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Climate and vegetation during the Miocene – evidence from Danish palynological assemblages

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Nullum magnum ingenium sine mixtura dementiae fuit

Salvo Errore et Omissione

Abstract

Several Danish exposures and one drill core spanning the upper Oligocene-upper Miocene interval of the Cenozoic (i.e., 24–5 Myr ago) were palynologically investigated. The sediments were deposited in alternating deltaic, marginal marine and fully marine settings, and reveal a rich and diverse miospore flora, associated with abundant dinoflagellate cysts. The results consistently demonstrate that coastal areas in what is now Denmark were inhabited by *Taxodium* swamp forests that also hosted a range of terrestrial angiosperms, such as *Nyssa*, *Betula, Alnus* and Myricaceae. Further inland, mixed deciduous-evergreen forests prevailed and in drained soils, or in elevated areas, conifer-forests dominated by *Pinus*, *Sequoia* and *Sciadopitys* thrived. By employing the Coexistence Approach, the mean annual temperatures were calculated to 15.5–21.1° C for the late Oligocene-late Miocene. The warmest periods occurred during the earliest Miocene and the middle Miocene, respectively. The latter period represents a prolonged climatic warming event approximately 17–14 Myr ago. This warming is globally recognized and referred to as the middle Miocene Climate Optimum. Following this event, a marked climatic cooling occurred at about 11 Ma, which coincides with the beginning of the globally identified late Miocene Cooling phase.

Svensk sammanfattning

Miocen – tidsperioden då Danmark täcktes av sumpcypress-skogar

Denna studie avhandlar vegetationsutveckling, klimat och miljöförändringar under tidsperioden miocen som inleddes för 23 miljoner år sedan och avslutades för 6 miljoner år sedan, och är baserad på pollenanalys (palynologi) av sediment från Jylland, Danmark. Paleo-palynologi baseras på palynomorfer, dvs. de mikroskopiskt små fossil (främst sporer, pollen och mikroalger) som är motståndskraftiga mot saltsyra, fluorvätesyra och liknande ämnen. En av många fördelar med att studera palynomorfer är att provmängden som krävs för den vetenskapliga studien oftast är liten (vissa bergarter kan innehålla miljontals mikrofossil per kilo sediment). Med hjälp av palynomorfer kan man knyta samman lagerföljder som avsatts i havet med sediment som deponerats på land. Detta förfarande är möjligt då pollen och sporer, som är de reproduktiva delarna av växter, ibland avsätts ute till havs och således förekommer tillsammans med marina mikroalger, s.k. dinoflagellater. På motsvarande sätt kan sediment som avsatts i kustnära miljöer, och som huvudsakligen innehåller palynomorfer från landlevande växter, innehålla små mängder marina mikroalger som avsatts vid tillfälliga havsytehöjningar.

Under de 17 miljoner år som miocen omfattar ägde ett antal viktiga klimatförändringar rum. Det som idag är Nordsjön var då en havsvik vars utbredning varierade p.g.a. havsyteförändringar, medan dagens Danmark låg i ett område med vidsträckta, kustnära deltaområden. Det ledde till avsättning av både sandiga och leriga sediment i marina såväl som brackvattensmiljöer. I sedimenten finns stora mängder pollen och sporer som bevarats sedan miocen. Genom att identifiera vilka växter som producerat pollen och sporer går det att få en uppfattning om växtlighetens beskaffenhet i Danmark under miocen. Då alla växter är anpassade till visst klimat och en viss miljö kan man använda palynomorfer som miljö- och klimatindikatorer.

Under miocen var klimatet i Danmark varmtempererat med årsmedeltemperaturer som varierade mellan 15.5 och 21.1° C. Detta kan jämföras med dagens årsmedeltemperatur om 7.7° C baserat på uppgifter från åren 1961 till 1990. Resultaten från denna undersökning tyder på att miocen omfattar två riktigt varma perioder. En i början av epoken och en under mellersta miocen. Den senare är globalt igenkännbar och var den senaste riktigt varma perioden i jordens historia. Under senare delen av miocen blev klimatet gradvis kallare och mer säsongsbetonat, vilket fortsatt under kvartärperioden, dvs. den tidsperiod som vi lever i idag.

