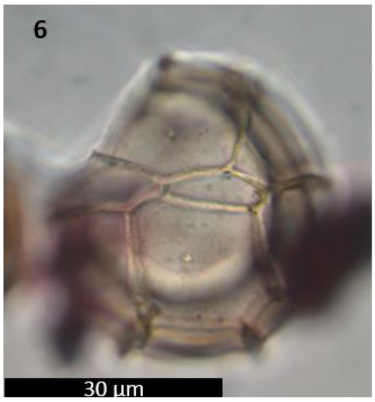

1
10 µm


2
10 µm


3
10 µm


4
30 µm


5
30 µm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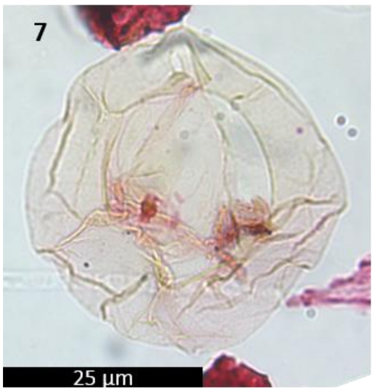
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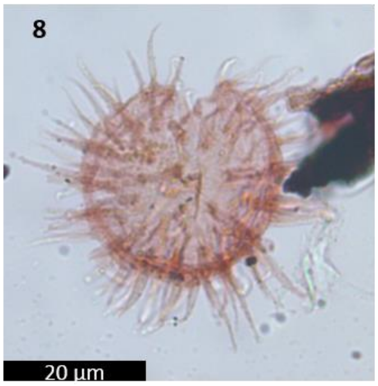
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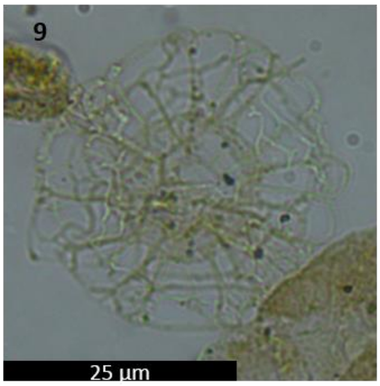
20 µm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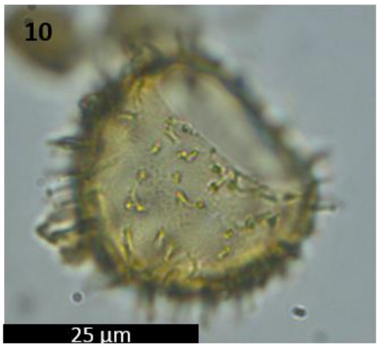
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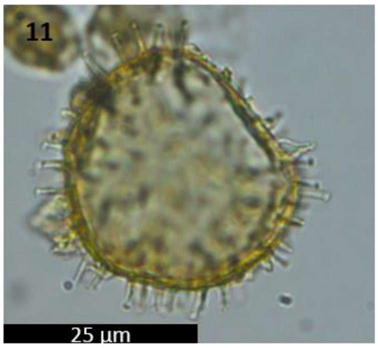
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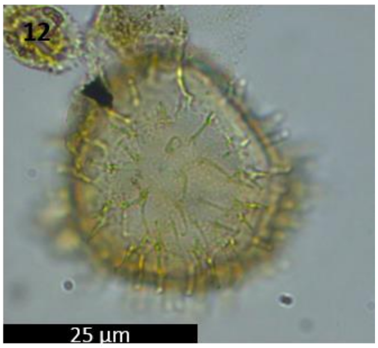
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Plate 4

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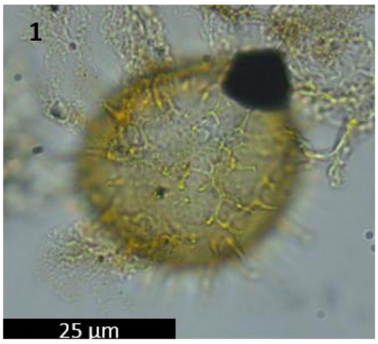

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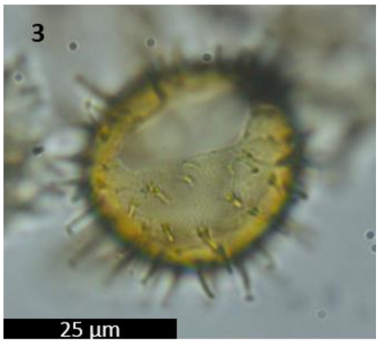

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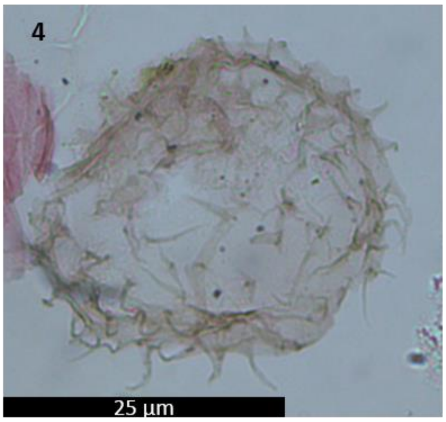

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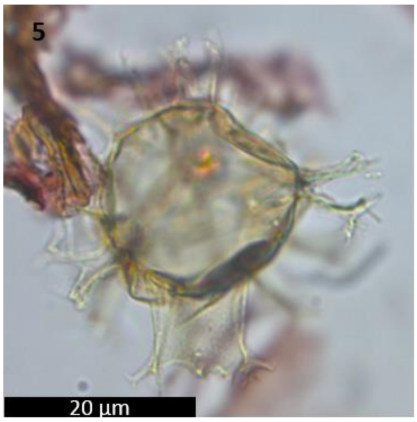

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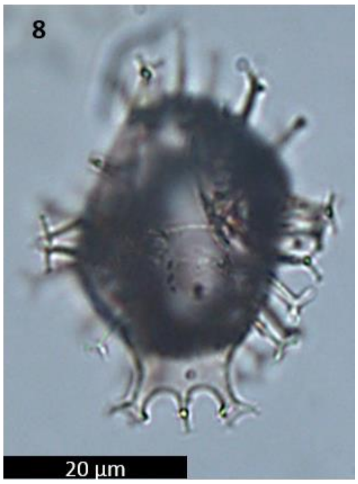

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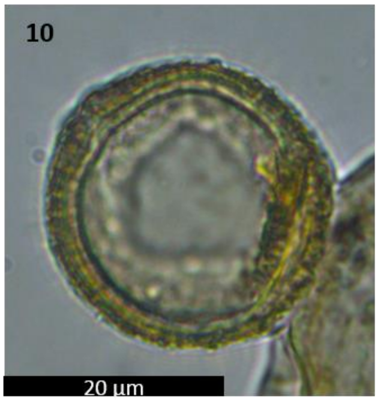

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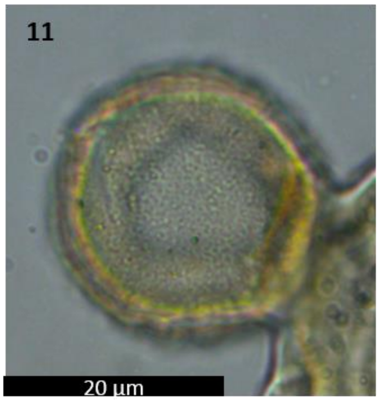
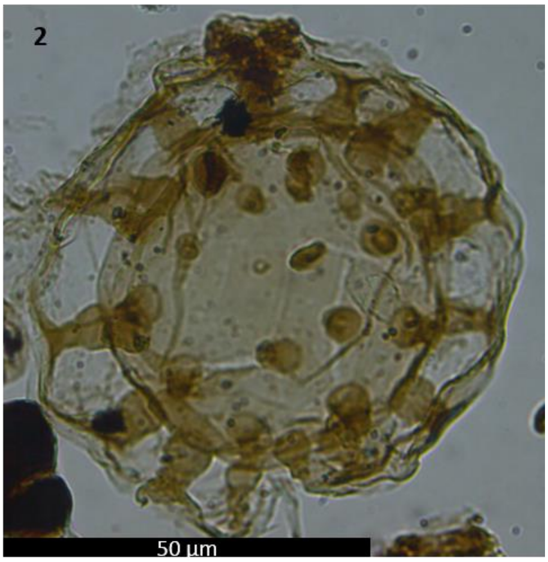


Plate 5



<u>Plate 1:</u> All images are taken under plain transmitted light.

1) *Achomosphaera* sp., MPA 66058, EF: G66/2.

2) *Achomosphaera* sp., MPA 66058; EF: D6/3

3) *Nannobarbophora* Habib and Knapp, 1982; MPA 66071; EF: B62/4.

4-6) Dinocyst sp. A; MPA 66067; EF: S60/1). (4) Low focus, (5) middle focus, (6) high focus.

7) Dinocyst sp. B; MPA 66059; EF: H67/1.

8-9) *Hystrichokolpoma cinctum* Klumpp, 1953; MPA 66071; EF: C64/4. (8) High focus, (9) low focus.

10-12) Dinocyst sp. C; MPA 66053; EF: W63/2. There is a possible apical archeopyle. (10) High focus, (11) middle focus, (12) low focus.

<u>Plate 2:</u> All images are taken under plain transmitted light.

1-3) *Hystrichokolpoma pusillum* Biffi and Manum, 1988; MPA 66056; EF: J66/0. (1) Low focus, (2) middle focus, (3) high focus.

4-6) *Hystrichokolpoma rigaudiae* Deflandre and Cookson, 1955; MPA 66061; EF: O66/3. (4) Low focus, (5) middle focus, (6) high focus.

7-9) *Hystrichokolpoma* Klumpp, 1953; MPA 66061; EF: O66/3. (7) High focus, (8) middle focus, (9) low focus.

10-12) *Hystrichokolpoma* Klumpp, 1953; MPA 66060; EF: U51/1. (10) High focus, (11) middle focus, (12) low focus.

Plate 3: All images are taken under plain transmitted light.

1-3) *Impagidinium paradoxum* (Wall, 1967) Stover and Evitt, 1978; MPA 66056; EF: F65/2.

4-6) *Impagidinium patulum* (Wall, 1967) Stover and Evitt, 1978; MPA 66063; EF: U60/1. (4) High focus, (5) middle focus, (6) low focus.

7) *Invertocysta lacrymosa* Edwards, 1984; MPA 66058; EF: L58/0.

8) *Lingulodinium machaerophorum* (Deflandre and Cookson, 1955) Wall, 1967; MPA 66061; EF: above F67/2.

9) *Nematosphaeropsis labyrinthus/lemniscata* (Ostenfeld, 1903) Reid, 1974 and Wrenn, 1988) MPA 66071; EF: R64/0.

10-12) *Operculodinium* spp. Wall, 1967; MPA 66070; EF: M57/0. The majority of the *Operculodinium* species are most likely *Operculodinium centrocarpum*. (10) Low focus, (11) middle focus, (12) high focus.

Plate 4: All images are taken under plain transmitted light.

1-3) *Operculodinium* spp. Wall, 1967; MPA 66070; EF: D59/0. The majority of the *Operculodinium* species are probably *Operculodinium centrocarpum*. (1) High focus, (2) middle focus, (3) low focus.

4) *Selenopemphix quanta* (Bradford, 1975) Matsuoka, 1985; MPA 66062; EF: U58/4.

5) *Spiniferites membranaceus* (Rossignol, 1964) Sarjeant, 1970; MPA 66059; EF: S59/0.

6-7) *Spiniferites* sp. A of Louwye and De Schepper (2010); MPA 66056; EF: K67/2. (6) Low focus, (7) high focus.

8) *Spiniferites mirabilis* (Rossignol, 1964) Sarjeant, 1970; MPA 66062; EF: Q48/1.

9-11) *Tectatodinium pellitum* (Wall, 1967) Head, 1994; MPA 66053; EF: K58/1. (9) Low focus, (10) middle focus, (11) high focus.

Plate 5: All images are taken under plain transmitted light

4) *Tuberculodinium vancampoae* (Rossignol, 1962) Wall, 1967; MPA 66055; EF: G53/4.

5) *Tuberculodinium vancampoae* (Rossignol, 1962) Wall, 1967; MPA 66053; EF: M60/0.

5.3.3 Palaeoecology

The majority of the species present in both the late Miocene and the Pliocene are still extant, and so have known ecological preferences. Species present that are known to thrive in warm waters include: *Tuberculodinium vancampoae, Spiniferites mirabilis, Spiniferites membranaceus, Impagidinium patulum, Impagidinium paradoxum, Lingulodinium machaerophorum, Tectatodinium pellitum, Hystrichokolpoma rigaudiae* and the acritarch *Nannobarbophora sp.* (Figure 5.7 and Table 5.3; Strauss et al., 2001; Head, 2003; 1997; Marret and Zonneveld, 2003; Zonneveld et al., 2013a). No species that prefer cold waters were present and so supports that the climate was warm temperate to sub-tropical for both the late Miocene the Pliocene.

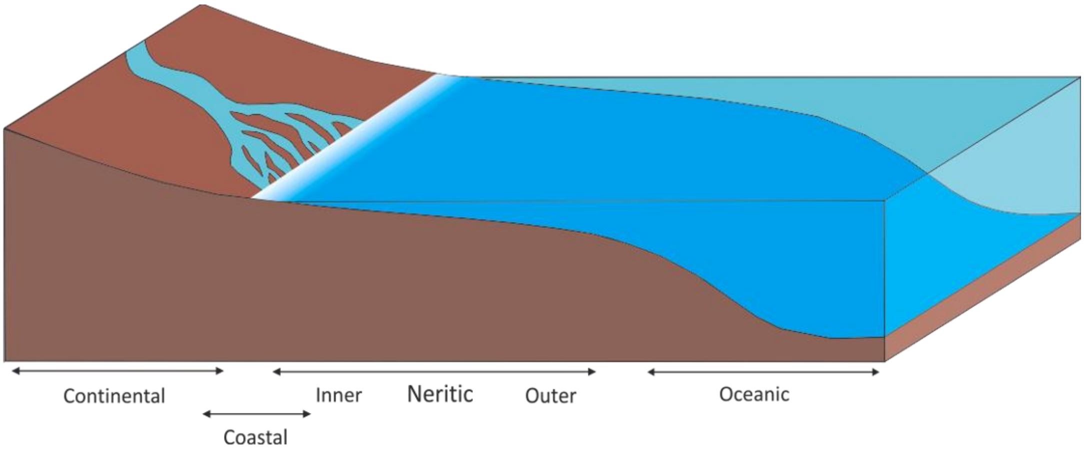


Figure 5-7: The main ocean settings discussed in this chapter.

Oceanic Preference	Warm Water Species
Inner neritic	*Tectatodinium pellitum* *Tuberculodinium vancampoae* *Lingulodinium machaerophorum*
Outer Neritic	*Invertocysta lacrymosa* *Nematosphaeropsis labyrinthus/lemniscata* *Spiniferites/Achomosphaera* spp.
Oceanic	*Impagidinium paradoxum* *Impagidinium patulum*

Table 5-3: Dinoflagellate cyst ecological preferences, used in the indices (Table 5.2)

Species present with known marine zonal preferences include *Impagidinium paradoxum* and *Impagidinium patulum,* oceanic species; *Invertocysta lacrymosa* and *Nematosphaeropsis labyrinthus/lemniscata,* which are outer neritic to oceanic species; and *Tectatodinium pellitum* and *Tuberculodinium vancampoae,* which are coastal species (Figure 5.7 and Table 5.3; Wrenn and Kokinos, 1986; Marret and Zonneveld, 2003; Warny et al., 2003; Zonneveld et al., 2013a). *Lingulodinium machaerophorum* can be found in a broad range of salinities. It is particularly abundant in areas of upwelling or river discharge and is generally an inner neritic species (Marret and Zonneveld, 2003; Zonneveld et al., 2013a). The majority of *Spiniferites* and *Achomosphaera* spp*.* are found in neritic environments and are classed as outer neritic in the IN/ON index (Marret and Zonneveld, 2003; Warny et al.. 2003; Zonneveld et al., 2013a).

Gypsum Canyon had the oceanic to outer neritic species *Impagidinium patulum* and *Nematosphaeropsis rigida* in low abundances along with *Lingulodinium machaerophorum* and *Tectatodinium pellitum.* At Chrysospiliotissa the coastal species *Tuberculodinium vancampoae* appeared and *Nematosphaeropsis labyrinthus/lemniscata* disappeared. The increase in the number (and abundance) of species with shallow water preferences indicates that the environment of deposition was shallower in the Pliocene than it was in the late Miocene, suggesting a change from middle-outer neritic conditions in the late Miocene to inner neritic conditions in the Pliocene. A shallower environment of deposition in the Pliocene is supported with the use of the IN/ON palaeoenvironmental indices (number of inner neritic species/the number of inner neritic species combined with the number of outer neritic species). The mean IN/ON value for the Gypsum Canyon samples is 0.15, whereas it is higher in the samples from the Chrysospiliotissa samples (0.32), indicating that the Pliocene site was closer to the coast (Table 5.2).

5.3.4 Comparison to the rest of the Mediterranean Sea

The assemblages from Cyprus have been compared to assemblages from the rest of the Mediterranean using the same methodology and statistical analyses described in Section 3.6. For example, questionably assigned species were not included in the analysis and only presence and absence data were used. Comparison was accomplished using separate non-metric multidimensional scaling (MDS; see Section 3.6.2 for a full description) and the late Miocene and Pliocene were analysed separately. In the late Miocene, only the three assemblages that contained dinoflagellate cysts were included in the analysis and all three assemblages clustered close to each other on the MDS. They are most closely related to assemblages from the Eastern and Western Mediterranean basins, although there are only two assemblages from the Western Mediterranean Basin to compare against (Figure 5.8a).

Pliocene assemblages from Cyprus cluster separately to the rest of the assemblages from the Mediterranean during the Pliocene, suggesting that the species making up the assemblages in Cyprus are different to the rest of the Mediterranean, although they are most closely related to assemblages from the Eastern Mediterranean Basin (Figure 5.8b).

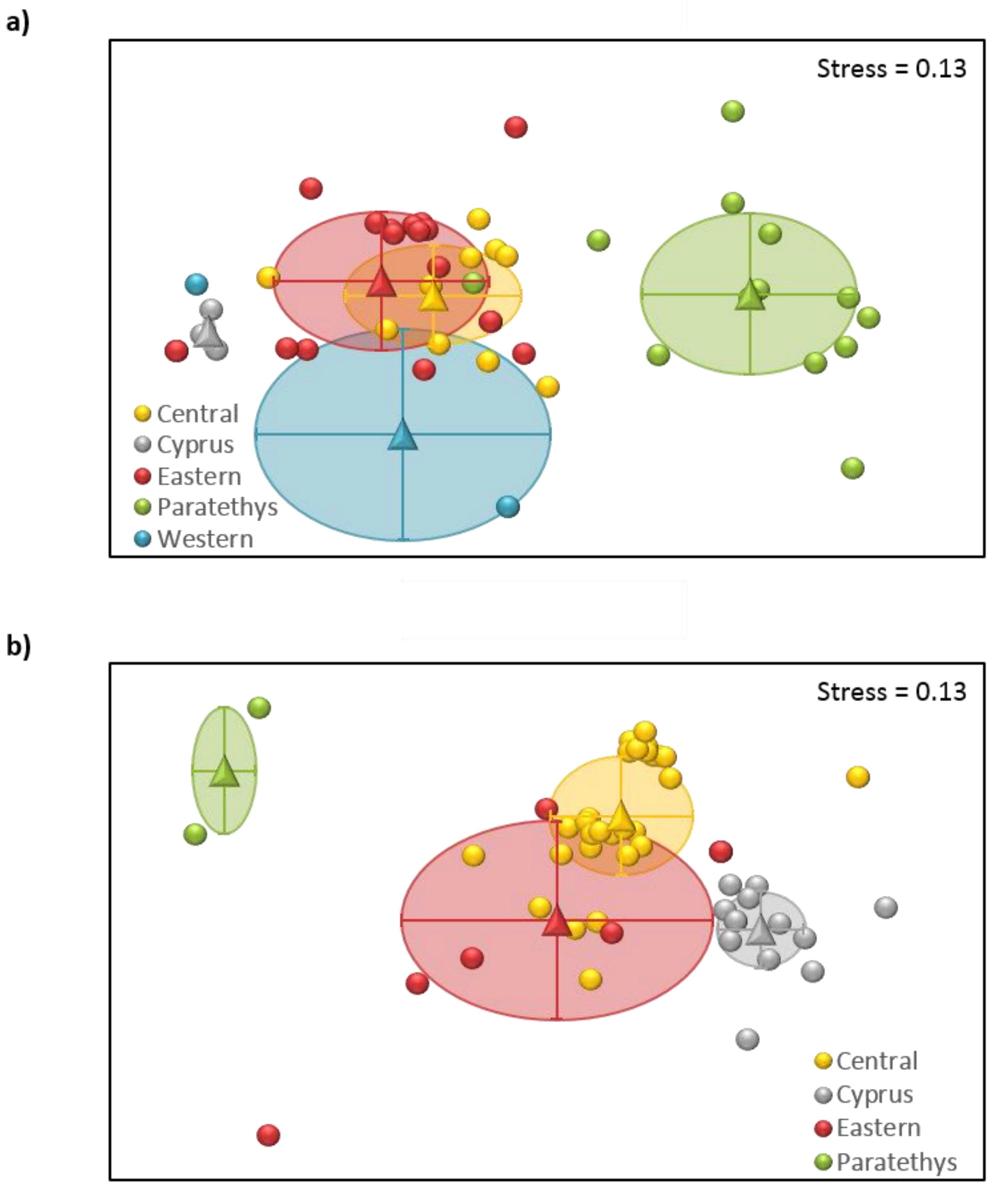


Figure 5-8: MDS plots for (a) the late Miocene and (b) the Pliocene. The triangle points represent the mean average position for each basin and the ellipses denote the standard deviation.