Pollendata från Danmarks miocen har visat att vidsträckta träskskogar som i mångt och mycket påminner om de sumpområden som återfinns i sydöstra USA idag, en gång bredde ut sig längs de dåvarande kusterna. De vanligaste växterna i dessa skogar var träskcypresser och andra fukttoleranta arter. I något mer dränerade marker, längre inåt land, frodades bl.a. ek, bok och alm, som finns i området än idag. Dock förekom även mer exotiska inslag, såsom *Engelhardtia* (en släkting till valnötsträdet), som idag endast återfinns i sydvästra Kina. I höglänta områden växte barrträd, bl.a. Redwoodträd, vilka idag uteslutande återfinns i varmtempererade områden. Bland de pollen som identifierats finns även representanter av växter som gran och lärkträd, vilka antagligen vuxit i bergsområden i lite kallare klimat.

Resultaten från denna avhandling är jämförbara med studier som gjorts i Tyskland och central Europa. Dock är de klimatdata som tagits fram de första numeriska resultaten från miocen i Norra Europa.

1. Introduction

The Miocene (23.03–5.33 Myr ago) heralded important changes in Earth's landscapes, biome structure and biological diversity. It encompasses the end of the prehistoric world as well as the birth of the one that we are familiar with today. On land, mammals and birds rapidly evolved and several mammal groups, such as ungulates, diversified in the new grassland and savanna ecosystems that formed around the globe (Strömberg 2002). In North America, equids reached their peak in diversity, and in east Africa the first hominids emerged (Senut et al. 1997).

During the Miocene, the continental configuration was similar to the one we see today. The African-Arabian plates were colliding with Eurasia resulting in the formation of the Alps. This, in turn, reduced the central European part of the Tethys Sea and thus the connection between the Mediterranean and Indian Ocean. Consequently, the main source of atmospheric moisture in southern Europe was cut off causing an increase in aridity in that region (Kazlev 1998; Bruch et al. 2007). Nonetheless, the reduction of the Tethys Sea facilitated more dynamic floral and faunal exchanges between Africa and Eurasia (Kazlev 1998). During the Miocene, the south circumpolar ocean circulation intensified as Australia and South America receded from Antarctica, which strongly affected the global ocean and atmospheric circulation through reduced north-south mixing of oceanic waters. This in turn caused the buildup of the Antarctic polar ice cap (e.g., Lear et al. 2003; Roberts et al. 2003), thus accelerating the development of seasonality, aridity, and enhanced cooling on a global scale. Accordingly, the Miocene was a period of profound climatic changes.

The Miocene is characterized by extreme climatic optima alternating with major climate coolings (Kashiwagi and Shikazono 2003; Lear et al. 2003). Studies of oxygen isotope (δ^{18}O/ δ^{16}O) curves have revealed significant changes throughout the Miocene (Kocsis et al. 2009). Miller et al. (1991) described several major oxygen isotope excursions based on measursments of oxygen in benthic foraminifera, whereas van der Burgh et al. (1993) used stomata index from multiple tree species in order to detect changes in the carbon dioxide levels. One of the most prominent isotopic excursions is the Mi-1 of Miller et al. (1991), which has been correlated with a chronostratigraphic scale based on foraminifera (Miller 1987) and magnetostratigraphy (Zachos et al. 2001). The Mi-1 excursion coincides with the Oligocene-Miocene epoch boundary and major turnovers affecting both terrestrial and marine taxa (Miller 1987). These ecosystem changes are interpreted to be the result of a global cooling event that coincided with the appearance of a continental-scale ice sheet on Antarctica (Zachos et al. 2001). This cooler period lasted until the late early Miocene and was succeeded by one of the warmest periods in the Neogene, i.e., the Miocene Climate Optimum (MCO), which peaked 15–17 Myr ago. At the transition between the middle and late Miocene, approximately 14 Ma ago, a marked event referred to as the middle Miocene Cooling occurred. This event is a major step in Earth's Cenozoic climate evolution (Shevenell et al. 2004) and was accompanied by growth of the Antarctic ice sheet and subsequent eustatic sea level changes.

From that period, and onwards, a global cooling is observed, which included decreasing temperatures and precipitation (Bruch et al. 2007). This caused an increase in both latitudinal and seasonal differentiation, which is also recorded in Europe (Bruch et al. 2007). The latest Miocene, approximately 6 Ma ago, is a period when the Mediterranean evaporated partly or completely, and has been described as the Messinian Event. From the late Miocene and onwards continuously decreasing temperatures and increased seasonal oscillations are reported (Utescher et al. 2000).

1.1 Palynology

Palynology is the science that studies organic-walled microfossils, also referred to as palynomorphs, which includes pollen, spores, dinoflagellate cysts, acritarchs, chitinozoans, scolecodonts and other organic-walled, acid-resistant microfossils. Palynology does not normally include the study of organisms with siliceous or calcareous exoskeletons (Traverse 1988). Palynomorphs in most pre-Quaternary studies are extracted from rocks and sediment cores by dissolution of the siliceous or calcareous rock matrix with hydrofluoric acid (HF) or hydrochloric acid (HCl) (Batten 1999). The sieved and concentrated organic residues are thereafter mounted on microscope slides and the palynomorphs are counted. The quantitative and/or qualitative data obtained can then be used to reconstruct past plant communities, and thereby infer palaeoenvironmental and palaeoclimatic changes by inferences from the distribution of modern vegetation categories. Palynology can also be applied in biostratigraphy to correlate strata and determine the relative age of a given bed or formation (Traverse 1988).

In this study I have investigated pollen, spores and, to a minor extent, dinoflagellate cysts assemblages. The study of pollen and spores is referred to as "terrestrial" palynology and it is a valuable tool for assessing the spatial and temporal distribution of past vegetation. In pre-Neogene strata, paly-
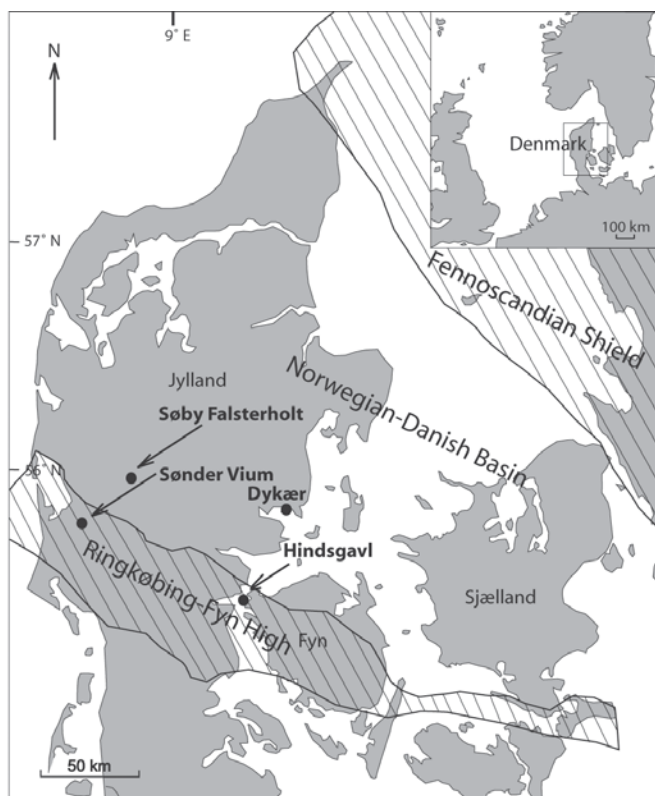
Figure 1. Location of the the Sdr. Vium drill and the outcrop sections in Dykær och Hindsgavl, which have been studied for this PhD-thesis. Included in the figure is also the location of the Søby Falsterholt section, which has previously been comprehensively studied by e.g., Ingwersen (1954), Koch et al. (1973), Christensen (1975, 1976), Friis (1975, 1977, 1978) and Koch (1989).

nology is also heavily applied in biostratigraphy. However, the stratigraphical value of miospore assemblages for the Miocene is somewhat limited because all recognized plant genera are long-ranging (Moreno et al. 2005). Nonetheless, palynology is an excellent tool for interpreting palaeoclimate variations as the world's climatic zones are closely reflected by the distribution of certain vegetation types. In order to interpret the palaeoenvironment, the pollen and spores have been assigned to botanical groups based on their extant relatives and modern eco-climatological tolerances (see below).