5.4 Discussion

There are very few studies on dinoflagellate cysts in the Eastern Mediterranean Sea and the only dinoflagellate cyst studies from Cyprus are on calcareous dinoflagellates (Bison et al., 2007; 2009). This study, therefore, while not contributing any new stratigraphic controls, provides information on the changes that took place in Cyprus before and after the MSC (the late Miocene and Pliocene). It also demonstrates the potential of using dinoflagellate cysts to determine changes to the ecology in Cyprus.

5.4.1 Comparison of Cyprus late Miocene and Pliocene palynology

The low diversity of the assemblages at Gypsum Canyon (late Miocene) can be attributed to the progressive restriction of the Mediterranean Sea and the increasingly saline conditions (Hsü et al., 1973; 1977). Similar changes in dinoflagellate cyst diversity are seen all over the Mediterranean; for example, Zakynthos (Kontopoulos et al., 1997), Morocco (Warny et al., 2003), Sicily (Londeix et al., 1999; 2007) and the Aegean Sea (Melinte-Dobrinescu et al., 2009). The hostile conditions were as a result of the closure of the Western Mediterranean gateways. However, when the Strait of Gibraltar opened (~5.33 Ma), the Mediterranean reflooded and allowed the species that were forced to migrate elsewhere to survive to move back into the areas, explaining the higher diversity in the Pliocene (ten additional species).

As well as the diversity, the species with known environmental preferences were different in the late Miocene and Pliocene. For example the additional species present in the Chrysospiliotissa (Pliocene) samples contained species with coastal preferences (*Tectatodinium pellitum* and *Tuberculodinium vancampoae).* This increase in coastal species reflects the uplifting of the Troodos Ophiolites, and the shallowing of the Mesaoria Basin (McCallum and Robertson, 1995). The presence of *Turritella communis* (a type of gastropod; Figure 5.9) was also present amongst the Pliocene sediment collected for this study, and suggests relatively shallow water depths, between 30 and 150 m deep (Pérès, 1967). This agrees with the environment of deposition provided by the dinoflagellate cysts of inner neritic for the Pliocene, compared to the middle-outer neritic of the late Miocene (Eaton and Robertson, 1993).

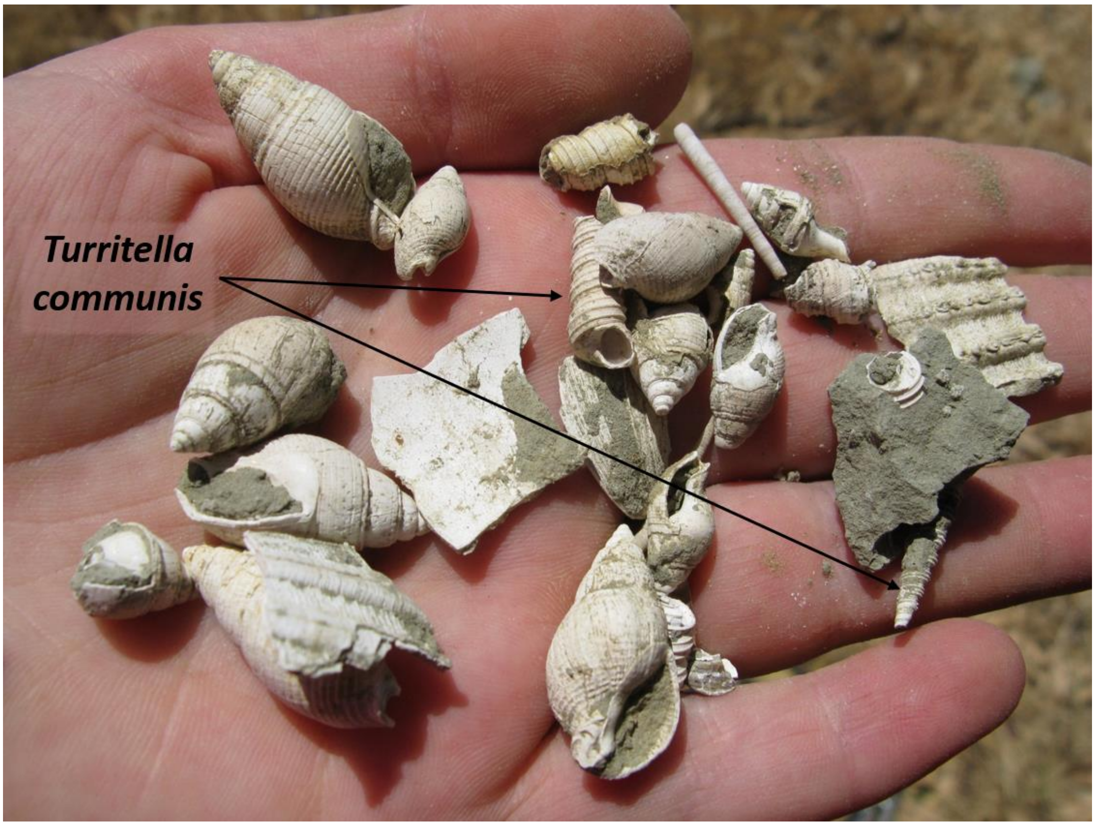


Figure 5-9: A selection of the marine macrofossils found at Chrysospiliotissa, including *Turritella communis,* which is presently found in water depths between 30 and 150 m deep (Pérès, 1967).

The increase (number of species and abundance) of coastal species (*Tectatodinium pellitum* and *Tuberculodinium vancampoae)* in the Chrysospiliotissa samples demonstrates that there was a general shallowing trend due to the uplifting of the Troodos Ophiolites. Whilst the IN/ON index indicates that the Pliocene site was closer to the coast than the late Miocene site, the P/D index values are higher in the late Miocene than in the Pliocene suggesting the opposite is true (Table 5.2). The reason for the higher percentages of pollen in the late Miocene relative to the Pliocene is possibly related to the debris flows and turbidites that were more common in the late Miocene (Eaton and Robertson, 1993). It may also signify a large river flowing into the region during the late Miocene, bringing in addition pollen, although with out more information of productivity (there is only one P-cyst for the P/G cyst index) this is difficult to prove. However, the most probable reason is likely related to the majority of the pollen at both sites being *Pinus. Pinus* is transported great distances in the wind, and thus its relative abundnace generally increases with distance from the shore explaining the higher P/D ratio in the late Miocene compared to the Pliocene (Heusser, 1983;

Mudie and McCarthy, 2006). One aspect that is common to both the late Miocene and the Pliocene is that no cold water species were present. This suggests that the temperature for both the late Miocene and the Pliocene was warm temperate to sub-tropical.

The presence of reworked species (e.g. *Hystrichokolpoma cinctum,* which had its last occurrence in the early Miocene, ~17 Ma; Brinkhuis et al., 1992) may be present due to the transport of the cysts in debris flows, which occurred more frequently in the late Miocene than the Pliocene. This may have been due to the late Miocene having a steeper palaeoslope, higher tectonic activity or a different position on the shelf. The most likely explanation is that there was more tectonic activity in the late Miocene, as the fragmentation of the piggy-back basin became more pronounced at this time (Calon et al., 2005). The sedimentology substantiates that the late Miocene and Pliocene had a different environmental setting. For example, the sediments from the Pliocene site (Chrysospiliotissa) are composed entirely of marls, whereas in the late Miocene sites (Gypsum Canyon) the marls are interbedded between chalks and marly chalks. The coarser material of the chalks is interpreted as the outer most limit of debris flows (Eaton and Robertson, 1993).

5.4.2 Comparison of Cyprus palynomorph assemblages to the rest of the Mediterranean Sea

Samples from the late Miocene of Cyprus (Gypsum Canyon), with dinoflagellate cysts present, are limited to just three samples making it difficult to determine any change over time, however, all three samples had a low species diversity (between five and seven). Prior to the Zanclean flood, as the Western Mediterranean Gateways were closing, the environment of deposition in the Mediterranean shallowed, salinity increased and dinoflagellate cyst diversity decreased (Ioakim et al., 1997; Kontopoulos et al., 1997; Warny et al., 2003). The diversity decrease is attributed to the closing of the Western Mediterranean Gateways as oceanic circulation became more restricted (Londeix et al., 2007). This effect is seen regionally (e.g. Crete: Ioakim et al., 1997; Santarelli et al., 1998; Sicily: Londeix et al., 1999; 2007; Morocco:

Warny et al., 2003) and is also represented by the disappearance of oceanic species. As mentioned, due to too few samples (in the late Miocene) containing dinoflagellate cysts it is difficult to determine a decrease in diversity. However, the fact the diversity in Cyprus was so low in the late Miocene could be attributed to the closing of the Western Mediterranean Gateways. What can be inferred is that the waters were most likely middle to outer neritic due to the high abundance of species from the *Spiniferites* genus (Warny et al., 2003) as well as the presence of outer neritic to oceanic species such as *Invertocysta lacrymosa* and *Nematosphaeropsis labyrinthus/lemniscata.*

When comparing the new data from Cyprus to previously published data from the rest of the Mediterranean (described in Section 3.6), it was found that the late Miocene assemblages cluster with other assemblages from the rest of the Mediterranean Sea, including the Eastern Mediterranean (Figure 5.8a). However, the assemblages from the Pliocene cluster separately (Figure 5.8b). This taxonomic isolation of the Pliocene Cyprus assemblages from the rest of the Mediterranean Sea suggests that the conditions in the Mesaoria Basin were different to the rest of the Mediterranean Sea, and did not allow the migration of all of the species provided by the Zanclean flood into the basin. Although the Cyprus assemblages are most similar to other assemblages from the Eastern Mediterranean (Crete; Ioakim et al., 1997).The reason for the taxonomic isolation of the Cyprus assemblages can be attributed to the uplifting environment of the region. The uplifting resulted in the Nicosia Formation changing from a shallow marine settings to a deltaic/fluvial environment of the Fanglomerates and Terrace deposits in the Pleistocene, which isolated the basin from the rest of the Mediterranean (McCallum and Robertson, 1995).

The uplifting that took place in Cyprus did not take place all over the Mediterranean Sea and in many regions, such as Sicily and Crete, after the Mediterranean Sea became reconnected with the Atlantic Ocean in the Pliocene, outer neritic/oceanic dinoflagellate cysts (e.g.

Impagidinium spp. and *Nematosphaeropsis* spp.) became more dominant, indicating a deepening of the waters (Ioakim et al., 1997; Londeix et al., 1999; 2007).

When the Western Mediterranean Gateway opened at the start of the Neogene, and reflooded the Mediterranean, an increase in dinoflagellate cyst diversity is reported to have occurred (e.g. Greece, Kontopoulos et al., 1997; Sicily, Londeix et al., 1999; 2007), similar to what is recorded in the Cyprus sections. The additional species that appeared in the studies mentioned above were mostly outer neritic species such as *Spiniferites* spp. and *Achomosphaera* spp., whereas the additional species appearing at Chrysospiliotissa were coastal species such as *Tuberculodinium vancampoae and Tectatodinium pellitum*, although additional *Spiniferites* species (e.g. *Spiniferites mirabilis)* did also appear. This again infers that the Mesaoria Basin was shallower than the majority of the Mediterranean Sea during the Pliocene.

An additional difference between the data from Cyprus, and data from the rest of the Mediterranean, is evident by comparing data from this chapter to the data in Section 3.6. In Section 3.6, the diversity of the overall Mediterranean decreased through the late Miocene and did not recover in the Pliocene, although the assemblage composition between the two sub-epochs were significantly different (see Section 3.6.4.1.2). Whereas in the Cyprus samples (this chapter), the diversity in the Pliocene is higher than in the late Miocene, demonstrating that local conditions do not always reflect the regional patterns.

5.4.3 Comparison with the Modern Mediterranean Sea

The modern Mediterranean Sea is split into two main basins, which are separated by the Strait of Sicily. These basins are the Eastern and Western Mediterranean basins. Modern Mediterranean dinoflagellate cyst assemblages are also split into two different associations (Elshanawany et al., 2010). The first association is composed of high abundances of *Impagidinium aculeatum, Impagidinium sphaericum, Impagidinium patulum, Impagidinium paradoxum, Impagidinium plicatum, Pyxidinopsis reticulata, Nematosphaeropsis labyrinthus* and *Operculodinium israelianum*. High abundances of these species are found in offshore Eastern Mediterranean Sites, where the waters are warm with high salinity and low productivity. The second group is composed of the species *Selenopemphix nephroides, Echinidinium* spp., *Selenopemphix quanta, Quinquecuspis concreta, Brigantedinium spp.* and *Lingulodinium machaerophorum* and have high abundances in Western Mediterranean, the Straits of Sicily as well as at the distal end of river plumes. The waters with assemblages composed of species from association two are generally considered to be cooler than those where association one is found, with a lower salinity and higher productivity (Elshanawany et al., 2010).

The high abundances of *Impagidinium spp.* in association one (Eastern Mediterranean), represent that the sites sampled (Elshanawany et al., 2010) are generally oceanic (Wall et al., 1977; Elshanawany et al., 2010). This does not correlate with the dinoflagellate cysts found in the Eastern Mediterranean during the Pliocene (this study), which suggest that the waters overlying the Chrysospiliotissa site were much shallower than they are at present, which is consistent with the continued uplift of the basin.

5.5 Conclusions

This chapter provides the first account of organic-walled dinoflagellate cysts from the Neogene of Cyprus. Two sections were sampled for palynomorphs and dinoflagellate cysts were present in 17 of the 21 samples. One late Miocene (11.63-5.33 Ma) and one Pliocene (5.33-2.58 Ma) section was selected with the aim of investigating the effects of the closure of the MSC on dinoflagellate cyst assemblages. The following results were found:

Did the MSC result in differing dinoflagellate cyst assemblages in Cyprus?

- Similar species were found before and after the MSC, but additional species were present in the Pliocene, possibly due to an influx from the reopening of the Western Mediterranean Gateway.

- There was both a higher number as well as a higher percentage of species preferring inner neritic/coastal environments in the Pliocene samples, which reflects the shallowing of the Mesaoria Basin as Cyprus continued to uplift as a result of the converging African and Eurasian plates.
- Species known to thrive under warm water conditions were present in both sections, indicating that temperatures were warm temperate to tropical.

Does the diversity of the Cyprus assemblages alter as a result of the MSC?

- The low diversity during the late Miocene has been attributed to the increasingly hostile conditions brought about by the MSC. The diversity increased in the Pliocene due to the reopening of the Western Mediterranean Gateway and the Zanclean flood.

Do the Cyprus assemblages demonstrate a similar trend to the regional pattern depicted in Section 3.6?

- Dinoflagellate cyst assemblages from the Pliocene do not resemble those from the rest of the Pliocene, or from the modern Mediterranean Sea. This is thought to be due to uplifting in the region, resulting in the Mesaoria Basin being isolated from the rest of the Mediterranean Sea.

This chapter demonstrates that the MSC did result in differing dinoflagellate cyst assemblages before and after the MSC. However, due to uplift of the Mesaoria Basin, a local signal dominates the results. This means that Cyprus, at least the Mesaoria Basin, is a poor case study to investigate the regional influence of the MSC. Nonetheless, it does demonstrate that the ‘diversity dump’, as a result of the Zanclean flood, reached small and semi isolated basins such as the Mesaoria Basin. It also demonstrates that local changes can affect the results, and hence the need for global databases to contain a significant number of studies over large regions to compensate for this.

Chapter 6: Conclusions

6.1 Significance of the project

The discovery of the utility of dinoflagellate cysts as a proxy for oceanic environmental parameters such as sea surface temperatures is relatively new, and their use in the Neogene has mainly been investigated in the last two decades. It is important to develop climate proxies so that multi-proxy studies can be carried out to produce robust, reliable and consistent results. This project helps to develop dinoflagellate cysts as a useful tool for palaeoecology, and explores their potential at regional and global scales. It also, represents the first time that the available published data on Neogene dinoflagellate cysts has been compiled into an internally consistent global database, TOPIS (Tertiary Oceanic Parameters Information System; Chapter 2).

Databasing allows palaeontologists to utilise the full potential of published information. Several global databases currently exist including Paleobiology/Fossilworks database (Alroy et al., 2009; 2013), Neogene Old World Mammal database (Fortelius, 2015), MorphoBank (O'Leary and Kaufman, 2011), Tertiary Environments Vegetation Information System (TEVIS; Salzmann et al., 2008; Pound et al., 2011) and the NEPTUNE Deep-Sea Microfossil Occurrence Database (Lazarus, 2013). However, TOPIS is the first global database for Neogene dinoflagellate cysts and has a similar structure to its terrestrial counterpart, TEVIS (Salzmann et al., 2008; Pound et al., 2011). The benefits of these large-scale databases are numerous. For example, having all of the required information in one place means that the data are readily accessible. This allows the data to be used effectively and efficiently, as inconsistencies and redundancies have already been taken into account. Large datasets represent a key tool for assessing previously published literature and evaluating change over larger regions, allowing a better comparison between general circulation models and data. They also provide a useful way of examining sampling bias, and determining where literature deficient areas are, allowing for a better justification for additional field work and data collection.

Many extant species of dinoflagellate cysts were present during the Neogene, therefore their environmental preferences are well established. This makes the Neogene a valuable interval to study, as does the fact that many of the Neogene changes helped sculpt the modern world. Such changes include: the closure of the Eastern Mediterranean Gateway (Rögl, 1999; Allen and Armstrong, 2008; Hüsing et al., 2009); the Middle Miocene Climatic Optimum (MMCO; Savin et al., 1975; Shackleton and Kennett, 1975; Zachos et al., 2001; Böhme, 2003; You et al., 2009); the Middle Miocene Climatic Transition (MMCT; Flower and Kennett, 1993a; Shevenell et al., 2004; Holbourn et al., 2005; 2013; Quaijtaal et al., 2014); the closure of the Panama gateway (Marshall et al., 1982; Groeneveld et al., 2014); the Messinian Salinity Crisis (Hsü et al., 1973; 1977; Martín et al., 2001; Krijgsman et al., 2002) and the initiation of Northern Hemisphere Glaciation (Bartoli et al., 2005; Mudelsee and Raymo, 2005; De Schepper et al., 2014).

The dynamic Neogene Earth, and the fact that the marine realm makes up ~70% of the planet, means that understanding Neogene oceanic changes can vastly improve the awareness of how the present conditions developed and how they might change in the future. This is especially important with the uncertainty of future climate changes and the consequences it might present. With the power of TOPIS and TEVIS (Salzmann et al., 2008; Pound et al., 2011), there is now palynological coverage of the whole globe, which can be used to determine the palaeoecology of the Neogene.

The construction of the original Neogene dinoflagellate cyst database (TOPIS) allowed for the first global synthesis of oceanic temperature development through the Neogene using this environmental parameters proxy (Chapter 3). It also meant that regional-scale analyses of the effects of gateway changes could be carried out, such as for the Mediterranean (Chapter 3, Section 3.6). TOPIS was also utilised to identify literature/sample deficient areas. Cyprus was recognised as one such location, which was then sampled and analysed (Chapter 5).

6.2 Summary of the project

This thesis provides the first global compilation of publications on Neogene dinoflagellate cysts, and is used to investigate their use and potential as a proxy for sea surface parameters, especially temperature. It uses dinoflagellate cysts to investigate the changing Neogene on global (Chapter 3), regional (Chapter 3. Section 3.6) and local (Chapter 5) scales. Variations to the distribution (Chapter 3), diversity (Chapters 3 and 5) and assemblage composition (Chapters 3 and 5) of dinoflagellate cysts were used to interpret alterations that took place in the Neogene such as climate and gateway changes. Specific research questions were asked in Chapter 1 and are summarised below:

6.2.1 Research question 1:

Can dinoflagellate cysts be used to demonstrate a progressive global cooling during the Neogene (Chapter 3)?