It is useful to calculate the ratio of dinoflagellate cysts to spores and pollen in order to evaluate the depositional environment. This is particularly important when examining sediments deposited in marginal settings in order to distinguish between palynoassemblage changes that might be generated by broad-scale climate change from those caused by modifications in local depositional setting (e.g., sea level changes). Mapping of freshwater algae versus other palynomorphs are used primarily to assess freshwater influence.

1.2 Aims and objectives

Several comprehensive studies on the Miocene sedimentary succession in Denmark (Fig. 1) have been carried out resulting in a well-established chronostratigraphic framework, biostratigraphic zonation based on dinoflagellate cysts (e.g., Dybkjær

2004; Piasecki 2005; Dybkjær & Rasmussen 2007; Dybkjær & Piasecki 2008), and detailed sequence stratigraphic framework (e.g. Rasmussen 2004a; Rasmussen & Dybkjær 2005) (Fig. 2). Studies of the Danish Miocene terrestrial record by e.g. Christensen (1975, 1976), Friis (1975, 1977, 1978), and Koch (1989) focused on the lignite-bearing middle Miocene deposits in the central parts of Jutland (the "Søby-Fasterholt flora"). However, a drill core penetrating the lower to upper Miocene taken on central Jutland, Denmark, provides a rare opportunity to apply palynology to examine the palaeoenvironment and palaeoclimate of a 20 Myr long stratigraphical interval. The study documented in this PhD thesis ties the terrestrial succession in Denmark to the international chronostratigraphic scheme, something that has previously been problematic. However, this study has correlated the pollen data with the dinoflagellate chronostratigraphy of Dybkjær (2004) and Dybkjær & Rasmussen (2007), thus achieving a better fit between globally documented climate change and floristic response in Denmark.

The aims of this thesis are to:
1) distinguish between variations in miospore assemblages related to vegetational changes from those related to changes in depositional facies;
2) interpret the palaeovegetation in Denmark during the latest Oligocene–late Miocene interval.
3) identify quantitative shifts in miospore assemblages corresponding to global climatic changes.
4) interpret the broader floristic responses to climate change across the Oligocene-Miocene boundary.