In order to investigate cooling in the Neogene using dinoflagellate cysts, all species with known temperature preferences were extracted from TOPIS, as were the sites in which they were present. A robust and reliable dataset was achieved by checking for synonyms, reworking and problematic taxonomy, as well as removing poorly dated sites. The data were then analysed, and it was found that changes to the distribution of dinoflagellate cysts with known temperature preferences can be used to track climate changes through the Neogene.

Cooling during the Neogene is indicated by an increase in the number of records with Cold Water Species (CWS) appearing, as demonstrated by Chapter 3. Cooling is also depicted in Chapter 3 by an increase in the percentage of CWS relative to the total number of species with known temperature preferences present in each record. Both the increase in the number of sites with CWS present, and the increase in the percentage of CWS indicate that during the Neogene, sea surface temperatures cooled significantly. This overall cooling trend is in general agreement with the global compilation of bottom water $\delta^{18}O$ values (Zachos et al., 2001; 2008) with the advantage that the dinoflagellate cyst record is not significantly influenced by ice volume, although it is not quantitative.

It was also possible to determine that the cooling was not uniform and that the rate of cooling varied, which again is in general agreement with the global compilation of benthic $\delta^{18}O$ values (Zachos et al., 2001; 2008). Temperatures in the early Miocene were warmest, with a slight decrease in the Serravallian. However, sea surface temperatures then dropped more significantly in the Tortonian followed by considerable cooling from the Pliocene to the modern. The cooling in the Pliocene has been attributed to a number of events such as the uplifting of the Tibetan Plateau (Raymo et al., 1988; Raymo and Ruddiman, 1992; Mudelsee and Raymo, 2005), the shoaling of the Indonesian seaway (Cane and Molnar, 2001), the closure of the Central American Seaway (Haug and Tiedemann, 1998; Steph et al., 2006) and the opening of the Bering Strait (Marincovich and Gladenkov, 1999; Verhoeven et al., 2011) and also to a decrease in atmospheric carbon dioxide (Lunt et al., 2008a).

The results presented here, also establish that cooling was not uniform at all latitudes and that the majority of the cooling occurred in the mid to high latitudes (Nikolaev et al., 1998). The low latitudes indicated minimal if no temperature change. This resulted in a steepening latitudinal temperature gradient throughout the Neogene, and reflects the evolving latitudinal temperature gradient of the terrestrial realm (Pound et al., 2012a).

6.2.2 Research question 2:

Can a global compilation of Neogene dinoflagellate cysts detect shorter term variations in global/regional climate, which are superimposed on the long term cooling trend (Chapters 3 and 4)?

Chapter 3 demonstrates that dinoflagellate cysts can be used to determine a general cooling trend in the Neogene. However, it struggles to demonstrate short term climate changes such as the MMCO. The MMCO was a global event, between 17 and 15 Ma, where deep-sea temperatures increased between 3 and 7 °C (Raymo and Ruddiman, 1992). This warming event is displayed in the bottom water $\delta^{18}O$ curve of Zachos et al. (2008) by a negative $\delta^{18}O$ excursion, representing a warming event. When the data from Chapter 3 are directly compared to the bottom water $\delta^{18}O$ curve, the trend displays a similar pattern with the exception of the MMCO. Data from Chapter 3 indicate no warming during this event, and percentages of CWS are very similar during the MMCO as they were both before and after the warming.

Whilst on first glance this suggests that dinoflagellate cysts can only be used to determine long term trends, this is not necessarily the case. The reason for the lack of any short term changes may be related to the temporal resolution of the data. For example, much of the data are dated to within a stage or in some cases a sub-epoch. This means that any evidence of short term changes are blurred by effects of the longer term change. To militate against this it would be essential to obtain data of a higher resolution. It may also help to increase the number of sites that have abundance data. Other short term changes, which analysis of the TOPIS data does not pick up, include changes to the Eastern Mediterranean Gateway, and changes to assemblages as a result of the Lago Mare. Reasons for this are also likely related to the resolution of the data.

6.2.3 Research question 3:

What were the regional effects of gateway changes on dinoflagellate cysts during the Neogene (Chapter 3)?

To investigate further changes that can impact dinoflagellate cyst assemblages on a large scale, the Mediterranean Sea was used as a case study. The reason for this is that there were three gateway changes during the Neogene in the Mediterranean region. These were the closure of the Eastern Mediterranean Gateway, the isolation of the Paratethys and the geologically brief closure of the Western Mediterranean Gateway. Understanding the effects of gateway changes on dinoflagellate cyst assemblages means that it may be possible to eliminate or confirm external sources of variation, aiding in further understanding of the complex climate and environmental proxy.

To explore the question regarding the effects of gateway changes on dinoflagellate cysts, and whether dinoflagellate cysts can provide any new information, Mediterranean/Paratethys assemblages were extracted from TOPIS and filtered to remove poorly dated assemblages as well as any questionably assigned species. The Neogene was split into 0.5 million year time bins and the diversity was calculated following the methodology provided in MacRae et al. (1996). The diversity in the Mediterranean was shown to follow a different pattern to the global diversity (MacRae et al., 1996), and the decrease in the number of species present from the late Tortonian (in the Mediterranean region) was attributed to the closing Western Mediterranean Gateway, which resulted in the Messinian Salinity Crisis (MSC). Unlike in more localised studies, this regional study shows that the Pliocene diversity of dinoflagellate cysts did not recover back to the original number of species before the MSC. However, the species making up the assemblages were statistically different before (late Miocene) and after (Pliocene) the event.

Climate change may also have impacted the assemblages found in the Mediterranean and Paratethys regions. For example, fluctuations in sea level, attributed to the melting of terrestrial ice, meant that the Paratethys and Mediterranean seas, as well as the Mediterranean and the Indian Ocean, were sporadically connected (Harzhauser et al., 2007; Harzhauser and Piller, 2007; Reuter et al., 2009). This allowed for the migration of animals and phytoplankton between the basins, increasing the diversity. Warming events have also been attributed to increases in diversity in the Paratethys, as species preferring cooler conditions migrated north to escape the warming conditions of the MMCO (Harzhauser et al., 2003). However, when presenting the mean percentage of CWS dinoflagellate cysts (relative to the total number of species with known temperature preferences in each record) for just the Mediterranean Sea, there are minimal qualitative differences in sea surface temperatures. This indicates that the changes seen in the diversity and assemblage composition is dominated by gateway changes rather than climate change.

6.2.4 Research question 4:

Can changes in dinoflagellate cyst assemblages elucidate complex histories of the opening/closing of marine gateways (Chapters 3 and 5)?

Chapter 3 (Section 3.6) demonstrates that dinoflagellate cysts can be used to determine some of the effects of the closure of the Western Mediterranean Gateway by means of assemblage composition and diversity variations through time. It also displays some of the consequences of the closure of the gateways between the Mediterranean Sea and the Paratethys Sea. However, it does not provide any new information on the timings or consequences of the Eastern Mediterranean Gateway closure. A possible reason for this is that dating of the assemblages does not have a sufficiently high resolution. The closing of the Eastern Mediterranean Gateway is thought to have occurred gradually with numerous recursions during the early and middle Miocene (Woodruff and Savin, 1989; Rögl, 1999; Harzhauser and Piller, 2007). The complex nature of this closing may have been blurred by poorly constrained dating. Further primary data, with a high temporal resolution, from the Eastern Mediterranean would help investigate this further.

Chapter 3 demonstrates that gateway changes can be recognised regionally. For example, it provides evidence for the consequences of the closure of the Western Mediterranean Gateway. The late Miocene was characterised by low diversities as the salinity of the waters increased. In Chapter 3, the diversity did not appear to recover, and remained low, although the species present were statistically significantly different to those found prior to the event. However, in Chapter 5 the diversity was higher after the MSC than before it. Reasons for this are postulated to relate to the Mesaoria Basin in which the dinoflagellate cysts were preserved and reflect a local signal dominating over the regional signal of Chapter 3.

The Mesaoria Basin was consistently being uplifted. This meant that when the rest of the Mediterranean Sea was reflooded at the beginning of the Pliocene (McCallum and Robertson, 1995), resulting in high numbers of oceanic species, the Mesaoria Basin was still shallow with few oceanic species. The uplifting of the Mesaoria Basin resulted in it being isolated from the rest of the Mediterranean and the assemblages in the Pliocene are depicted as being statistically significantly different to the rest of the Mediterranean. This effect is similar to the disconnection of the Paratethys Sea described in Chapter 3.

Statistical analysis (Chapter 3) demonstrates that when the Paratethys had numerous gateways connecting it with the Mediterranean Sea, migration could take place between the two basins and no discernible differences could be identified between the assemblages of each ocean basin. As time progressed through the Neogene, and the Paratethys became more isolated, statistically significant differences can be noted between the Paratethys and the basins of the Mediterranean. By the late Miocene and the Pliocene, the Paratethys gateway became even more restricted and eventually cut off the Paratethys from the Mediterranean (Rögl, 1997; 1999; Harzhauser and Piller, 2007). As this geographical isolation occurred, taxonomic isolation also took place with increased numbers of endemic species.

6.3 Future Outlook

TOPIS does not represent the completion of the Neogene dinoflagellate cyst literature. As further primary data are published, it should be added to the database and included in any future syntheses. Another point regarding TOPIS is that it is important to concentrate further efforts on gaining more primary data in areas with limited data points such as the Indian, Pacific and Southern oceans as well as attaining data of a higher temporal resolution. With a higher number of entries, with well constrained dates, it may be possible to observe short scale changes such as the MMCO. It would also be useful to detect and constrain changes in the lead up to and aftermath of an event to see how quickly dinoflagellate cysts responded to the changes. At present, due to the large number of publications where each assemblage is dated at stage level, TOPIS characterises general climate and assemblage turnover trends. If more publications are added that have a higher temporal resolution, it would be possible to apply and use dinoflagellate cysts to observe a much larger range of research questions.

A greater uniformity of available data would also be welcomed. For example, if regions lacking data points could be sampled, research questions relating to global change would be less likely to be biased. An example from this project is displayed in Chapter 3, where the analysis is only reliable for the Northern Hemisphere due to a lack of data from the Southern Hemisphere. Chapter 3 also highlights where over sampling (for example, in the Gulf of Saint Lawrence) can produce anomalies, and the importance of having an even coverage of data sites. Preferential sampling should concentrate on the Indian, South Atlantic and Pacific oceans to compensate for limited data from those regions. The Indian Ocean in particular would be interesting to study in order to compare Indian Ocean assemblages to Mediterranean assemblages, thereby increasing the understanding of the Eastern Mediterranean Gateway closure.

It is equally important to obtain more data with quantifiable abundance counts to allow more quantitative analysis of ocean parameters and permit further statistical analyses. Additional information that would be useful to have for every site/assemblage is the environment of deposition. This information would enable further evaluation as to the cause of any changes to the assemblages and would aid in determining if the effects of change were seen everywhere, or just selective environments. If abundance counts and the environment of deposition was consistently included, along with the rest of the information from TOPIS, then further research questions could be explored. For example, did surface waters in neritic and oceanic regions cool at the same rate and did the evaporites of the MSC precipitate in deep and shallow water synchronously? With more quantifiable environmental parameters, as has been developed with modern dinoflagellate cysts (Marret and Zonneveld, 2003; Zonneveld et al., 2013a), it would be possible to provide further information on boundary conditions in the

Neogene. It is therefore important that future studies should contain, where possible, both environmental information and abundance counts, which are calculated in a consistent manner.

The benefits of having a large compilation of data are numerous, and many other research questions can be posed that time did not permit for in this project. One such question would be to use them to evaluate changes to ocean currents that impact climate. An example is the North Atlantic Current (NAC) that helps keep the UK warmer than expected at its current latitude. De Schepper et al. (2009) demonstrate how the dinoflagellate cyst *Operculodinium centrocarpum* can be used to assess variability in the NAC from 3.35–3.24 Ma. Three very well constrained sites from the North Atlantic were used, but with the aid of TOPIS, and further high resolution data, it may be possible to track the path of the NAC since its initiation. This would potentially assist with understanding the consequences of any alterations to its flow in the future, which would have important controls on climate. Another avenue that would be useful to explore further is to examine latitudinal distributions of dinoflagellate cyst species with known temperature preferences (as per Masure and Vrielynck, 2009; Masure et al., 2013; Woods et al., 2014). Chapter 3 touches on this, but does not establish any biomes or quantifiable temperature changes.

It is hoped that with the initial research on Neogene dinoflagellate cysts from Cyprus (Chapter 5), that more sites and assemblages can be analysed from Cyprus in order to further understand the consequences of the Mediterranean Gateway changes to the region. It would be interesting to also sample the older sediment to investigate any effects of the Eastern Mediterranean Gateway closure on the dinoflagellate cysts, which may help establish the timing of the closure. The closure of the Eastern Mediterranean Gateway is hotly debated and some authors speculate that its closure partly resulted in the MMCT by changing ocean circulation patterns (Allen and Armstrong, 2008). Further dinoflagellate cyst analysis from the Eastern Mediterranean, and the Indian Ocean, may help to investigate the nature of the closure, i.e. its intermittent nature, as dinoflagellate cysts may have the potential to detect any climate variation as a result of the closure. By comparing Mediterranean assemblages to those of the Indian Ocean, as well as using their ability to determine palaeoenvironments, it may be possible to establish a more constrained timing of the events that led to the final closure of the Eastern Mediterranean Gateway.

TOPIS demonstrates the value of big datasets covering large intervals of time to investigate global long term changes. The results presented in this thesis provide an insight into climate and ecological changes over the Neogene and was able to compare Neogene changes to the conditions of the present on a global scale. Due to the utility of large palynological databases it is hoped that TOPIS will become accessible to the rest of the palynological community to aid in further research.

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Appendix A: References and location of the data used in Chapter 3

Main ID	Nearest Country	Latitude	Longitude	Pal Latitude	Pal Longitude	Nearest Ocean	Reference
1	Greenland	85.5	-108.2	85.5	-108.2	Arctic	(Aksu and Mudie, 1985)
2	Canada	70.3	-64.4	69.9	-62.5	Labrador Sea	(El Beialy, 1997)
3	Greenland	58.4	-48.4	57.3	-45.2	Atlantic	(Head et al., 1989a)
4	Canada	58.1	-48.2	57.7	-47.0	Atlantic	(Edwards et al., 1991)
5	Greenland	58.1	-48.2	57.7	-46.9	Labrador Sea	(de Vernal and Mudie, 1989)
6	Greenland	58.1	-48.2	56.9	-44.8	Atlantic	(Head et al., 1989b)
7	Canada	54.2	-54.5	52.8	-50.4	Atlantic	(Williams and Bujak, 1977)
8	Canada	55.1	-56.6	53.8	-52.3	Atlantic	(Williams and Bujak, 1977)
9	Canada	55.1	-56.6	53.8	-52.3	Atlantic	(Williams and Bujak, 1977)
10	Canada	48.4	-51.6	46.3	-46.4	Atlantic	(Williams and Bujak, 1977)
11	Canada	47.4	-51.2	45.4	-46.0	Atlantic	(Williams and Bujak, 1977)
12	Canada	47.0	-50.3	45.0	-45.2	Atlantic	(Williams and Bujak, 1977)
13	Canada	46.4	-51.1	44.4	-46.0	Atlantic	(Williams and Bujak, 1977)
14	Canada	45.6	-52.3	44.2	-48.5	Atlantic	(Williams, 1975b)
15	Canada	44.4	-51.3	42.4	-46.2	Atlantic	(Williams and Bujak, 1977)
16	Canada	44.3	-52.0	41.2	-44.9	Atlantic	(Williams and Bujak, 1977)
17	Canada	44.5	-52.5	42.5	-47.4	Atlantic	(Williams and Bujak, 1977)
18	Canada	44.1	-52.3	42.1	-47.2	Atlantic	(Williams and Bujak, 1977)
19	Canada	43.5	-52.4	41.5	-47.3	Atlantic	(Williams and Bujak, 1977)
20	Canada	45.0	-53.2	43.6	-49.4	Atlantic	(Williams, 1975a)
21	Canada	44.3	-53.2	42.3	-48.1	Atlantic	(Williams and Bujak, 1977)
22	Canada	44.3	-53.4	42.3	-48.2	Atlantic	(Williams and Bujak, 1977)
23	Canada	44.7	-53.7	43.3	-49.9	Atlantic	(Jenkins, 1974)

24	Canada	44.6	-54.1	42.6	-48.9	Atlantic	(Williams and Bujak, 1977)
25	Canada	44.3	-57.1	42.4	-51.9	Atlantic	(Williams and Bujak, 1977)
26	Canada	43.3	-59.4	41.5	-54.1	Atlantic	(Williams and Bujak, 1977)
27	Canada	44.2	-59.3	42.3	-54.0	Atlantic	(Williams and Bujak, 1977)
28	Canada	44.1	-59.5	42.2	-54.2	Atlantic	(Williams and Bujak, 1977)
29	Canada	42.5	-61.2	40.7	-55.9	Atlantic	(Williams and Bujak, 1977)
30	Canada	42.3	-62.3	40.5	-56.9	Atlantic	(Williams and Bujak, 1977)
31	Canada	39.5	-61.5	38.3	-57.7	Atlantic	(Lentin et al., 1994)
32	USA	38.6	-72.5	37.6	-68.6	Atlantic	(de Verteuil, 1996)
33	USA	38.6	-72.5	37.8	-69.5	Atlantic	(de Verteuil, 1996)
34	USA	35.3	-70.2	35.0	-69.1	Atlantic	(de Vernal, 1989)
35	USA	38.6	-72.5	37.8	-69.5	Atlantic	(de Verteuil, 1996)
36	USA	38.5	-72.5	37.5	-68.6	Atlantic	(de Verteuil, 1996)
37	USA	38.6	-72.5	37.1	-67.3	Atlantic	(de Verteuil, 1996)
38	USA	39.2	-74.3	37.4	-67.7	Atlantic	(de Verteuil, 1997)
39	USA	38.6	-74.5	37.4	-69.9	Atlantic	(de Verteuil, 1997)
40	USA	38.3	-76.3	38.0	-75.0	Atlantic	(De Verteuil and Norris, 1996)
41	USA	37.5	-75.8	36.9	-73.3	Atlantic	(De Verteuil and Norris, 1996)
42	USA	38.0	-76.7	37.3	-73.7	Atlantic	(De Verteuil and Norris, 1996)
43	USA	37.1	-76.4	36.5	-73.7	Atlantic	(Edwards, 2005)
44	USA	37.1	-76.7	36.6	-74.1	Atlantic	(De Verteuil and Norris, 1996)
45	USA	37.5	-77.4	37.0	-74.8	Atlantic	(De Verteuil and Norris, 1996)
46	USA	33.1	-77.3	30.7	-69.7	Atlantic	(Stover, 1977)
47	USA	32.2	-80.3	29.9	-72.7	Atlantic	(Edwards, 1986)
48	USA	25.4	-80.6	25.0	-78.4	Atlantic	(Weedman et al., 1999)
49	USA	25.5	-80.5	24.8	-77.4	Atlantic	(Weedman et al., 1999)
50	USA	25.5	-80.6	25.1	-78.7	Atlantic	(Weedman et al., 1999)
51	USA	25.5	-81.0	24.7	-77.3	Atlantic	(Weedman et al., 1999)
52	USA	25.5	-81.1	25.1	-78.9	Atlantic	(Weedman et al., 1999)
53	USA	26.1	-81.4	25.3	-77.8	Atlantic	(Edwards, 1998)

54	USA	26.0	-81.4	25.2	-77.9	Atlantic	(Edwards, 1998)
55	USA	26.0	-81.4	25.1	-77.8	Atlantic	(Edwards, 1998)
56	USA	26.0	-81.6	25.2	-78.0	Atlantic	(Edwards, 1998)
57	USA	29.2	-87.0	29.0	-85.8	Atlantic	(Wrenn and Kokinos, 1986)
58	USA	29.3	-87.0	28.6	-83.2	Atlantic	(Wrenn, 1986)
59	USA	32.8	-91.1	32.3	-87.7	Atlantic	(Wrenn et al., 2003)
60	USA	29.2	-92.9	27.9	-86.1	Atlantic	(Lenoir and Hart, 1986)
61	USA	30.5	-114.5	28.0	-107.5	Pacific	(Helenes, 2009)
62	USA	30.8	-114.2	28.3	-107.2	Pacific	(Helenes, 2009)
63	USA	31.6	-114.4	29.1	-107.5	Pacific	(Helenes, 2009)
64	USA	32.4	-114.8	29.9	-107.8	Pacific	(Helenes, 2009)
65	USA	33.5	-120.5	32.0	-116.9	Pacific	(Ballog and Malloy, 1981)
66	Canada	33.5	-120.5	30.8	-113.4	Pacific	(Ballog and Malloy, 1981)
67	Mexico	2.7	-113.6	1.5	-110.6	Pacific	(Jarvis, 1984)
68	Mexico	3.4	-113.2	2.1	-110.2	Pacific	(Jarvis and Tocher, 1985)
69	Venezuela	9.5	-63.2	6.8	-57.3	Caribbean Sea	(Helenes and Cabrera, 2003)
70	Argentina	-38.6	-62.0	-40.1	-57.7	Atlantic	(Quattrocchio et al., 1986)
71	Argentina	-39.0	-61.0	-40.5	-56.8	Atlantic	(Guler and Guerstein, 2002)
72	Argentina	-39.0	-59.0	-40.5	-54.7	Atlantic	(Guler and Guerstein, 2002)
73	Argentina	-39.0	-59.0	-40.5	-54.7	Atlantic	(Guler and Guerstein, 2002)
74	Antarctica	-62.1	-58.6	-64.8	-55.7	Southern	(Troedson and Riding, 2002)
75	Antarctica	-62.0	-58.0	-64.7	-55.0	Southern	(Stover et al., 1996)
76	Antarctica	-65.0	-78.5	-65.0	-78.5	Southern	(Pudsey and Harland, 2001a)
77	Antarctica	-67.0	-78.5	-67.0	-78.5	Southern	(Harland and Pudsey, 2002)
78	Antarctica	-67.6	-80.2	-67.6	-80.2	Southern	(Pudsey and Harland, 2001b)
79	Antarctica	-67.3	-76.5	-67.3	-76.5	Southern	(Pudsey and Harland, 2001a)
80	Antarctica	-67.6	-76.3	-67.6	-76.3	Southern	(Pudsey and Harland, 2001b)
81	South Africa	-31.7	14.1	-32.1	14.2	Atlantic	(Udeze and Oboh-Ikuenobe, 2005)
82	South Africa	-23.3	14.1	-23.6	14.2	Atlantic	(Udeze and Oboh-Ikuenobe, 2005)
83	Equatorial Guinea	3.5	8.4	2.9	8.4	Atlantic	(Dunay et al., 1999)
84	Angola	-11.1	11.2	-12.2	11.3	Atlantic	(Partridge, 1978)
85	Nigeria	4.2	5.9	3.9	5.9	Atlantic	(Durugbo et al., 2010)

86	Nigeria	4.1	6.3	3.8	6.3	Atlantic	(Durugbo et al., 2010)
87	Ghana	3.4	-2.4	1.8	-2.5	Atlantic	(Hulth, 2009)
88	Western Sahara	24.0	-20.0	23.6	-20.0	Atlantic	(Andrejeva-Grigorovich et al., 1996)
89	Morocco	34.0	-6.8	32.9	-6.8	Atlantic	(Warny and Wrenn, 2009)
90	Spain	37.5	-5.6	36.6	-6.1	Atlantic	(Jan Du Chene, 1977)
91	Spain	37.3	-7.0	36.4	-7.5	Atlantic	(Raymo et al., 1989)
92	Portugal	38.6	-9.1	37.6	-9.6	Atlantic	(Sousa, 2003)
93	Portugal	38.4	-9.9	37.4	-10.3	Atlantic	(Antunes et al., 1997)
94	Spain	40.9	-11.7	40.6	-11.8	Atlantic	(Mc Carthy et al., 1996)
95	Portugal	41.4	-11.4	41.1	-11.5	Atlantic	(Mc Carthy et al., 1996)
96	Portugal	41.4	-11.4	40.3	-11.9	Atlantic	(Mc Carthy et al., 1996)
97	Portugal	41.4	-12.7	40.4	-13.2	Atlantic	(Mc Carthy et al., 1996)
98	Portugal	41.0	-32.6	40.5	-31.6	Atlantic	(De Schepper et al., 2011)
99	Portugal	41.0	-32.6	40.6	-31.8	Atlantic	(Versteegh, 1997)
100	Spain	47.4	-9.2	46.4	-10.0	Atlantic	(Engel, 1992)
101	France	47.4	-9.2	47.1	-9.5	Atlantic	(Harland, 1979)
102	Ireland	48.5	-12.1	47.8	-12.7	Atlantic	(Brown and Downie, 1985)
103	Ireland	48.9	-12.2	48.1	-12.8	Atlantic	(Downie, 1984)
104	United Kingdom	49.5	-24.1	49.1	-24.3	Atlantic	(De Schepper et al., 2011)
105	Ireland	53.1	-18.5	52.8	-18.8	Atlantic	(De Schepper et al., 2009a)
106	Ireland	53.1	-18.5	52.8	-18.8	Atlantic	(De Schepper and Head, 2008)
107	United Kingdom	53.3	-20.1	52.1	-20.9	Atlantic	(Costa and Downie, 1979)
108	Ireland	56.6	-20.8	55.4	-21.7	Atlantic	(Edwards, 1984)
109	Ireland	56.0	-23.1	55.7	-23.4	Atlantic	(Edwards et al., 1991)
110	Ireland	56.0	-23.2	54.8	-24.1	Atlantic	(Edwards, 1984)
111	Ireland	56.3	-23.5	55.0	-24.4	Atlantic	(Edwards, 1984)
112	Iceland	56.3	-23.5	55.0	-24.4	Atlantic	(Engel, 1992)
113	United Kingdom	55.6	-25.0	54.3	-25.8	Atlantic	(Costa and Downie, 1979)
114	Iceland	63.4	-28.9	61.8	-25.6	Arctic	(Engel, 1992)
115	Iceland	66.3	-17.5	65.9	-18.2	Arctic	(Verhoeven et al., 2011)
116	Iceland	66.9	-17.5	66.5	-18.3	Arctic	(Verhoeven and Louwye, 2012)
117	Greenland	77.5	-17.3	77.0	-16.4	Arctic	(Bennike et al., 2002)

118	Greenland	77.5	-17.4	77.0	-16.5	Arctic	(Bennike et al., 2002)
119	Greenland	77.5	-17.4	77.0	-16.5	Arctic	(Bennike et al., 2002)
120	Greenland	78.1	-2.8	77.4	-2.4	Arctic	(Boulter and Manum, 1996)
121	Norway	76.5	5.2	73.8	4.1	Norwegian Sea	(Manum, 1976)
122	Spitsbergen	80.3	8.1	80.1	5.7	Arctic	(Matthiessen and Brenner, 1993)
123	Greenland	77.5	10.5	77.3	9.0	Arctic	(Smelor, 1999)
124	Norway	68.3	1.4	67.5	-1.4	Atlantic	(Manum et al., 1989)
125	Norway	67.5	1.0	66.7	-1.7	North Sea	(Mudie, 1989)
126	Norway	67.1	2.6	66.9	1.8	Atlantic	(Edwards et al., 1991)
127	Norway	67.2	3.7	67.0	3.0	Atlantic	(De Schepper et al., 2015)
128	Norway	67.2	3.7	66.9	2.4	Atlantic	(Mudie, 1989)
129	Norway	67.2	3.7	67.0	2.9	Atlantic	(Mudie, 1989)
130	Norway	66.3	4.4	66.1	3.5	North Sea	(Mudie, 1989)
131	Norway	66.6	9.3	65.6	3.5	Atlantic	(Eidvin et al., 2007)
132	Norway	66.5	10.4	65.8	6.7	Atlantic	(Eidvin et al., 2007)
133	Norway	64.2	7.5	64.1	6.7	Atlantic	(Eidvin et al., 2007)
134	Norway	64.2	7.5	64.0	6.7	Atlantic	(Eidvin et al., 2007)
135	Norway	64.2	7.4	63.9	6.3	Atlantic	(Eidvin et al., 2007)
136	Norway	56.7	3.5	56.4	2.8	North Sea	(Bennike et al., 2002)
137	Denmark	56.1	5.4	55.0	2.7	North Sea	(Dybkjaer et al., 2012)
138	Denmark	56.2	8.4	55.6	6.7	North Sea	(Piasecki, 1980)
139	Denmark	56.1	9.1	55.6	7.4	North Sea	(Costa and Downie, 1979)
140	Denmark	56.0	9.1	55.4	7.5	North Sea	(Costa and Downie, 1979)
141	Denmark	55.6	9.1	55.0	7.5	North Sea	(Piasecki, 1980)
142	Denmark	56.0	10.6	55.5	8.9	North Sea	(Costa and Downie, 1979)
143	Denmark	55.5	8.4	54.9	6.8	North Sea	(Piasecki, 1980)
144	Denmark	55.2	8.6	54.6	7.0	North Sea	(Piasecki, 1980)
145	Germany	54.9	9.0	54.4	7.5	North Sea	(Fechner, 1994)
146	Germany	53.8	8.6	53.1	7.0	North Sea	(Lund and Heilmann-Clausen, 2001)
147	Germany	53.5	9.2	52.8	7.3	North Sea	(Laursen, 1998)
148	Germany	53.4	9.2	52.8	7.7	North Sea	(Strauss et al., 2001)
149	Germany	53.4	10.2	52.6	8.3	North Sea	(Strauss and Lund, 1992)

150	Germany	53.3	10.3	52.7	8.7	North Sea	(Daniels et al., 1990)
151	Germany	52.7	11.2	52.2	9.8	North Sea	(Fechner, 1994)
152	Netherlands	51.7	10.0	51.1	8.6	North Sea	(Zonnevald, 1989)
153	Germany	52.7	8.3	52.1	6.9	North Sea	(Gerlach, 1961)
154	Netherlands	52.2	6.9	51.6	5.5	North Sea	(Herngreen, 1984)
155	Netherlands	52.3	6.9	51.7	5.5	North Sea	(Herngreen, 1984)
156	Netherlands	52.3	6.9	51.7	5.6	North Sea	(Herngreen, 1984)
157	Germany	51.2	6.7	50.4	5.2	North Sea	(Donders et al., 2009)
158	Netherlands	51.7	5.9	51.0	4.7	North Sea	(Zonnevald, 1989)
159	Belgium	51.8	5.5	51.1	4.2	North Sea	(Vandenberghe et al., 2005)
160	Netherlands	51.4	5.4	51.2	5.0	North Sea	(Wijnker et al., 2008)
161	Netherlands	51.5	5.5	50.5	3.8	North Sea	(Donders et al., 2009)
162	Belgium	51.1	5.7	50.6	4.8	North Sea	(Louwye et al., 1999)
163	Belgium	51.2	5.1	50.9	4.5	North Sea	(Louwye et al., 1999)
164	Belgium	51.2	5.1	50.9	4.5	North Sea	(Louwye et al., 2007)
165	Belgium	51.3	5.1	50.8	4.3	North Sea	(Louwye et al., 1999)
166	Belgium	51.1	4.9	50.8	4.3	North Sea	(Louwye et al., 2007)
167	Belgium	51.2	4.8	50.9	4.3	North Sea	(Louwye et al., 1999)
168	Belgium	51.3	4.7	51.0	4.2	North Sea	(Louwye et al., 1999)
169	Belgium	51.4	4.5	51.1	3.9	North Sea	(Louwye et al., 1999)
170	Belgium	51.4	4.5	50.9	3.5	North Sea	(Louwye and Laga, 1998)
171	Belgium	51.2	4.5	50.6	3.3	North Sea	(Louwye, 2002)
172	Belgium	51.2	4.4	50.6	3.3	North Sea	(Louwye, 2002)
173	Belgium	51.3	4.3	51.1	3.8	North Sea	(De Schepper et al., 2004)
174	Belgium	51.1	4.3	50.2	2.7	North Sea	(Louwye et al., 2000)
175	Belgium	51.1	4.3	50.1	2.6	North Sea	(Louwye et al., 2000)
176	Belgium	51.1	4.2	49.9	2.2	North Sea	(Louwye et al., 2000)
177	Belgium	51.1	4.2	50.1	2.6	North Sea	(Louwye et al., 2000)
178	Belgium	51.1	4.2	49.9	1.9	North Sea	(Louwye et al., 2000)
179	Belgium	51.2	4.2	51.0	3.8	North Sea	(De Schepper et al., 2009b)
180	Belgium	51.2	4.2	51.0	3.8	North Sea	(Louwye et al., 2004)
181	Belgium	51.2	4.1	50.9	3.7	North Sea	(Louwye et al., 2004)

182	Belgium	51.1	2.3	50.1	0.7	North Sea	(Louwye et al., 2010)
183	United Kingdom	52.6	1.3	52.4	0.9	North Sea	(Head, 1997)
184	United Kingdom	52.4	1.3	52.2	0.9	North Sea	(Head, 1998)
185	United Kingdom	49.1	6.0	48.0	4.1	Atlantic	(Powell, 1988)
186	United Kingdom	48.5	7.3	48.3	6.9	Atlantic	(Powell, 1988)
187	United Kingdom	48.6	7.5	48.0	6.4	Atlantic	(Powell, 1988)
188	France	43.8	-1.3	42.9	-2.1	Atlantic	(Mauroux and Platel, 2002)
189	France	44.4	-0.4	43.1	-1.6	Atlantic	(Londeix and Du Chene, 1998)
190	France	44.4	-0.3	43.1	-1.6	Atlantic	(Londeix and Du Chene, 1998)
191	France	44.4	-0.3	43.1	-1.7	Atlantic	(Londeix and Du Chene, 1998)
192	France	44.4	-0.4	43.1	-1.7	Atlantic	(Londeix and Du Chene, 1998)
193	France	44.1	6.1	43.2	5.0	Mediterranean	(Bialkowski et al., 2006)
194	France	44.0	6.1	42.9	4.4	Mediterranean	(Bialkowski et al., 2006)
195	Italy	44.3	8.2	43.5	7.0	Mediterranean	(Zevenboom, 1995)
196	Italy	44.4	8.2	43.4	6.4	Mediterranean	(Brinkhuis et al., 1992)
197	Italy	44.4	8.2	43.4	6.4	Mediterranean	(Prins, 1991)
198	Italy	44.4	8.3	43.6	7.1	Mediterranean	(Zevenboom, 1995)
199	Italy	44.5	8.3	43.8	7.3	Mediterranean	(Zevenboom, 1995)
200	Italy	44.5	8.6	44.1	8.0	Mediterranean	(Zevenboom, 1995)
201	Italy	44.4	8.6	43.4	6.8	Mediterranean	(Brinkhuis et al., 1992)
202	Italy	44.5	8.6	43.5	6.8	Mediterranean	(Powell, 1986c)
203	Italy	44.8	8.6	43.7	8.2	Mediterranean	(Powell, 1986a)
204	Italy	44.7	9.0	43.7	8.7	Mediterranean	(Zevenboom, 1995)
205	Italy	44.4	9.3	43.3	8.9	Mediterranean	(Powell, 1986b)
206	Italy	44.3	10.0	44.0	9.9	Mediterranean	(Habib, 1971)
207	Italy	43.4	11.5	41.3	10.7	Mediterranean	(Bucefalo Palliani et al., 1997)
208	Italy	43.2	12.3	41.6	11.7	Mediterranean	(Montanari et al., 1997)
209	Italy	43.2	12.3	41.2	11.6	Mediterranean	(Montanari et al., 1997)
210	Italy	43.2	12.3	41.1	11.6	Mediterranean	(Brinkhuis et al., 1992)
211	Italy	43.3	12.4	41.2	11.6	Mediterranean	(Brinkhuis et al., 1992)

212	Italy	43.3	12.4	41.6	11.8	Mediterranean	(Biffi and Manum, 1988)
213	Italy	43.4	12.4	41.3	11.7	Mediterranean	(Biffi and Manum, 1988)
214	Italy	43.3	12.6	41.2	11.8	Mediterranean	(Biffi and Manum, 1988)
215	Italy	43.4	13.3	41.3	12.5	Mediterranean	(Biffi and Manum, 1988)
216	Austria	48.1	13.3	47.3	11.5	Mediterranean	(Jimenez-Moreno et al., 2006)
217	Australia	48.1	14.1	47.5	11.8	Mediterranean	(Banerjee and Misra, 1972)
218	Austria	48.1	16.4	47.7	15.2	Mediterranean	(Harzhauser et al., 2008)
219	Austria	47.6	16.1	47.1	14.6	Mediterranean	(Jimenez-Moreno et al., 2006)
220	Austria	46.5	15.6	46.2	14.5	Mediterranean	(Soliman et al., 2013)
221	Croatia	45.5	15.4	44.6	15.0	Mediterranean	(Bakrač et al., 2012)
222	Croatia	45.5	17.1	44.4	16.5	Mediterranean	(Bakrač, 2007)
223	Hungary	47.4	18.2	47.1	17.3	Mediterranean	(Cziczer et al., 2009)
224	Hungary	46.5	18.7	46.1	17.3	Mediterranean	(Jimenez-Moreno et al., 2006)
225	Poland	50.4	20.3	50.0	18.6	North Sea	(Gedl, 1996)
226	Poland	50.6	21.7	50.3	20.4	Baltic Sea	(Gedl, 1999)
227	Ukraine	48.5	23.2	48.4	20.7	Black Sea	(Andrejeva-Grigorovich et al., 1996)
228	Ukraine	48.4	26.2	48.2	24.8	Black Sea	(Gedl and Peryt, 2011)
229	Romania	47.2	26.1	47.1	24.9	Black Sea	(Chirila and Tabara, 2008)
230	Russia	45.8	36.4	45.9	35.7	Black Sea	(Filippova, 2002)
231	Russia	44.3	40.5	45.2	38.6	Black Sea	(Zaporozhets, 1999)
232	Russia	42.6	44.2	43.7	42.5	Black Sea	(Filippova et al., 2010)
233	Russia	42.6	44.3	43.7	42.6	Black Sea	(Filippova et al., 2010)
234	Spain	40.0	4.5	39.3	3.8	Mediterranean	(Corradini et al., 1978)
235	Spain	40.0	4.8	39.4	4.1	Mediterranean	(Corradini et al., 1978)
236	Sardinia	39.5	8.5	37.3	7.9	Mediterranean	(Corradini, 1985)
237	Sardinia	39.4	8.5	37.2	8.0	Mediterranean	(Corradini, 1985)
238	Sardinia	39.4	8.6	37.8	8.1	Mediterranean	(Corradini, 1985)
239	Sardinia	39.4	9.1	37.8	8.7	Mediterranean	(Corradini, 1985)
240	Sardinia	39.2	9.4	37.8	9.0	Mediterranean	(Corradini, 1985)
241	Portugal	38.4	9.8	37.3	9.5	Mediterranean	(Legoinha et al., 2002)
242	Tunisia	36.4	10.4	36.2	10.3	Mediterranean	(Londeix et al., 1999)