2. Study area

2.1 Regional palaeogeography

This thesis is based on studies conducted on two coastal exposures and one drill core on Jutland, the Danish mainland (Fig. 1). The study area is situated near the eastern border of the North Sea Basin, which during the Cenozoic was developed into an epicontinental basin (Fig. 3). It had periodic connections with the Tethys Sea towards the south and east, and to the North Atlantic through a narrow strait between present-day Norway and Scotland (Ziegler 1990). The basin was bounded to the north and north-east by the Fennoscandian Shield. The southern limit was located within the area of northern Poland, via Germany through northern France and the western border was probably located in the region of the British Isles. The basin was influenced by several tectonic events associated with the Alpine Orogeny (Vejbæk & Andersen 1987; Ziegler 1990) and was also subjected to several other phases of tectonism from the Permian to the present (Rasmussen 2004a). Over time, the basin was filled with large amounts of sediment of various ages, generating a complex stratigraphic architecture. The geological history of the Miocene sedimentary succession in Jutland is relatively well known and is represented by an almost complete sedimentary succession (Fig. 2). The succession dips towards the southwest and has been partially removed by Neogene uplift and erosion to the east (Rasmussen 2005). Consequently, the most complete Miocene depo-
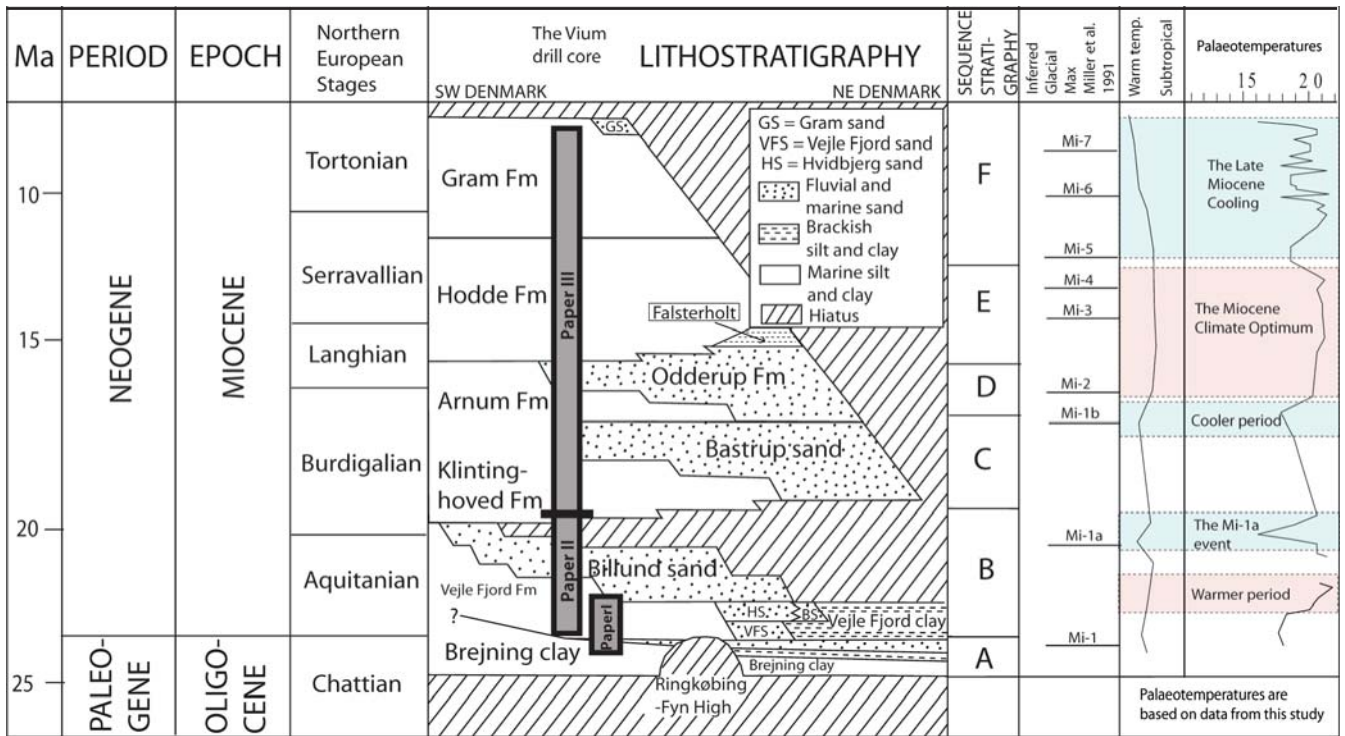
Figure 2. Diagram presenting the Miocene stratigraphy (modified from Rasmussen 2005) in Denmark and the lithostratigrapic extension of the studied sections in this thesis. Included are also the Miocene isotop excursions in comparison with the the mean annual temperatures calculated herein.