243	Tunisia	36.4	10.4	35.9	10.3	Mediterranean	(Londeix et al., 1992)
244	Tunisia	36.1	10.6	35.6	10.4	Mediterranean	(Londeix, 1995)
245	Italy	37.2	13.2	36.6	13.0	Mediterranean	(Bertini et al., 1998)
246	Italy	37.2	13.3	36.5	13.1	Mediterranean	(Londeix et al., 1999)
247	Italy	37.2	13.4	36.6	13.2	Mediterranean	(Bertini et al., 1998)
248	Italy	37.5	14.1	37.0	13.9	Mediterranean	(Londeix et al., 2007)
249	Italy	38.2	16.3	38.0	16.2	Mediterranean	(Versteegh and Zonneveld, 1994)
250	Italy	38.2	16.3	38.0	16.2	Mediterranean	(Versteegh, 1997)
251	Albania	41.2	19.3	40.0	18.8	Mediterranean	(Gjani et al., 2003)
252	Greece	39.4	20.4	37.4	19.5	Mediterranean	(Janssen, 1991)
253	Greece	35.2	24.5	34.7	24.3	Mediterranean	(Ioakim et al., 1992)
254	Greece	35.2	26.1	34.6	25.8	Mediterranean	(Santarelli et al., 1998)
255	Greece	35.2	26.1	34.3	25.6	Mediterranean	(Ioakim et al., 1997)
256	Greece	35.9	26.6	35.5	26.4	Mediterranean	(Carvalho, 2003)
257	Greece	35.1	26.9	34.7	26.7	Mediterranean	(Edwards, 1984)
258	Egypt	31.2	27.2	29.9	26.6	Mediterranean	(Mahmoud, 1998)
259	Canada	54.3	-54.6	52.9	-50.4	Atlantic	(Williams and Bujak, 1977)
260	Turkey	36.4	35.6	36.6	34.9	Mediterranean	(Ediger et al., 1996)
261	Egypt	31.0	30.1	29.5	29.3	Mediterranean	(El Beialy, 1988)
262	USA	24.4	-79.1	24.1	-77.8	Atlantic	(Head and Westphal, 1999)
263	Egypt	31.1	30.4	30.7	30.2	Mediterranean	(El Beialy, 1992)
264	Egypt	31.2	30.7	30.3	30.2	Mediterranean	(El Beialy, 1997)
265	Egypt	30.6	31.0	29.7	30.5	Mediterranean	(Edwards, 1998)
266	Egypt	31.0	32.1	30.2	31.7	Mediterranean	(El Beialy, 1990)
267	Egypt	29.2	32.4	28.1	31.8	Mediterranean	(El Beialy and Ali, 2002)
268	Egypt	28.5	32.5	27.6	32.0	Red Sea	(Soliman and Ibrahim, 2012)
269	Egypt	28.1	33.0	27.0	32.5	Mediterranean	(Mahmoud, 1993)
270	Egypt	28.3	33.4	26.8	32.7	Red Sea	(Soliman and Ibrahim, 2012)
271	Egypt	27.5	33.2	26.0	32.5	Red Sea	(Soliman and Ibrahim, 2012)
272	USA	38.3	75.0	38.4	74.6	Atlantic	(McLaughlin et al., 2008)
273	India	18.2	67.2	13.5	69.2	Arabian Sea	(Mehrotra)
274	India	15.2	80.2	14.1	80.5	Indian	(Kumar and Saxena, 1997)
275	India	15.7	81.2	11.9	81.9	Arabian Sea	(Nallapa Reddy, 2005)
276	India	21.7	87.6	15.0	89.1	Indian	(Mehrotra and Rawat, 1992)

277	India	25.9	92.2	15.1	94.3	Indian	(Saxena and Rao, 1984)
278	India	12.1	93.6	7.9	100.4	Indian	(Daneshian et al., 2007)
279	USA	24.3	-78.6	24.0	-77.4	Atlantic	(Westphal et al., 1999)
280	China	18.0	110.0	21.0	112.9	South China Sea	(Dequan, 1997)
281	China	19.8	114.3	21.5	115.5	South China Sea	(Yichun et al.)
282	China	19.3	113.6	20.9	114.8	South China Sea	(Yichun et al.)
283	China	19.5	114.5	21.0	115.6	South China Sea	(Mao and Lei, 1996)
284	China	24.3	121.1	28.7	123.2	South China Sea	(Mao et al., 2002)
285	Korea	35.5	129.3	39.1	130.0	Sea of Japan	(Yun, 1987)
286	Japan	34.4	135.5	36.3	134.5	Sea of Japan	(Matsuoka, 1974)
287	Japan	37.7	138.1	38.4	137.6	Sea of Japan	(Matsuoka, 1983)
288	France	43.5	0.4	42.6	-0.5	Atlantic	(Gardère and Pais, 2009)
289	Japan	39.9	139.8	42.0	138.7	Sea of Japan	(Matsuoka et al., 1987)
290	Japan	39.9	139.8	42.0	138.7	Sea of Japan	(Matsuoka et al., 1987)
291	Japan	39.1	144.8	38.0	157.6	Pacific	(Kurita, 2003)
292	Borneo	6.4	115.9	8.5	118.8	South China Sea	(Naih, 2008)
293	Borneo	3.3	117.9	5.6	121.2	South China Sea	(Besems, 1993)
294	Indonesia	-6.5	107.1	-5.2	111.2	Indian	(Morgenroth, 2008)
295	Australia	-16.0	117.4	-23.3	114.3	Indian	(McMinn, 1992)
296	Australia	-16.9	147.7	-22.5	146.5	Pacific	(McMinn, 1993)
297	Australia	-18.8	148.9	-24.3	147.8	Pacific	(McMinn, 1993)
298	Australia	-32.6	140.5	-42.9	138.5	Pacific	(Truswell et al., 1985)
299	Australia	-38.4	142.5	-45.8	141.5	Pacific	(Deflandre and Cookson, 1955)
300	Australia	-38.2	144.4	-45.6	143.6	Pacific	(Deflandre and Cookson, 1955)
301	Australia	-42.9	144.6	-48.3	143.9	Tasman Sea	(Brinkhuis, 2003)
302	Australia	-42.8	154.2	-48.1	154.6	Tasman Sea	(Macphail, 1993)
303	New Zealand	-45.3	174.6	-46.2	176.6	Pacific	(McMinn et al., 2001)
304	Antarctica	-77.5	165.2	-76.6	157.2	Ross Sea	(Warny et al., 2009)
305	Argentina	-38.4	-62.8	-40.0	-58.6	Atlantic	(Quattrocchio et al., 1986)
306	USA	38.4	-72.2	37.7	-69.6	Atlantic	(de Verteuil, 1996)

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Appendix B: Species with known temperature preferences and references

Species with known temperature preferences used in the Neogene

Taxa	Temperature Preference	Species Original Publication	Temperature Preference Reference
Ataxiodinium choane	**CWS**	Reid, 1974	Zonneveld et al. (2013)
Batiacasphaera complex (B. micropapillata and B.minuta	**CWS**	Stover, 1977	Schreck and Matthiessen (2013), Schreck et al. (2013)
Bitectatodinium tepikiense	**CWS**	Wilson, 1973	Zonneveld et al. (2013)
Filisphaera filifera	**CWS**	Bujak, 1984	Head (1996); De Schepper et al. (2009)
Filisphaera microornata	**CWS**	(Head et al., 1989b) Head, 1994b	Wijnker et al. (2008)
Habibacysta tectata	**CWS**	Head et al. 1989b	Head (1994); Head (1996); Wijnker et al. (2008)
Headinium miocenicum	**CWS**	Zevenboom, 1995 Name not validly published	Wijnker et al. (2008)
Impagidinium japonicum	**CWS**	Matsuoka, 1983	Schreck et al. (2013)
Impagidinium pallidum	**CWS**	Bujak, 1984	Zonneveld et al. (2013)
Lejeunecysta communis	**CWS**	Biffi and Grignani, 1983	Strauss et al. (2001)
Pyxidinopsis braboi	**CWS**	De Schepper et al., 2004	Warny et al. (2009); Hennissen et al. (2014)
Spiniferites elongatus/frigidus	**CWS**	Reid, 1974; Harland et al., 1980	Zonneveld et al. (2013)
Achomosphaera andalousiensis	**WWS**	Jan du Chêne, 1977	Wijnker et al. (2008)
Ataxiodinium confusum	**WWS**	Versteegh, 1995	Udeze and Oboh-Ikuenobe (2005); De Schepper et al. (2011)
Barssidinium pliocenicum	**WWS**	(Head, 1993) Head, 1994	Head (1997)
Bitectatodinium raedwaldii	**WWS**	Head, 1997	Head (1997)
Bitectatodinium spongium	**WWS**	(Zonneveld, 1997) Zonneveld and Jurkschat, 1999	Zonneveld et al. (2013)
Caligodinium pychnum	**WWS**	Biffi and Manum, 1988	McCarthy and Mudie (1996)

Capisocysta lata	**WWS**	Head, 1998	Head (1998)
Capisocysta lyellii	**WWS**	Head, 1998	Head (1998)
Cerebrocysta poulsenii	**WWS**	de Verteuil and Norris, 1996a	Strauss et al. (2001)
Dapsilidinium pastielsii	**WWS**	(Stover, 1977) Bujak et al., 1980	Head and Westphal (1999)
Echinidinium euaxum	**WWS**	(Head, 1993) Head et al., 2001	Marret and Zonneveld (2003)
Edwardsiella sexispinosa	**WWS**	Versteegh, 1995	De Schepper et al. (2011)
Geonettia clineae	**WWS**	de Verteuil and Norris, 1996	de Verteuil and Norris (1996)
Geonettia waltonensis	**WWS**	Head, 2000	Head (2000)
Homotryblium aculeatum	**WWS**	Williams, 1978	Williams and Bujak (1977)
Homotryblium floripes	**WWS**	(Deflandre and Cookson, 1955) Stover, 1975	McCarthy and Mudie (1996)
Homotryblium oceanicum	**WWS**	Eaton, 1976	Williams and Bujak (1977)
Homotryblium pallidum	**WWS**	Davey and Williams, 1966	de Verteuil and Norris (1996)
Homotryblium plectilum	**WWS**	Drugg and Loeblich Jr., 1967	de Verteuil and Norris (1996)
Homotryblium tenuispinosum	**WWS**	Davey and Williams, 1966	Williams and Bujak (1977)
Homotryblium vallum	**WWS**	Stover, 1977	Williams and Bujak (1977)
Hystrichokolpoma cinctum	**WWS**	Klumpp, 1953	McCarthy and Mudie (1996)
Hystrichokolpoma rigaudiae	**WWS**	Deflandre and Cookson, 1955	Strauss et al. (2001)
Impagidinium aculeatum	**WWS**	(Wall, 1967) Lentin and Williams, 1981	Zonneveld et al. (2013)
Impagidinium bacatum	**WWS**	Londeix et al., 1992	Londeix et al. (1992)
Impagidinium paradoxum	**WWS**	(Wall, 1967) Stover and Evitt, 1978	Zonneveld et al. (2013)
Impagidinium patulum	**WWS**	(Wall, 1967) Stover and Evitt, 1978	Zonneveld et al. (2013)
Impagidinium plicatum	**WWS**	Versteegh, 1995	Zonneveld et al. (2013)
Impagidinium strialatum	**WWS**	(Wall, 1967) Stover and Evitt, 1978	Zonneveld et al. (2013)
Impagidinium velorum	**WWS**	Bujak, 1984	Zonneveld et al. (2013)
Invertocysta lacrymosa	**WWS**	Edwards, 1984	De Schepper et al. (2011)
Invertocysta tabulata	**WWS**	Edwards, 1984	De Schepper et al. (2011)
Lingulodinium machaerophorum	**WWS**	(Deflandre and Cookson, 1955) Wall, 1967	Zonneveld et al. (2013)
Melitasphaeridinium choanophorum	**WWS**	(Deflandre and Cookson, 1955) Harland and Hill, 1979	Wijnker et al. (2008)

Operculodinium crassum	**WWS**	Harland, 1979b	Strauss et al. (2001)
Operculodinium israelianum	**WWS**	(Rossignol, 1962) Wall, 1967	Zonneveld et al. (2013)
Operculodinium janduchenei	**WWS**	Head et al., 1989b	Zonneveld et al. (2013)
Operculodinium tegillatum	**WWS**	Head, 1997	Head (1997)
Operculodinium? eirikianum	**WWS**	Head et al., 1989, Emendation: Head, 1997	Head (1993)
Pentadinium laticinctum	**WWS**	Gerlach, 1961	McCarthy and Mudie (1996)
Polysphaeridium subtile	**WWS**	Davey and Williams, 1966b	Gedl and Peryt (2011)
Polysphaeridium zoharyi	**WWS**	(Rossignol, 1962) Bujak et al., 1980	Zonneveld et al. (2013)
Selenopemphix nephroides	**WWS**	Benedek, 1972	Zonneveld et al. (2013)
Spiniferites hyperacanthus	**WWS**	(Deflandre and Cookson, 1955) Cookson and Eisenack, 1974	Marret and Zonneveld (2003)
Spiniferites membranaceus	**WWS**	(Rossignol, 1964) Sarjeant, 1970	Zonneveld et al. (2013)
Spiniferites mirabilis	**WWS**	(Rossignol, 1964) Sarjeant, 1970	Zonneveld et al. (2013)
Tectatodinium pellitum	**WWS**	Wall, 1967	Zonneveld et al. (2013)
Thalassiphora delicata	**WWS**	Williams and Downie, 1966c	McCarthy and Mudie (1996)
Tuberculodinium vancampoae	**WWS**	(Rossignol, 1962) Wall, 1967	Zonneveld et al. (2013)

Species with known temperature preferences used in the Modern

Taxa	**Temperature Preference**	**Species Original Publication**	**Temperature Preference Reference**
Bitectatodinium tepikiense	**CWS**	Wilson, 1973	Zonneveld et al. (2013)
Echinidinium karaense	**CWS**	Head et al., 2001	Zonneveld et al. (2013)
Impagidinium pallidum	**CWS**	Bujak, 1984	Zonneveld et al. (2013)
Islandinium minutum	**CWS**	(Harland and Reid, in Harland et al., 1980) Head et al., 2001	Zonneveld et al. (2013)
Operculodinium centrocarpum (var. arctica)	**CWS**	Deflandre et Cookson 1955)Wall 1967 var. arctica sensu Radi and de Vernal 2008	Zonneveld et al. (2013)

Selenopemphix antarctica	**CWS**	Marret and de Vernal, 1997	Zonneveld et al. (2013)
Spiniferites elongatus/frigidus	**CWS**	Reid, 1974; Harland et al., 1980	Zonneveld et al. (2013)
Spiniferites lazus	**CWS**	Reid 1974	Zonneveld et al. (2013)
Cyst of *Gymnodinium catenatum*	**WWS**	Graham 1943	Zonneveld et al. (2013)
Cyst of *Gymnodinium nolleri*	**WWS**	Ellegaard and Moestrup 1999	Zonneveld et al. (2013)
Echinidinium "aculeatum"	**WWS**	Zonneveld, 1997 Name not validly published	Zonneveld et al. (2013)
Echinidinium delicatum	**WWS**	Zonneveld, 1997	Zonneveld et al. (2013)
Impagidinium aculeatum	**WWS**	(Wall, 1967) Lentin and Williams, 1981	Zonneveld et al. (2013)
Impagidinium paradoxum	**WWS**	(Wall, 1967) Stover and Evitt, 1978	Zonneveld et al. (2013)
Impagidinium patulum	**WWS**	(Wall, 1967) Stover and Evitt, 1978	Zonneveld et al. (2013)
Impagidinium plicatum	**WWS**	Versteegh, 1995	Zonneveld et al. (2013)
Impagidinium strialatum	**WWS**	(Wall, 1967) Stover and Evitt, 1978	Zonneveld et al. (2013)
Impagidinium velorum	**WWS**	Bujak, 1984	Zonneveld et al. (2013)
Lejeunecysta oliva	**WWS**	(Reid, 1977) Turon and Londeix, 1988	Zonneveld et al. (2013)
Lingulodinium machaerophorum	**WWS**	(Deflandre and Cookson, 1955) Wall, 1967	Zonneveld et al. (2013)
Operculodinium israelianum	**WWS**	(Rossignol, 1962) Wall, 1967	Zonneveld et al. (2013)
Operculodinium janduchenei	**WWS**	Head et al., 1989b	Zonneveld et al. (2013)
Operculodinium longispinigerum	**WWS**	Matsuoka, 1983	Zonneveld et al. (2013)
Polykrikos schwarztii	**WWS**	(Bütschli 1873) sensu Matsuoka et al., 2009	Zonneveld et al. (2013)
Polysphaeridium zoharyi	**WWS**	(Rossignol, 1962) Bujak et al., 1980	Zonneveld et al. (2013)
Protoperidinium monospinum	**WWS**	(Gran et Braarud 1930) Balech 1974	Zonneveld et al. (2013)
Pyxidinopsis psilata	**WWS**	Wall et Dale 1973	Zonneveld et al. (2013)
Quinquecuspis concreta	**WWS**	(Reid 1977) Harland 1977	Zonneveld et al. (2013)
Selenopemphix nephroides	**WWS**	Benedek, 1972	Zonneveld et al. (2013)
Spiniferites bentorii	**WWS**	(Rossignol 1964) Wall et Dale 1970	Zonneveld et al. (2013)
Spiniferites delicatus	**WWS**	Reid 1974	Zonneveld et al. (2013)
Spiniferites membranaceus	**WWS**	(Rossignol, 1964) Sarjeant, 1970	Zonneveld et al. (2013)
Spiniferites mirabilis	**WWS**	(Rossignol, 1964) Sarjeant, 1970	Zonneveld et al. (2013)

Spiniferites pachydermus	**WWS**	(Rossignol, 1964) Reid, 1974	Zonneveld et al. (2013)
Stelladinium robustum	**WWS**	Zonneveld 1997	Zonneveld et al. (2013)
Stelladinium stellatum	**WWS**	(Wall et Dale 1968) Reid 1977	Zonneveld et al. (2013)
Tectatodinium pellitum	**WWS**	Wall, 1967	Zonneveld et al. (2013)
Tuberculodinium vancampoae	**WWS**	(Rossignol, 1962) Wall, 1967	Zonneveld et al. (2013)
Votadinium spinosum	**WWS**	Reid 1977	Zonneveld et al. (2013)
Xandarodinium xanthum	**WWS**	Head et al. 1989	Zonneveld et al. (2013)

CWS = Cold Water Species

WWS = Warm Water Species

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Appendix C: References and location of the sites used in Chapter 4

ID	Latitude	Longitude	Palaeo lat.	Palaeo long.	Sub-epoch	Max Age	Min Age	Basin	Literature
1	48.1	13.3	47.3	11.5	Early Miocene	19.5	18.1	Paratethys	(Jimenez-Moreno et al., 2006)
2	48.1	14.1	47.5	11.8	Early Miocene	23.03	20.44	Paratethys	(Grunert et al., 2010)
3	46.5	15.3	45.8	13.8	Early Miocene	17.9	13.5	Paratethys	(Soliman and Piller, 2007)
4	46.5	15.6	46.2	14.5	Late Miocene	11.608	7.246	Paratethys	(Soliman et al., 2013)
5	47.6	16.1	47.1	14.6	Middle Miocene	15.97	13.65	Paratethys	(Jimenez-Moreno et al., 2006)
6	45.5	15.4	44.1	14.8	Middle Miocene	15.97	15	Paratethys	(Bakrač et al., 2012)
7	45.5	15.4	44.2	14.8	Middle Miocene	15	13.82	Paratethys	(Bakrač et al., 2012)
8	45.5	15.4	44.3	14.9	Middle Miocene	13.82	11.9	Paratethys	(Bakrač et al., 2012)
9	45.5	15.4	44.4	14.9	Middle Miocene	11.9	11.62	Paratethys	(Bakrač et al., 2012)
10	45.5	15.4	44.5	14.9	Late Miocene	11.62	9.6	Paratethys	(Bakrač et al., 2012)
11	45.5	15.4	44.6	15.0	Late Miocene	9.6	8.2	Paratethys	(Bakrač et al., 2012)
12	45.5	15.4	44.8	15.1	Late Miocene	8.2	7.246	Paratethys	(Bakrač et al., 2012)
13	45.5	15.4	44.9	15.1	Late Miocene	7.246	5.33	Paratethys	(Bakrač et al., 2012)

14*	48.1	16.4	47.7	15.2	Late Miocene	11.61	5.3	Paratethys	(Harzhauser et al., 2008)
15*	45.5	17.1	44.1	16.4	Early-Middle Miocene	16.4	13.02	Paratethys	(Bakrač, 2007)
16	45.5	17.1	44.4	16.5	Middle Miocene	13.02	11.5	Paratethys	(Bakrač, 2007)
17	45.5	17.1	44.5	16.6	Late Miocene	11.5	9.78	Paratethys	(Bakrač, 2007)
18*	45.5	17.1	44.9	16.8	Late-Miocene-Pliocene	7.25	3.6	Paratethys	(Bakrač, 2007)
19	47.3	18.0	47.0	17.1	Late Miocene	9.4	8.9	Paratethys	(Cziczer et al., 2009)
20	47.4	18.2	47.1	17.3	Late Miocene	9.4	8.9	Paratethys	(Cziczer et al., 2009)
21	46.5	18.7	46.1	17.3	Middle Miocene	15.97	14.4	Paratethys	(Jimenez-Moreno et al., 2006)
22	46.5	18.7	46.2	17.4	Middle Miocene	14.4	13.65	Paratethys	(Jimenez-Moreno et al., 2006)
23	46.5	18.7	46.2	17.5	Middle Miocene	13.65	12.8	Paratethys	(Jimenez-Moreno et al., 2006)
24	46.5	18.7	46.2	17.5	Middle Miocene	12.8	11.6	Paratethys	(Jimenez-Moreno et al., 2006)
25	50.4	20.3	50.0	18.6	Middle Miocene	15	13.65	Paratethys	(Gedl, 1996)
26	50.6	21.7	50.3	20.4	Late Miocene	11.6	7.25	Paratethys	(Gedl, 1999)
27	48.5	23.2	48.4	20.7	Early Miocene	23.03	20.43	Paratethys	(Andrejeva-Grigorovich et al., 1996)
28	48.5	23.2	48.2	21.1	Early Miocene	20.43	15.97	Paratethys	(Andrejeva-Grigorovich et al., 1996)
29	44.5	23.5	44.5	23.0	Pliocene	5.33	3.6	Paratethys	(Demetrescu, 1989)

30	45.8	24.4	45.7	23.8	Late Miocene	6.25	6	Paratethys	(Demetrescu, 1992)
31	45.5	24.6	45.4	24.1	Pliocene	5.332	3.6	Paratethys	(Baltes, 1971)
32	45.2	24.7	45.1	24.2	Pliocene	5.33	3.6	Paratethys	(Demetrescu, 1989)
33	45.3	25.1	45.2	24.6	Pliocene	5.33	3.6	Paratethys	(Demetrescu, 1989)
34	48.4	26.2	48.2	24.8	Middle Miocene	13.65	12.01	Paratethys	(Gedl and Peryt, 2011)
35	47.2	26.1	47.1	24.9	Middle Miocene	12.7	11.9	Paratethys	(Chirilă and Tabara, 2008)
36	46.4	26.6	46.3	25.4	Middle Miocene	12.7	11.6	Paratethys	(Chirilă, 2010)
37	45.3	26.2	45.2	25.7	Pliocene	5.33	3.6	Paratethys	(Demetrescu, 1989)
38	45.8	36.4	45.9	35.6	Late Miocene	7.9	7.4	Paratethys	(Filippova, 2002)
39*	45.8	36.4	45.9	35.7	Late Miocene	7.4	6.05	Paratethys	(Filippova, 2002)
40	45.8	36.4	45.9	35.8	Late Miocene	6.05	5.2	Paratethys	(Filippova, 2002)
41	45.8	36.4	45.9	35.9	Pliocene	5.2	4.4	Paratethys	(Filippova, 2002)
42*	44.3	40.5	45.2	38.6	Early Miocene	23.03	15.97	Paratethys	(Zaporozhets, 1999)
43	42.6	44.2	43.7	42.5	Early Miocene	23.7	21.4	Paratethys	(Filippova et al., 2010)
44	42.6	44.3	43.7	42.6	Early Miocene	23.7	21.4	Paratethys	(Filippova et al., 2010)
45*	40.0	4.5	38.9	3.1	Early Miocene	23.03	15.97	Western	(Corradini et al., 1978)
46	40.0	4.5	39.1	3.5	Middle Miocene	15.97	11.62	Western	(Corradini et al., 1978)
47*	40.0	4.5	39.3	3.8	Late Miocene	11.62	5.33	Western	(Corradini et al., 1978)

48	40.0	4.8	39.4	4.1	Late Miocene	11.6	7.2	Western	(Corrandini)
49*	39.5	8.5	37.3	7.9	Early Miocene	23.2	18.2	Western	(Corradini, 1985)
50	39.5	8.5	37.3	7.9	Early Miocene	23.2	22.8	Western	(Corradini, 1985)
51*	39.4	8.5	37.2	8.0	Early Miocene	23.2	18.2	Western	(Corradini, 1985)
52*	39.4	8.5	37.3	8.0	Early Miocene	22.8	17.9	Western	(Corradini, 1985)
53	39.4	8.6	37.8	8.1	Early Miocene	17.9	15	Western	(Corradini, 1985)
54	39.4	9.1	37.8	8.7	Early Miocene	17.9	15	Western	(Corradini, 1985)
55	39.2	9.4	37.8	9.0	Middle Miocene	15	13.5	Western	(Corradini, 1985)
56	38.4	9.8	36.7	9.4	Early Miocene	18	15.97	Western	(Legoinha et al., 2002)
57	38.4	9.8	36.9	9.4	Middle Miocene	15.97	13.82	Western	(Legoinha et al., 2002)
58	38.4	9.8	37.1	9.5	Middle Miocene	13.82	11.62	Western	(Legoinha et al., 2002)
59	38.4	9.8	37.3	9.5	Late Miocene	11.62	7.246	Western	(Legoinha et al., 2002)
60	44.0	6.1	42.9	4.4	Early Miocene	23.03	20.43	Central	(Bialkowski et al., 2006)
61	44.1	6.1	43.2	5.0	Middle Miocene	15.97	13.65	Central	(Bialkowski et al., 2006)
62	44.1	6.1	43.4	5.1	Middle Miocene	13.65	11.608	Central	(Bialkowski et al., 2006)
63	44.4	8.2	43.4	6.4	Early Miocene	23.03	20.43	Central	(Brinkhuis et al., 1992)
64*	44.4	8.2	43.4	6.4	Early Miocene	23.03	15.97	Central	(Prins, 1991)

65	44.3	8.2	43.4	6.7	Early Miocene	20.44	15.97	Central	(Zevenboom, 1995)
66	44.4	8.6	43.4	6.8	Early Miocene	23.03	20.43	Central	(Brinkhuis et al., 1992)
67	44.5	8.6	43.5	6.8	Early Miocene	23.03	20.43	Central	(Powell, 1986c)
68	44.3	8.2	43.5	7.0	Middle Miocene	15.97	13.82	Central	(Zevenboom, 1995)
69	44.4	8.3	43.6	7.1	Middle Miocene	15.97	13.82	Central	(Zevenboom, 1995)
70	44.5	8.3	43.7	7.2	Middle Miocene	15.97	13.82	Central	(Zevenboom, 1995)
71	44.5	8.3	43.8	7.3	Middle Miocene	13.82	11.62	Central	(Zevenboom, 1995)
72	44.5	8.6	44.1	8.0	Late Miocene	7.246	5.33	Central	(Zevenboom, 1995)
73*	44.8	8.6	43.3	8.1	Middle Miocene	15.97	11.61	Central	(Powell, 1986a)
74	44.8	8.6	43.7	8.2	Late Miocene	11.6	7.2	Central	(Powell, 1986a)
75	44.8	8.6	44.1	8.4	Late Miocene	7.25	5.33	Central	(Powell, 1986a)
76	44.7	9.0	43.5	8.6	Middle Miocene	13.82	11.62	Central	(Zevenboom, 1995)
77	44.4	9.3	42.3	8.6	Early Miocene	23.03	20.44	Central	(Powell, 1986b)
78	44.7	9.0	43.7	8.7	Late Miocene	11.6	7.25	Central	(Zevenboom, 1995)
79	44.4	9.3	42.5	8.7	Early Miocene	20.44	15.97	Central	(Powell, 1986b)
80	44.4	9.3	42.8	8.8	Early Miocene	17.6	15.97	Central	(Powell, 1986b)
81	44.4	9.3	43.0	8.8	Middle Miocene	15.97	14.8	Central	(Powell, 1986b)
82	44.4	9.3	43.1	8.9	Middle Miocene	14.8	13.8	Central	(Powell, 1986b)
83	44.4	9.3	43.2	8.9	Middle Miocene	13.8	13.4	Central	(Powell, 1986b)
84	44.4	9.3	43.2	8.9	Middle Miocene	13.4	11.8	Central	(Powell, 1986b)
85	44.4	9.3	43.3	8.9	Middle Miocene	11.8	11.62	Central	(Powell, 1986b)
86	44.3	10.0	43.9	9.8	Pliocene	5.333	3.6	Central	(Habib, 1971)

87	44.3	10.0	44.0	9.9	Pliocene	3.6	2.588	Central	(Habib, 1971)
88*	36.4	10.4	35.9	10.3	Pliocene	5.332	2.588	Central	(Londeix et al., 1992)
89	36.4	10.4	36.0	10.3	Pliocene	4.1	3.7	Central	(Londeix et al., 1999)
90*	36.4	10.4	36.1	10.3	Pliocene	3.7	3.4	Central	(Londeix et al., 1999)
91	36.4	10.4	36.1	10.3	Pliocene	3.4	2.9	Central	(Londeix et al., 1999)
92	36.4	10.4	36.1	10.3	Pliocene	2.9	2.6	Central	(Londeix et al., 1999)
93*	36.1	10.6	35.6	10.4	Pliocene	5.33	2.59	Central	(Londeix, 1995)
94	43.4	11.5	41.3	10.7	Early Miocene	23.8	20.5	Central	(Bucefalo Palliani et al., 1997)
95	43.2	12.3	41.1	11.6	Early Miocene	23.03	20	Central	(Montanari et al., 1997)
96*	43.2	12.3	41.2	11.6	Early Miocene	22.8	15.97	Central	(Montanari et al., 1997)
97	43.3	12.4	41.2	11.6	Early Miocene	23.03	20.43	Central	(Brinkhuis et al., 1992)
98*	43.3	12.4	41.2	11.6	Early Miocene	23.03	17.9	Central	(Biffi and Manum, 1988)
99	43.4	12.4	41.3	11.7	Early Miocene	23.03	21.1	Central	(Biffi and Manum, 1988)
100*	43.4	12.4	41.5	11.7	Early Miocene	21.1	17.6	Central	(Biffi and Manum, 1988)
101	43.3	12.4	41.6	11.8	Early Miocene	17.9	15.97	Central	(Biffi and Manum, 1988)

102*	43.3	12.6	41.2	11.8	Early Miocene	23.03	15.97	Central	(Biffi and Manum, 1988)
103	43.4	13.3	41.3	12.5	Early Miocene	23.03	22.8	Central	(Biffi and Manum, 1988)
104	43.4	13.3	41.3	12.5	Early Miocene	23.03	22.8	Central	(Biffi and Manum, 1988)
105*	43.4	13.3	41.3	12.6	Early Miocene	22.8	15.97	Central	(Biffi and Manum, 1988)
106*	43.4	13.3	41.3	12.6	Early Miocene	22.8	18.2	Central	(Biffi and Manum, 1988)
107	43.4	13.3	41.7	12.7	Early Miocene	18.2	15.97	Central	(Biffi and Manum, 1988)
108	37.2	13.2	36.6	13.0	Late Miocene	7.246	5.332	Central	(Bertini et al., 1998)
109	37.2	13.3	36.5	13.1	Late Miocene	7.25	5.33	Central	(Londeix et al., 1999)
110	37.2	13.3	36.7	13.2	Pliocene	5.33	5.08	Central	(Londeix et al., 1999)
111	37.2	13.3	36.7	13.2	Pliocene	5.08	4.52	Central	(Londeix et al., 1999)
112	37.2	13.3	36.8	13.2	Pliocene	4.52	3.92	Central	(Londeix et al., 1999)
113*	37.2	13.3	36.8	13.2	Pliocene	4.3	2.4	Central	(Londeix et al., 1992)
114	37.2	13.3	36.8	13.2	Pliocene	3.92	3.82	Central	(Londeix et al., 1999)
115	37.2	13.3	36.8	13.2	Pliocene	3.82	3.58	Central	(Londeix et al., 1999)
116	37.2	13.4	36.6	13.2	Late Miocene	7.246	5.332	Central	(Bertini et al., 1998)
117	37.2	13.3	36.9	13.2	Pliocene	3.31	3.2	Central	(Londeix et al., 1999)

118	37.2	13.3	36.8	13.2	Pliocene	3.58	3.31	Central	(Londeix et al., 1999)
119	37.2	13.3	36.9	13.2	Pliocene	3.2	2.69	Central	(Londeix et al., 1999)
120*	37.2	13.3	36.9	13.2	Pliocene-Pleistocene	2.69	1.81	Central	(Londeix et al., 1999)
121	37.5	14.1	36.5	13.7	Late Miocene	11.6	7.25	Central	(Londeix et al., 2007)
122	37.6	14.2	36.6	13.8	Late Miocene	11.61	7.246	Central	(de Capoa et al., 2004)
123	37.6	14.2	36.6	13.8	Late Miocene	11.62	7.246	Central	(de Capoa et al., 2004)
124	37.5	14.1	36.9	13.9	Late Miocene	7.25	5.33	Central	(Londeix et al., 2007)
125	37.5	14.1	37.0	13.9	Pliocene	5.33	3.6	Central	(Londeix et al., 2007)
126	38.1	15.4	36.7	14.9	Middle Miocene	15.97	11.62	Central	(de Capoa et al., 2004)
127	38.0	15.5	36.6	15.0	Middle Miocene	15.97	13.82	Central	(de Capoa et al., 2004)
128	38.2	16.3	38.0	16.2	Pliocene	2.8	2.2	Central	(Versteegh and Zonneveld, 1994)
129	38.2	16.3	38.0	16.2	Pliocene	2.8	2.75	Central	(Versteegh, 1997)
130	38.2	16.3	38.0	16.2	Pliocene	2.75	2.7	Central	(Versteegh, 1997)
131	38.2	16.3	38.0	16.2	Pliocene	2.7	2.65	Central	(Versteegh, 1997)
132	38.2	16.3	38.0	16.2	Pliocene	2.65	2.6	Central	(Versteegh, 1997)
133*	41.2	19.3	40.0	18.8	Middle-Late Miocene	13.65	7.246	Eastern	(Gjani et al., 2003)

134	39.4	20.4	37.4	19.5	Early Miocene	23.03	20.44	Eastern	(Janssen, 1991)
135	35.2	24.5	34.7	24.3	Pliocene	5.3	3.6	Eastern	(Ioakim et al., 1992)
136	35.2	26.1	34.3	25.6	Late Miocene	11.61	7.25	Eastern	(Ioakim et al., 1997)
137	35.2	26.1	34.6	25.8	Late Miocene	7.59	7.56	Eastern	(Santarelli et al., 1998)
138*	35.2	26.1	34.6	25.8	Late Miocene	7.55	5.52	Eastern	(Santarelli et al., 1998)
139	35.2	26.1	34.6	25.8	Late Miocene	7.51	7.46	Eastern	(Santarelli et al., 1998)
140	35.2	26.1	34.6	25.8	Late Miocene	7.45	7.39	Eastern	(Santarelli et al., 1998)
141	35.2	26.1	34.7	25.8	Late Miocene	7.38	7.31	Eastern	(Santarelli et al., 1998)
142	35.2	26.1	34.7	25.8	Late Miocene	7.31	7.24	Eastern	(Santarelli et al., 1998)
143	35.2	26.1	34.7	25.8	Late Miocene	7.24	7.2	Eastern	(Santarelli et al., 1998)
144	35.2	26.1	34.6	25.8	Late Miocene	7.246	5.332	Eastern	(Ioakim et al., 1997)
145	35.2	26.1	34.8	25.9	Pliocene	5.332	3.6	Eastern	(Ioakim et al., 1997)
146	35.9	26.6	35.3	26.3	Late Miocene	7.25	5.33	Eastern	(Ioakim et al., 1997)
147	35.9	26.6	35.5	26.4	Pliocene	5.33	3.6	Eastern	(Ioakim et al., 1997)
148	35.1	26.9	34.2	26.4	Late Miocene	11.61	7.25	Eastern	(Edwards, 1984)
149*	31.2	27.2	29.9	26.6	Middle Miocene	15.978	11.608	Eastern	(Mahmoud, 1998)
150	35.1	26.9	34.5	26.6	Late Miocene	7.25	5.33	Eastern	(Edwards, 1984)
151	35.1	26.9	34.7	26.7	Pliocene	5.33	3.6	Eastern	(Edwards, 1984)
152*	31.0	30.1	29.3	29.2	Early Miocene	23.03	20.7	Eastern	(El Beialy, 1988)

153	31.0	30.1	29.5	29.3	Early Miocene	20.7	15.97	Eastern	(El Beialy, 1988)
154*	31.0	30.1	29.9	29.5	Middle Miocene	15.97	11.61	Eastern	(El Beialy, 1988)
155*	31.0	30.1	30.2	29.6	Late Miocene	11.6	5.3	Eastern	(El Beialy, 1988)
156*	31.1	30.4	29.9	29.8	Middle Miocene	15.97	11.608	Eastern	(El Beialy, 1997)
157	31.1	30.4	30.7	30.2	Pliocene	5.332	3.6	Eastern	(El Beialy, 1997)
158*	31.2	30.7	30.3	30.2	Late Miocene	11.6	5.33	Eastern	(Beialy, 1997)
159*	31.1	30.4	30.8	30.3	Pliocene-Pleistocene	3.6	1.806	Eastern	(El Beialy, 1997)
160	30.6	31.0	29.7	30.5	Middle Miocene	12.2	11.7	Eastern	(El Beialy, 1992)
161*	30.6	31.0	29.8	30.5	Late Miocene	11.608	5.332	Eastern	(El Beialy, 1992)
162	30.6	31.0	30.2	30.7	Pliocene	5.332	3.6	Eastern	(El Beialy, 1992)
163*	31.0	32.1	29.4	31.2	Early Miocene	23.03	15.97	Eastern	(El Beialy, 1990)
164*	31.0	32.1	29.9	31.5	Middle Miocene	15.97	11.608	Eastern	(El Beialy, 1990)
165	29.2	32.4	27.8	31.6	Early Miocene	20.44	15.97	Eastern	(El Beialy and Ali, 2002)
166*	31.0	32.1	30.2	31.7	Late Miocene	11.608	5.332	Eastern	(El Beialy, 1990)

167	28.5	32.5	27.1	31.8	Early Miocene	20.44	15.97	Eastern	(Soliman and Ibrahim, 2012)
168*	31.0	32.2	30.2	31.8	Late Miocene	11.6	5.3	Eastern	(El Beialy, 1990)
169*	29.2	32.4	28.1	31.8	Middle Miocene	15.97	11.62	Eastern	(El Beialy and Ali, 2002)
170*	28.5	32.5	27.4	31.9	Middle Miocene	15.97	12.7	Eastern	(Soliman and Ibrahim, 2012)
171	31.0	32.1	30.6	31.9	Pliocene	5.332	3.6	Eastern	(El Beialy, 1990)
172	28.5	32.5	27.6	32.0	Middle Miocene	12.7	11.62	Eastern	(Soliman and Ibrahim, 2012)
173*	28.1	33.0	27.0	32.5	Middle Miocene	15.97	11.61	Eastern	(Mahmoud, 1993)
174	27.5	33.2	26.0	32.5	Early Miocene	20.44	15.97	Eastern	(Soliman and Ibrahim, 2012)
175	28.3	33.4	26.8	32.7	Early Miocene	20.44	15.97	Eastern	(Soliman and Ibrahim, 2012)
176*	36.4	35.6	36.6	34.9	Late Miocene	11.62	5.333	Eastern	(Ediger et al., 1996)
177	36.4	35.6	36.5	35.1	Late Miocene	7.2	5.333	Eastern	(Ediger et al., 1996)

ID numbers followed by an asterisk are the additional assemblages used in the two stage method.