sits are present in the western part of Jutland. Several studies (e.g. Larsen & Dinesen 1957; Rasmussen 1961; Rasmussen 2004a, b; Rasmussen & Dybkjær 2005) have revealed that a complicated interplay between climatic changes, eustatic sea-level changes and regional and local tectonics are reflected in the development of the Miocene sedimentary sequences in Denmark.
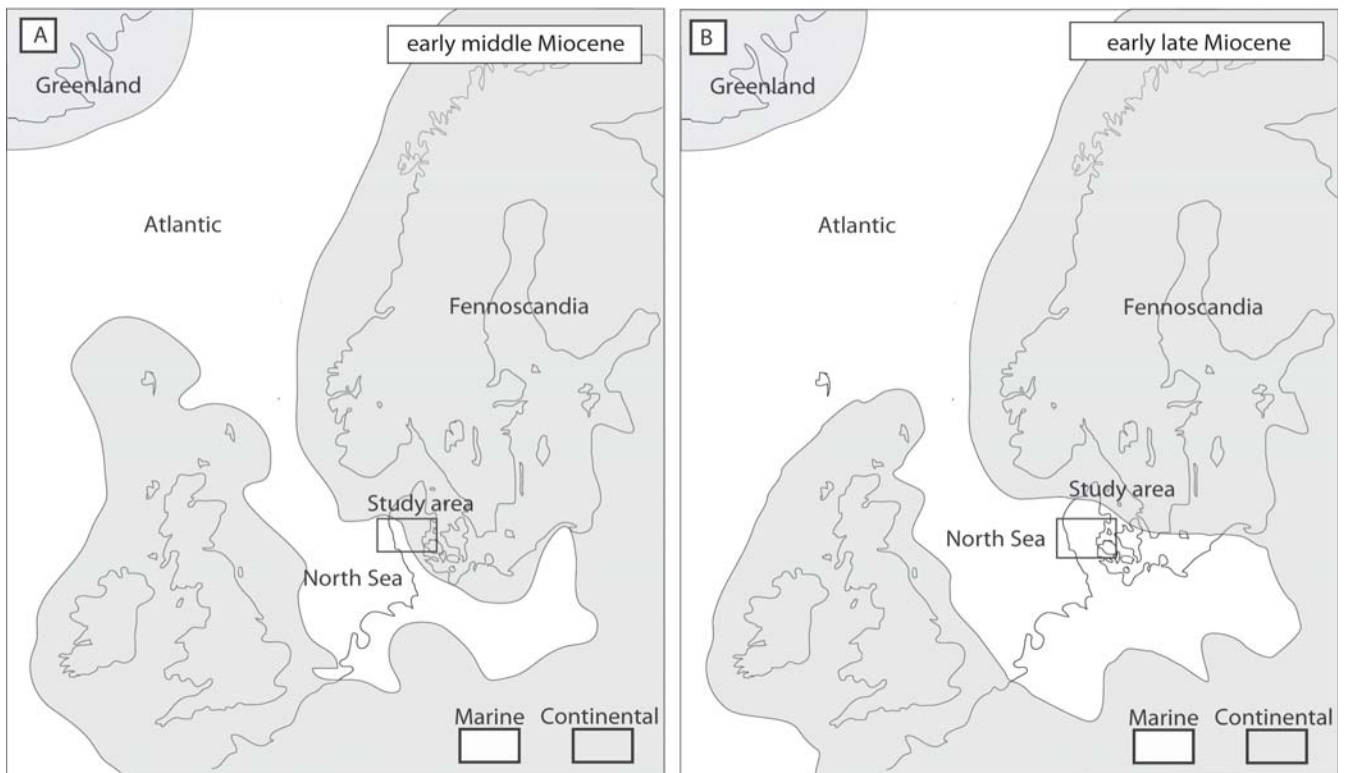
Figure 3. Palaeogeographic maps of A) early middle Miocene (15 Ma) and B) early late Miocene (11 Ma) based on Ziegler (1991) and Rasmussen (2005).
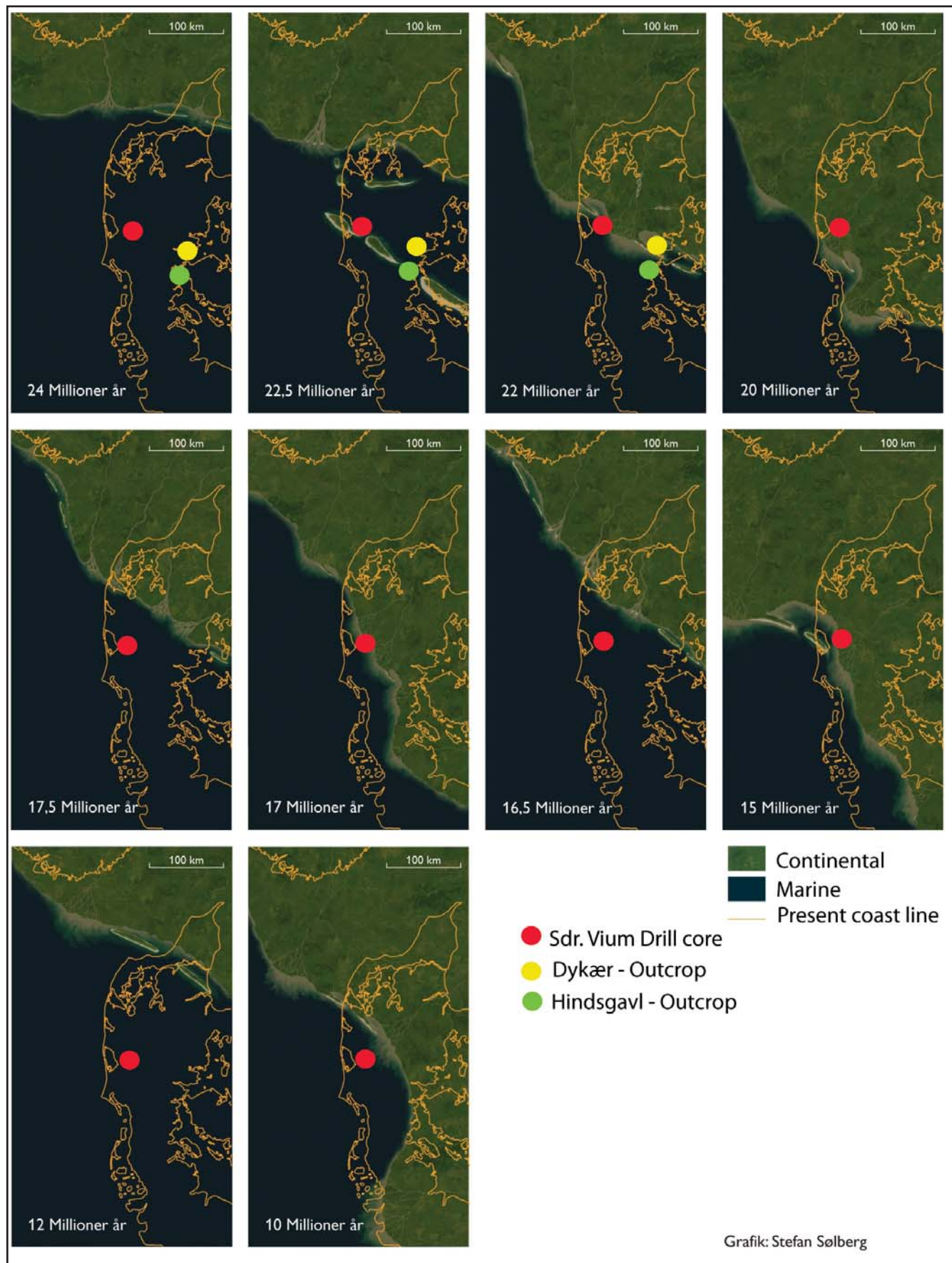
Figure 4. The dynamics of the coast line during the Miocene and the locations of the studied sections in this thesis after Rasmussen (2005). The text in the figures is in Danish and the translation of "Millioner år" is million years (Ma).