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Appendix D: The species used in Chapter 4 (and their original publications)

Taxa	Original Publication
Achomosphaera alcicornu	(Eisenack, 1954) Davey and Williams, 1966
Achomosphaera andalousiensis	Jan du Chêne, 1977. Emendation: Jan du Chêne and Londeix, 1988
Achomosphaera argesensis	Demetresçu, 1989
Achomosphaera callosa	Matsuoka, 1983
Achomosphaera crassipellis	(Deflandre and Cookson, 1955) Stover and Evitt, 1978
Achomosphaera ramosasimilis	(Yun Hyesu, 1981) Londeix et al., 1999
Achomosphaera ramulifera	(Deflandre, 1937) Evitt, 1963
Amiculosphaera umbraculum	Harland, 1979
Apteodinium australiense	(Deflandre and Cookson, 1955) Williams, 1978
Apteodinium emslandense	(Gerlach, 1961) Stover and Evitt, 1978
Apteodinium spiridoides	Benedek, 1972. Emendation: Benedek and Sarjeant, 1981
Apteodinium tectatum	Piasecki, 1980
Ataxiodinium choane	Reid, 1974
Ataxiodinium confusum	Versteegh and Zevenboom in Versteegh, 1995
Barssidinium olymposum	Warny and Wrenn, 1997
Barssidinium pliocenicum	(Head, 1993) Head, 1994
Batiacasphaera baculata	Drugg, 1970
Batiacasphaera biornata	(Jiabo, 1978) Jan du Chêne et al., 1985
Batiacasphaera compta	Drugg, 1970
Batiacasphaera gemmate	Head et al., 1989
Batiacasphaera hirsute	Stover, 1977
Batiacasphaera micropapillata complex	Stover, 1977
Batiacasphaera sphaerica	Stover, 1977
Bitectatodinium tepikiense	Wilson, 1973
Bitectatodinium? Serratum	(Head et al., 1989) Lentin and Williams, 1993
Brigantedinium cariacoense	(Wall, 1967) Lentin and Williams, 1993
Caligodinium amiculum	Drugg, 1970
Caligodinium pychnum	Biffi and Manum, 1988
Capillicysta fusca	Matsuoka and Bujak in Matsuoka et al., 1987
Cerebrocysta mediterranea	Biffi and Manum, 1988
Cerebrocysta poulsenii	de Verteuil and Norris, 1996
Cerebrocysta? namocensis	Head et al., 1989
Chiropteridium galea	(Maier, 1959) Sarjeant, 1983
Chytroeisphaeridia tuberosa	Sütő-Szentai, 1982
Cleistosphaeridium ancyreum	(Cookson and Eisenack, 1965a) Eaton et al., 2001
Cleistosphaeridium placacantha	(Deflandre and Cookson, 1955) Eaton et al., 2001
Cordosphaeridium cantharellus	(Brosius, 1963) Gocht, 1969
Cordosphaeridium minimum	(Morgenroth, 1966) Benedek, 1972

Corrudinium harlandii	Matsuoka, 1983
Corrudinium? labradori	Head et al., 1989
Cousteaudinium aubryae	de Verteuil and Norris, 1996
Cribroperidinium giuseppei	(Morgenroth, 1966) Helenes, 1984
Cribroperidinium tenuitabulatum	(Gerlach, 1961) Helenes, 1984
Cribroperidinium? granomembranaceum	(Matsuoka, 1983) Lentin and Williams, 1985
Dapsilidinium pseudocolligerum	(Stover, 1977) Bujak et al., 1980
Deflandrea hialina	Balteş, 1969 ex Lentin and Williams, 1973
Deflandrea phosphoritica	Eisenack, 1938
Distatodinium apenninicum	Brinkhuis et al., 1992
Distatodinium craterum	Eaton, 1976
Distatodinium fusiforme	(Matsuoka, 1974) Bujak and Matsuoka, 1986
Distatodinium paradoxum	(Brosius, 1963) Eaton, 1976
Echinidinium euaxum	(Head, 1993) Head et al., 2001
Ectosphaeropsis burdigalensis	Londeix and Jan du Chêne, 1988
Edwardsiella sexispinosum	Versteegh and Zevenboom in Versteegh, 1995
Exochosphaeridinium insigne	de Verteuil and Norris, 1996
Fibrocysta? fusiforma	Edwards, 1984
Filisphaera microornata	(Head et al., 1989) Head, 1994
Florentinia stellatum	(Maier, 1959) Below, 1982
Galeacysta etrusca	Corradini and Biffi, 1988
Glaphyrocysta reticulosum	(Gerlach, 1961) Stover and Evitt, 1978
Habibacysta tectata	Head et al., 1989
Heteraulacacysta campanula	Drugg and Loeblich Jr., 1967
Homotryblium aculeatum	Williams, 1978
Homotryblium floripes	(Deflandre and Cookson, 1955) Stover, 1975
Homotryblium oceanicum	Eaton, 1976
Homotryblium plectilum	Drugg and Loeblich Jr., 1967
Homotryblium tasmaniense	Cookson and Eisenack, 1967
Homotryblium tenuispinosum	Davey and Williams, 1966
Homotryblium vallum	Stover, 1977
Hystrichokolpoma cinctum	Klumpp, 1953
Hystrichokolpoma denticulatum	Matsuoka, 1974
Hystrichokolpoma ellipticum	Matsuoka, 1974
Hystrichokolpoma okinawaium	Matsuoka, 1979
Hystrichokolpoma pacificum	Matsuoka, 1979
Hystrichokolpoma poculum	Maier, 1959
Hystrichokolpoma rigaudiae	Deflandre and Cookson, 1955
Hystrichokolpoma salacium	Eaton, 1976
Hystrichokolpoma truncatum	Biffi and Manum, 1988
Hystrichosphaeropsis obscura	Habib, 1972
Hystrichosphaeropsis pontiana	(Balteş, 1969) Stover and Evitt, 1978
Hystrichostrogylon membraniforum	Agelopoulos, 1964
Impagidinium aculeatum	(Wall, 1967) Lentin and Williams, 1981

Impagidinium aliferum	Mudie, 1987
Impagidinium bacatum	Londeix et al., 1992
Impagidinium cornutum	Matsuoka and Bujak, 1988
Impagidinium dispertitum	(Cookson and Eisenack, 1965) Stover and Evitt, 1978
Impagidinium eugubinum	Biffi and Manum, 1988
Impagidinium fenestroseptatum	Head et al., 1989
Impagidinium pallidum	Bujak, 1984
Impagidinium paradoxum	(Wall, 1967) Stover and Evitt, 1978
Impagidinium patulum	(Wall, 1967) Stover and Evitt, 1978
Impagidinium plicatum	Versteegh and Zevenboom in Versteegh, 1995
Impagidinium sphaericum	(Wall, 1967) Lentin and Williams, 1981
Impagidinium spongianum	Sütő-Szentai, 1985
Impagidinium strialatum	(Wall, 1967) Stover and Evitt, 1978
Impagidinium tectum	Biffi and Manum, 1988
Impagidinium velorum	Bujak, 1984
Impagidinium? obesum	(Sütő-Szentai, 1982) Lentin and Williams, 1989
Impagidinium? pecsvaradense	(Sütő-Szentai, 1982) Lentin and Williams, 1989
Invertocysta lacrymosa	Edwards, 1984
Invertocysta tabulata	Edwards, 1984
Islandinium? cezare	de Vernal et al., 1989 ex de Vernal in Rochon et al., 1999
Komewuia inequicornutum	(Balteş, 1971. ex Stover and Evitt, 1978) Chen, 1982
Labyrinthodinium truncatum	Piasecki, 1980
Leipokatium invisitatum	Bradford, 1975
Lejeunecysta beninensis	Biffi and Grignani, 1983
Lejeunecysta catomus	(Harland in Harland et al., 1991) Lentin and Williams, 1993
Lejeunecysta cinctoria	(Bujak in Bujak et al., 1980) Lentin and Williams, 1981
Lejeunecysta communis	Biffi and Grignani, 1983
Lejeunecysta convexa	Matsuoka and Bujak, 1988
Lejeunecysta diversiforma	(Bradford, 1977) Artzner and Dörhöfer, 1978
Lejeunecysta fallax	(Morgenroth, 1966) Artzner and Dörhöfer, 1978
Lejeunecysta globosa	Biffi and Grignani, 1983
Lejeunecysta hyalina	(Gerlach, 1961) Artzner and Dörhöfer, 1978
Lejeunecysta lata	Biffi and Grignani, 1983
Lejeunecysta marieae	(Harland in Harland et al., 1991) Lentin and Williams, 1993
Lejeunecysta oliva	(Reid, 1977) Turon and Londeix, 1988
Lejeunecysta sabrina	(Reid, 1977) Bujak, 1984
Lejeunecysta tenella	(Morgenroth, 1966) Wilson and Clowes, 1980
Leptodinium italicum	Biffi and Manum, 1988
Leptodinium? bacculatum	Balteş, 1971
Lingulodinium machaerophorum	(Deflandre and Cookson, 1955) Wall, 1967
Melitasphaeridium angustum	Matsuoka, 1983
Melitasphaeridium choanophorum	(Deflandre and Cookson, 1955) Harland and Hill, 1979

Melitasphaeridium pseudorecurvatum	(Morgenroth, 1966) Bujak et al., 1980
Membranilarnacia? picena	Biffi and Manum, 1988
Membranophoridium aspinatum	Gerlach, 1961
Nematosphaeropsis balcombiana	Deflandre and Cookson, 1955
Nematosphaeropsis downiei	Brown, 1986
Nematosphaeropsis labyrinthus	(Ostenfeld, 1903) Reid, 1974
Nematosphaeropsis lativittata	Wrenn, 1988
Operculodinium centrocarpum	(Deflandre and Cookson, 1955) Wall, 1967
Operculodinium crassum	Harland, 1979
Operculodinium israelianum	(Rossignol, 1962) Wall, 1967
Operculodinium janduchenei	Head et al., 1989
Operculodinium longispinigerum	Matsuoka, 1983
Operculodinium piaseckii	Strauss and Lund, 1992
Operculodinium? borgerholtense	Louwye, 2001
Operculodinium? eirikianum	Head et al., 1989
Operculodinium? placitum	Drugg and Loeblich Jr., 1967
Palaeocystodinium golzowense	Alberti, 1961
Palaeocystodinium minor	Strauss in Strauss et al., 2001
Palaeocystodinium miocaenicum	Strauss in Strauss et al., 2001
Palaeocystodinium powellense	Strauss et al., 2001
Palaeocystodinium stritogranulasum	Zevenboom and Santarelli in Zevenboom, 1995
Pentadinium goniferum	Edwards, 1982
Pentadinium laticinctum	Gerlach, 1961
Pentadinium spinulum	Strauss and Lund, 1992
Pentadinium taeniagerum	Gerlach, 1961
Polysphaeridium subtile	Davey and Williams, 1966
Polysphaeridium zoharyi	(Rossignol, 1962) Bujak et al., 1980
Pyxidiella? scrobiculata	(Deflandre and Cookson, 1955) Cookson and Eisenack, 1958
Pyxidiella? simplex	Harland, 1979
Pyxidinopsis elliptica	Biffi and Manum, 1988
Pyxidinopsis pastilliformis	Head in Matsuoka and Head, 1992
Pyxidinopsis psilatum	(Wall and Dale in Wall et al., 1973) Head, 1994
Pyxidinopsis tuberculata	Versteegh and Zevenboom in Versteegh, 1995
Quinquecuspis concreta	(Reid, 1977) Harland, 1977
Reticulatosphaera actinocoronata	(Benedek, 1972) Bujak and Matsuoka, 1986
Romanodinium areolatum	Balteş, 1971
Selenopemphix? indentata	Head et al., 1989
Selenopemphix armageddonensis	de Verteuil and Norris, 1992
Selenopemphix armata	Bujak in Bujak et al., 1980
Selenopemphix brevispinosa	Head et al., 1989
Selenopemphix coronata	Bujak in Bujak et al., 1980
Selenopemphix crenata	Matsuoka and Bujak, 1988
Selenopemphix dionaeacysta	Head et al., 1989

Selenopemphix nephroides	Benedek, 1972
Selenopemphix quanta	(Bradford, 1975) Matsuoka, 1985
Selenopemphix selenoides	Benedek, 1972
Selenopemphix warriensis	Biffi and Grignani, 1983
Spiniferella cornutus	(Gerlach, 1961) Stover and Hardenbol, 1994
Spiniferites balcanicus	(Balteş, 1971) Sütő-Szentai, 2000
Spiniferites bentorii	(Rossignol, 1964) Wall and Dale, 1970
Spiniferites bulloideus	(Deflandre and Cookson, 1955) Sarjeant, 1970
Spiniferites cruciformis	Wall and Dale in Wall et al., 1973
Spiniferites delicatus	Reid, 1974
Spiniferites ellipseideus	Matsuoka, 1983
Spiniferites elongatus	Reid, 1974
Spiniferites firmus	Matsuoka, 1983
Spiniferites galeaformis	Sütő, 1994
Spiniferites hyperacanthus	(Deflandre and Cookson, 1955) Cookson and Eisenack, 1974
Spiniferites lazus	Reid, 1974
Spiniferites maisensis	Sütő, 1994
Spiniferites membranaceus	(Rossignol, 1964) Sarjeant, 1970
Spiniferites mirabilis	(Rossignol, 1964) Sarjeant, 1970
Spiniferites nodosus	(Wall, 1967) Sarjeant, 1970
Spiniferites ovatus	Matsuoka, 1983
Spiniferites pachydermus	(Rossignol, 1964) Reid, 1974
Spiniferites paradoxus	(Cookson and Eisenack, 1968) Sarjeant, 1970
Spiniferites pseudofurcatus	(Klumpp, 1953) Sarjeant, 1970
Spiniferites ramosus	(Ehrenberg, 1838) Mantell, 1854
Spiniferites rubinus	Rossignol, 1962, ex Rossignol, 1964
Spiniferites tengelicensis	Sütő-Szentai, 1982
Spiniferites twistringiensis	(Maier, 1959) Fensome et al., 1990
Spiniferites virgulaeformis	Sütő, 1994
Stoveracysta conerae	Biffi and Manum, 1988
Sumatradinium druggii	Lentin et al., 1994
Sumatradinium hispidum	(Drugg, 1970a) Lentin and Williams, 1976
Sumatradinium pustulosum	Lentin et al., 1994
Sumatradinium soucouyantiae	de Verteuil and Norris, 1992
Systematophora urbinii	Biffi and Manum, 1988
Tectatodinium pellitum	Wall, 1967
Thalassiphora delicate	Williams and Downie, 1966
Thalassiphora pelagica	(Eisenack, 1954) Eisenack and Gocht, 1960
Trinovantedinium applanatum?	(Bradford, 1977) Bujak and Davies, 1983
Trinovantedinium glorianum	(Head et al., 1989) de Verteuil and Norris, 1992
Trinovantedinium harpagonium	de Verteuil and Norris, 1992
Trinovantedinium variabile	(Bujak, 1984) de Verteuil and Norris, 1992
Trinovantedinium xylochoporum	de Verteuil and Norris, 1992
Tuberculodinium vancampoae	(Rossignol, 1962) Wall, 1967
Unipontidinium aquaeductum?	(Piasecki, 1980) Wrenn, 1988

Appendix E: Comparing datasets of different temporal resolution

E.1 The one stage method

Appendix E presents the results of an alternative method to the two stage method discussion in Chapter 3. Here the one stage method is applied to the data meaning that only assemblages that have dating constrained to one stage are included in the analysis. This resulted 41 fewer assemblages being utilised compared to the two stage method. A smaller dataset that has a higher resolution of dating was investigate in order to investigate whether the temporal resolution of the dataset alters the results. The one stage method results are very similar to the results from the two stage method and because of this the main differences will be highlighted.

E.1.1 Diversity

Changes to the diversity are very similar in both methods. The main difference is that in the one stage method there are several times where a diversity of zero is related to a lack of publications, for example in the Eastern and Western Mediterranean basins (Figure E.1c and e). Another difference is, when all of the data are combined (Figure E.1a), the diversity in the Messinian drops more rapidly in the one stage method then in the two stage method, which decreases in a step like manner. The number and percentage of species that appeared/disappeared in the Mediterranean during the Neogene is also similar for both methods (Figure E.2).

The R^2 and P values, when comparing the number of publications, sites, assemblages and species in each time bin, are similar for the individual basins. However, when all of the basins are combined (Table E.1). The R^2 values are significantly lower in the one stage method than in the two stage method (Table E.1) and the P values are significantly higher. This suggests that the data used in the one stage method are potentially less biased (i.e. the number of publications is less likely to be controlled by the number of species).

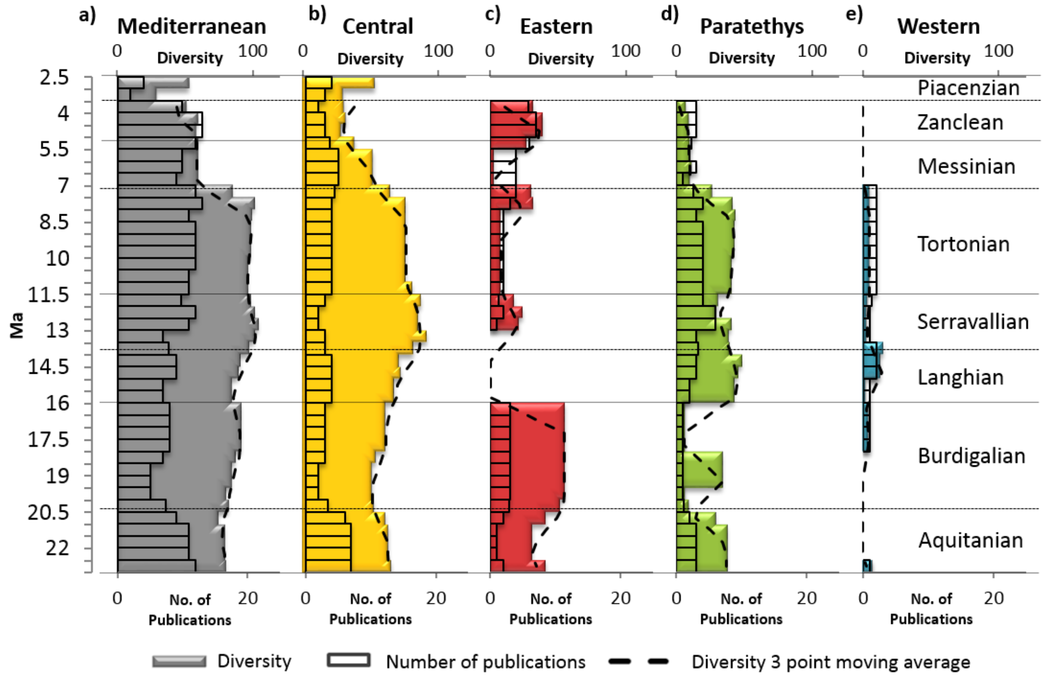

Figure E-1: The number of species present in each 0.5 Myr time bin for (a) the whole Mediterranean, (b) the Central Mediterranean Basin, (c) the Eastern Mediterranean Basin, (d) the Paratethys Basin and (e) the Western Mediterranean Basin. The three point running mean for diversity is represented by dashed lines. The number of publications for each 0.5 Myr time bin is indicated by black outlined boxes.

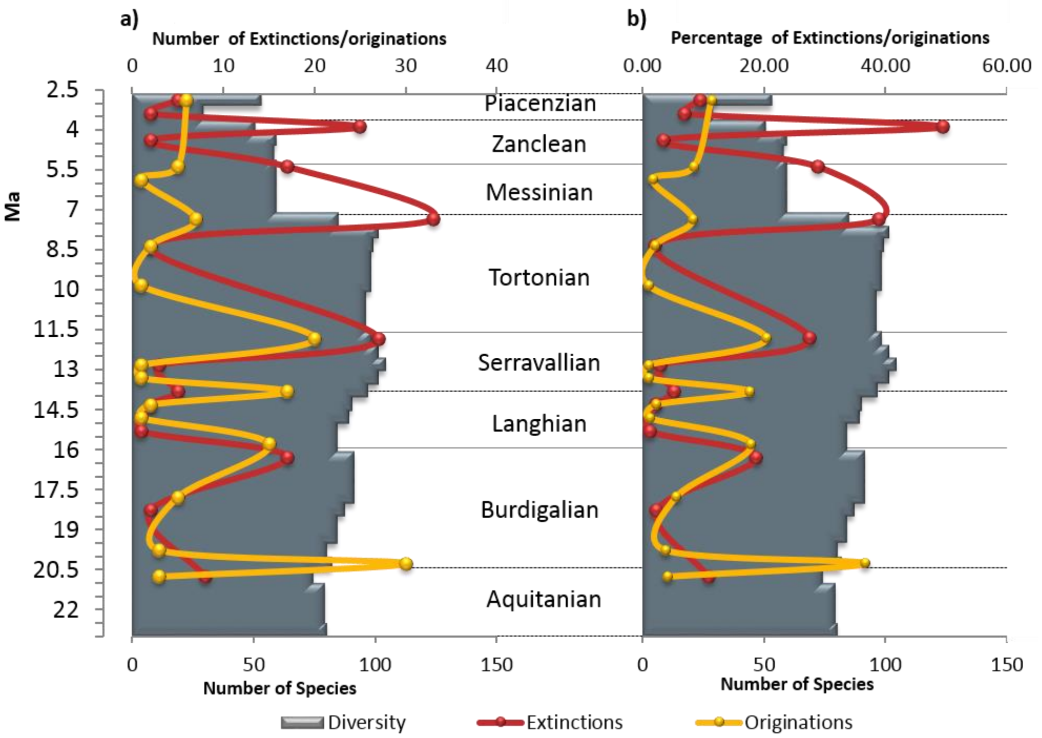

Figure E-2: The diversity (grey background) and (a) the number and (b) the percentage of species that disappeared or appeared in each 0.5 Myr time bin.

One stage		All Mediterranean	Central	Eastern	Paratethys	Western
Publications	**R^2**	0.074	0.007	0.219	0.351	0.661
	P value	0.086	0.597	0.002	4.48E-05	1.04E-10
	Number	51	16	14	18	4
Sites	**R^2**	0.046	0.037	0.489	0.212	0.661
	P value	0.18	0.227	3.71E-07	2.44E-03	1.04E-10
	Number	78	31	16	25	7
Assemblages	**R^2**	0.067	0.019	0.367	0.284	0.650
	P value	0.101	0.39	2.67E-05	3.31E-04	2.04E-10
	Number	137	60	27	39	10

Table E-1: Potential biases of diversity change for the whole of the Mediterranean, the Central Mediterranean Basin, the Eastern Mediterranean Basin, the Paratethys Basin and the Western Mediterranean Basin. The P and R^2 value are from the number of species present (diversity) versus the number of publications for each 0.5 million year time bin. The higher the R^2 value, and the lower the P value, the higher the correlation between the two, and the more likely that the diversity is controlled by the number of publications. For example, the Central Mediterranean Basin has a low R^2 value and a high P value. This suggests that the number of publications and the number of species are unlikely to be causally related to each other. Both the R^2 and P values relate to the smoothed data (Figure 4.5).

Residual models using the one stage method also produce similar results to the two stages method. The main difference is when all of the basins are combined where the majority of the points plot outside of the confidence intervals, suggesting that the diversity is not likely to be controlled by the number of assemblage (Figure E.3a). A further difference is that the diversity of the Eastern Basin appears to be potentially controlled by the number of assemblages between 16 and 13 Ma, however, this is where no data is provided (Figure E.3c).

E.1.2 Quantifying assemblage change through the Neogene

There are practically no differences between the one and two stage methods when analysing the assemblage composition for each sub-epoch, suggesting that using a higher resolution of data does not make a difference (Figure E.4). This is also the case when comparing the assemblages of individual consecutive sub-epochs (Figure E.5). Although the stress values are slightly higher in the two stage methods meaning that the one stage method MDS plots represent the spread of the data in two dimensions more accurately than in the two stage method. The R values in the one stage method are slightly lower than for the two stage method. This indicates that the assemblages change more between the late Miocene and Pliocene in the two stage method than in the one stage method (Figure E.5c). The reason for this must be related to the additional data (of a lower temporal resolution) included in the two stage method creating different assemblage either side of the Messinian-Zanclean boundary.

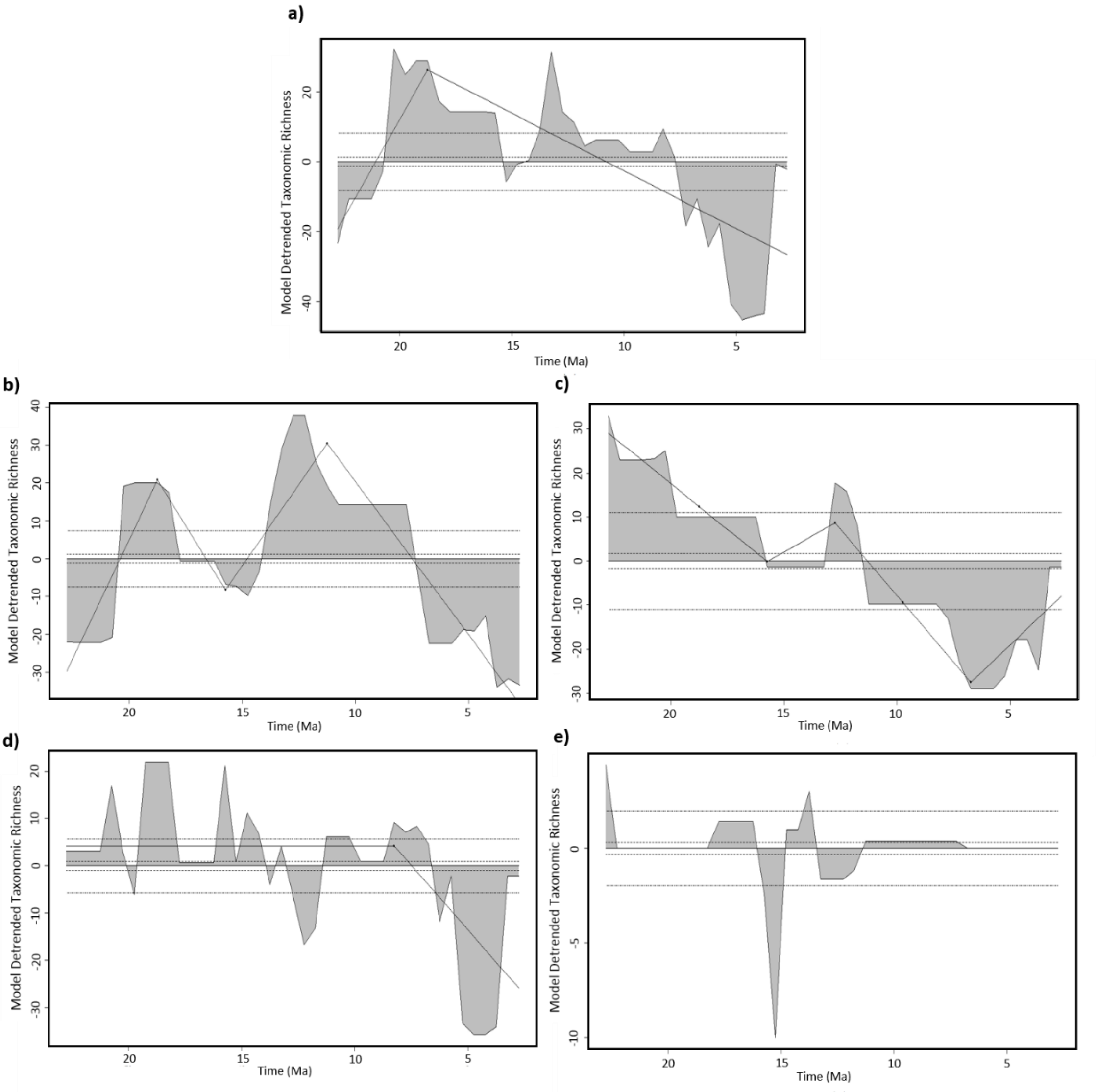

Figure E-3: Residual models for (a) the whole Mediterranean, (b) the Central Mediterranean Basin, (c) the Eastern Mediterranean Basin, (d) the Paratethys Basin and (e) the Western Mediterranean Basin. Grey polygons represent the model-detrended diversity (sampling proxy is the number of assemblages). The horizontal lines represent the confidence interval. The dashed lines is the 95% standard error and the dashed-dot horizontal lines (outside) represent the 95% standard deviation of the model. The solid lines that move with the polygons represents the medium term diversity trends.

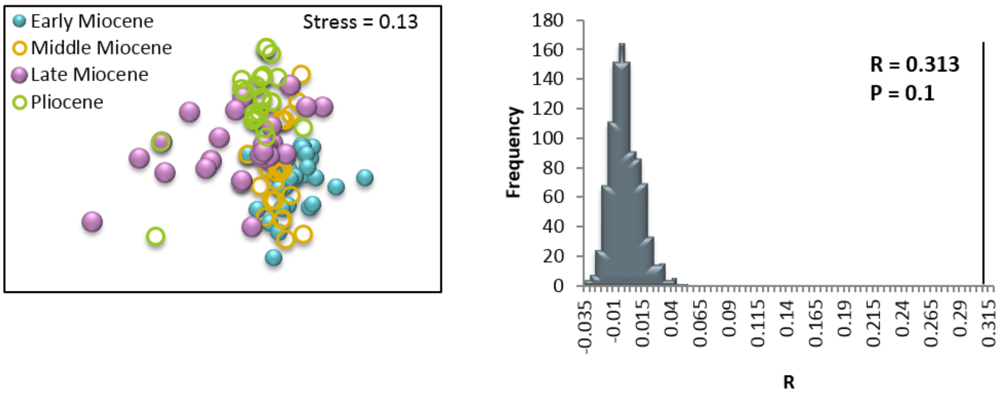

Figure E-4: MDS (left) and ANOSIM (right) analyses of data distinguished by sub-epochs (early Miocene, middle Miocene, late Miocene and Pliocene).

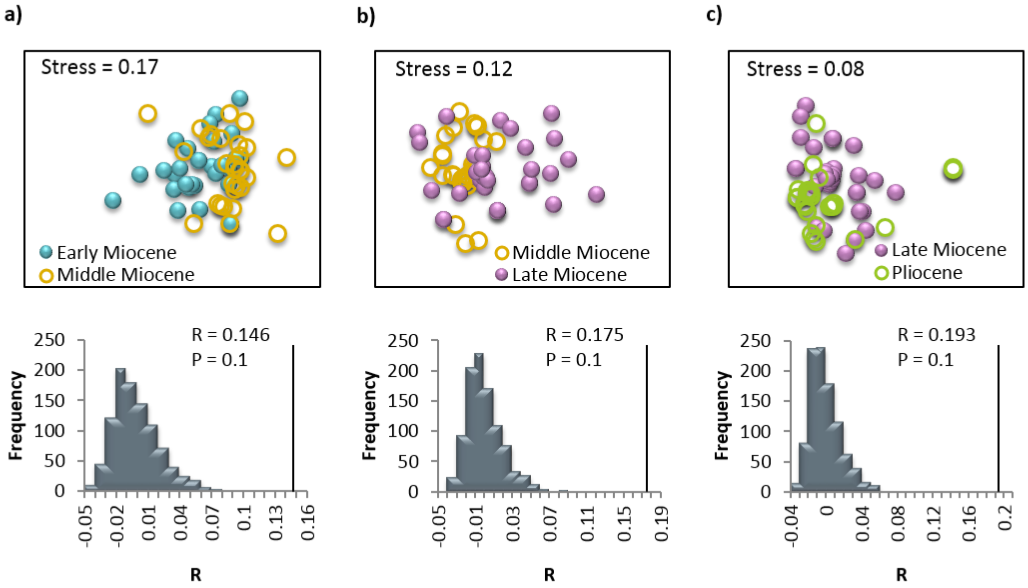

Figure E-5: MDS and ANOSIM analyses using the two stage method, with two sub-epochs shown in each panel to indicate where the largest changes in assemblage took place. (a) Early to middle Miocene, (b) middle to late Miocene and (c) late Miocene to Pliocene.

E.1.3 Changes in assemblages over the Mediterranean and Paratethys basins

As for when using age as the factor, when using location to determine how the assemblages differ in the Mediterranean/Paratethys for the entire Neogene (Figure E.6) the MDS and ANOSIM produce very similar results to those for the two stage method. However when the data from the different sub-epochs are separated out (Figure E.7) the stress values are all slightly lower in the one stage method, meaning that the MDS plots (for the one stage method) represent the spread of the data in two dimensions more accurately than in the two stage method. The R values in the one stage method (particularly for the early Miocene

(Figure E.7a) are slightly different too. In the early Miocene the one stage method has an R value of 0.12 compared to 0.222 in the two stage method. The different values in the one stage method result in the analysis indicating that the dinoflagellate cyst assemblages in the one stage method become more taxonomically isolated through the Neogene than in the two stage method.

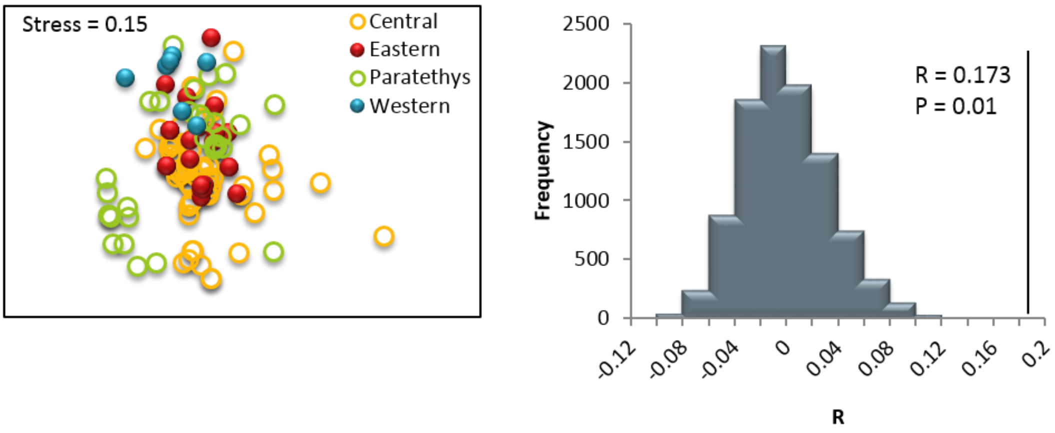

Figure E-6: MDS (left) and ANOSIM (right) analyses for the entire Neogene, with basins (Central, Eastern and Western Mediterranean basins and the Paratethys Basin) as the factor.

E.2 One and two stage methods

Two different datasets were used in this study. The first included assemblages that were dated to within one stage (the one stage method). The second encompassed these assemblages as well as assemblages dated to within two stages, to avoid any potential boundary biases (the two stage method). The one stage method can be considered to contain a better quality of data, as the dating is of a higher resolution. However, it disregards high resolution data that happen to span a stage boundary, which means assemblages either side of a stage boundary may appear less similar than they actually were. The two stage method has a greater quantity of data, helping to guard against statistics of small number biases, but the dating of the additional data is less accurate. This results in a resolution versus range debate, which has been explored by using both methods.

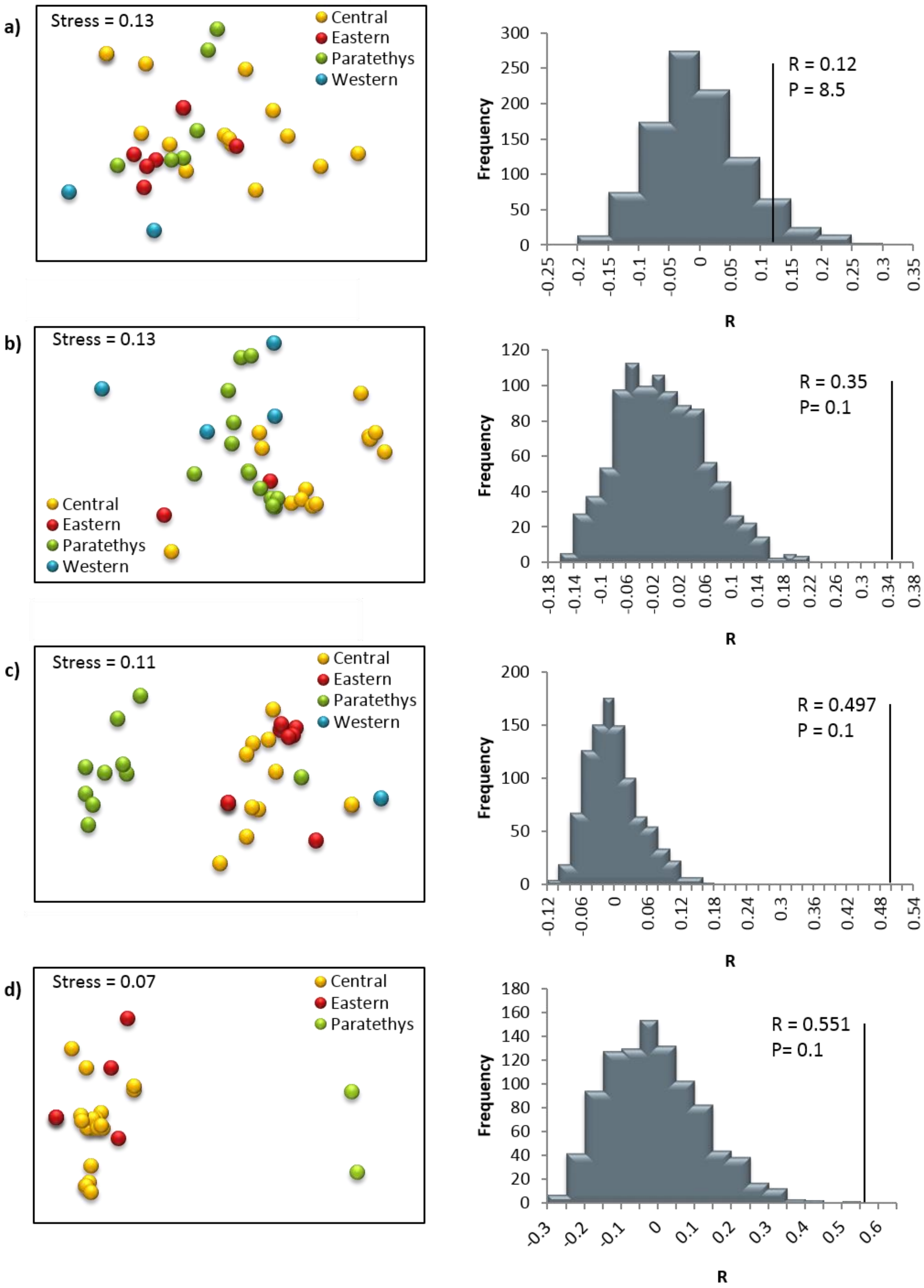

Figure E-7: MDS and ANOSIM analyses for individual sub-epochs with location as the factor (Central, Eastern and Western Mediterranean basins and the Paratethys Basin). (a) Early Miocene, (b) middle Miocene, (c) late Miocene, (d) Pliocene.

		One stage method			Two stage method		
		R	P	Stress	R	P	Stress
Age	Entire Neogene	0.313	0.1	0.13	0.299	0.1	0.13
	Early to middle Miocene	0.146	0.1	0.17	0.143	0.1	0.17
	Middle to late Miocene	0.175	0.1	0.12	0.147	0.1	0.13
	Late Miocene to Pliocene	0.193	0.1	0.08	0.271	0.1	0.11
Location	Entire Neogene	0.173	0.01	0.15	0.164	0.01	0.15
	Early Miocene	0.12	8.5	0.13	0.222	0.4	0.14
	Middle Miocene	0.35	0.1	0.13	0.207	0.1	0.15
	Late Miocene	0.497	0.1	0.11	0.449	0.1	0.15
	Pliocene	0.551	0.1	0.07	0.517	0.1	0.09

Table E-2: Comparison of the statistical values from the one and two stage methods.

Despite these differences in dating, the results for both methods yield similar results, which suggests that the methods are equally reliable. For example, the R^2 values and P values from the correlation between number of species and number of publications (Table 4.1 and E.1) are not consistently higher or lower in one method compared to the other. When the diversity is separated into the Central and Eastern Mediterranean basins and the Paratethys Basin, the R^2 values for both methods are very similar and both methods show a comparable diversity trend.

The MDS and ANOSIM analysis also display very similar trends, and the largest difference in the global R value, between the two methods, was 0.164 (Table E.2), and the largest different in the stress value was just 0.04 (Table E.2). In general the one stage method has higher global R values than the two stage method indicating that the factors used to determine which assemblage were most closely related, (age or location) have a more significant impact on which species make up the assemblages. The one stage methods also generally has lower stress values, implying that the one stage method more faithfully represents the multidimensional relationship of the assemblages. However, one benefit of the two stage method over the one stage method is that there are fewer data gaps where there is no literature, for example in the one stage method there are no data for the Eastern Mediterranean Basin during the Langhian.

In the case of this study (Chapter 4 and Appendix E) there is little difference between the two methods and both have positives and negatives. However, the best way to move forward in order to answer additional research questions, such as constraining the closure of the Eastern Mediterranean Gateway would be to expand TOPIS with additional high resolution data.

Appendix F: The species identified in Chapter 5 (and their original publications)

Taxa name	**Original Publication**
Achomosphaera sp.	Evitt, 1963
Acritarch *Nannobarbaphora* sp.	Habib and Knapp, 1982. Emendation: Head, 2003b
Dinocyst sp. A	
Dinocyst sp. B	
Dinocyst sp. C	
Hystrichokolpoma cinctum	Klumpp, 1953
Hystrichokolpoma pusilla	Biffi and Manum, 1988
Hystrichokolpoma rigaudiae	Deflandre and Cookson, 1955
Hystrichokolpoma sp.	Klumpp, 1953. Emendations: Williams and Downie, 1966a
Hystrichokolpoma sp?	
Impagidinium paradoxum	(Wall, 1967) Stover and Evitt, 1978,
Impagidinium patulum	(Wall, 1967) Stover and Evitt, 1978
Indeterminate dinoflagellate cysts	
Invertocysta lacrymosa	Edwards, 1984
Lingulodinium machaerophorum	(Deflandre and Cookson, 1955) Wall, 1967
Lingulodinium machaerophorum?	
Nematosphaeropsis labyrinthus/lemniscata	(Ostenfeld, 1903) Reid, 1974 and Wrenn, 1988
Operculodinium spp.	Wall, 1967. Emendation: Matsuoka et al., 1997
Operculodinium? sp.	
Selenopemphix quanta	(Bradford, 1975) Matsuoka, 1985a
Spiniferites membranaceus	(Rossignol, 1964) Sarjeant, 1970
Spiniferites mirabilis	(Rossignol, 1964) Sarjeant, 1970
Spiniferites Sp. A of Louwye and De Schepper (2010)	After Louwye and De Schepper, 2010
Spiniferites/Achomosphaera spp.	
Spiniferites/Achomosphaera? spp.	
Tectatodinium pellitum	Wall, 1967. Emendation: Head, 1994a
Tuberculodinium vancampoae	(Rossignol, 1962) Wall, 1967