2.2 Depositional history and stratigraphy of the Danish Miocene succession

Paleocene and Eocene sediments of the Eastern North Sea were deposited in a fully marine depositional setting, and consist primarily of clays. Uplift of the Fennoscandian area during the Eocene and Oligocene transition, resulted in deposition of fluvio-deltaic sands north of present day Jutland and marine clays in Jutland. Due to a global eustatic sea-level fall in the latest Oligocene and beginning of the Miocene (Mi-1), distinct shallowing is evident in the Danish succession. This shallowing in the beginning of the early Miocene is the focus of this thesis. The Miocene stratigraphic succession is characterized by several transgressive-regressive cycles, which generated six distinct depositional sequences named A to F in ascending order by Rasmussen (2004a) (Fig. 2). The first zone, A, is referred to the latest Chattian (latest late Oligocene) and consists of glauconite-rich marine clay. The depositional setting was interpreted as a sediment-starved, open marine setting, based on the high glauconite content and a high relative abundance and diversity of dinocysts (Rasmussen & Dybkjær 2005) (Fig. 4).

Sequence B represents the earliest Miocene transgression with the deposition of marine clayey pro-deltaic sediments of the Vejle Fjord Formation (Sorgenfrei 1958; Larsen & Dinesen 1957; Rasmussen 1961; Rasmussen 2004b; Rasmussen et al. 2005) and sand-rich fluvio-deltaic deposits of the Billund Sand (sequence B of Rasmussen 2004a, b). Subsequently, a minor transgression resulted in the accumulation of the marine Klintinghoved Formation. This was followed by the deposition of a wedge of sediment, informally named the Bastrup Sand (Rasmussen 2003), which represents a second progradation of a delta complex during the early Miocene (sequence C). This unit is overlain by the marine, clay-rich Arnum Formation. The third and final deltaic progradation, caused by the tectonic uplift of the hinterland, occurred at the early to middle Miocene transition and is represented by the coal-bearing Odderup Formation (sequence D; Rasmussen 1961; Koch 1989). Major parts of the North Sea Basin subsided during the late Langhian to Tortonian, which produced the fully marine clays of the Hodde and Gram formations, representing sequences E and F (Rasmussen 1961; Piasecki 1980) (Fig. 2).

2.3 Previous Miocene palynological studies in Denmark

Thorough pollen-based vegetation and climate studies have been conducted in western and central Europe (e.g., Thomson & Pflug 1953; Mai 1965, 1995; von der Brelie 1967; Krutzsch 1971; Ashraf & Mosbrugger 1995, 1996; Sadowska 1997; Zetter 1998; Kolcon & Sachsenhofer 1999; Figueiral et al. 1999; Kovar-Eder et al., 2001; Ivanov et al. 2002). The pollen spectra generally indicate a warm temperate to subtropical climate during the Miocene (Zetter, 1998; Kolcon & Sachsenhofer, 1999; Kovar-Eder et al. 2001). The Miocene pollen assemblages are typically dominated by taxa derived from mixed mesop-

hytic broad-leafed forests consisting of both evergreen and deciduous trees that characterize humid, subtropical climates (Ivanov et al. 2007). Previous pollen records from Scandinavia have focused on the lignite-bearing middle Miocene deposits in central Denmark (e.g., Ingwersen 1954; Koch et al. 1973; Christensen 1975, 1976; Friis 1975, 1977, 1978, Koch 1989). Koch (1989) comprehensively described the "Søby-Fasterholt flora" of the Falsterholt Member (Fig. 2), which was collected from the lignite-bearing middle Miocene deposits in the central parts of Jutland. He concluded that the dominant vegetation was a swamp forest association bordered by a mixed hardwood forest. The swamp forest mainly included taxa such as *Taxodium* and *Nyssa*, whereas the mixed hard-wood forest hosted taxa such as *Betula, Carya, Engelhardtia* and *Quercus*. He also found indications of upland vegetation, which he entitled "slope- or upland forest", consisting mainly of gymnosperms that thrive in well-drained environments, such as *Sequoia*.

Taxodiaceae pollen are also abundant in samples from contemporaneous sediments north of Denmark (from i.e., Greenland and Ellesmere Island) where taxodiacean macrofossils also were identified (Manum 1962). Middle Miocene terrestrial records are derived from macrofossils and indicate two types of vegetation. The first, which is adapted to moist lowland environments, consists of taxodiacean species. The other is dominated by taxa from better-drained forests such as *Quercus* and *Fagus* (Grìmsson & Denk 2007).

3. Material and methods

3.1 Palynological approach

Plant taxa produce morphologically distinctive pollen grains. Plants also have specific demands on the environment they grow in, so called eco-climatological preferences, which are dependent on e.g., temperature, moisture and soil nutrients. Consequently, this allows interpretation of the palaeovegetation, ecology and climate (Suc 1981). Because the majority of the plant genera recorded in this thesis have existed since the Eocene and are represented in the modern flora, I have used the botanical determination of the pollen grains. However, in some cases the pollen taxa have an uncertain affinity and in those cases classical pollen morpho-taxonomy has been employed.

3.2 Sampled exposures and the Vium drill core

The palynomorphs examined in this study were extracted from two exposures (at Dykær and Hindsgavl), and a 289 metres succession in the Sønder (Sdr.) Vium bore hole (DGU 102.948) (Fig. 1). Data in Paper I is based on samples collected from the Dykær and Hindsgavl exposures. From Dykær, a total of 23 samples were collected from an interval of 17.65 metres and at Hindsgavl eight samples were collected covering a total of 3.55 metres of the outcrop. The sedimentary sequences have previously been dated by dinocyst stratigraphy (Piasecki 1980;
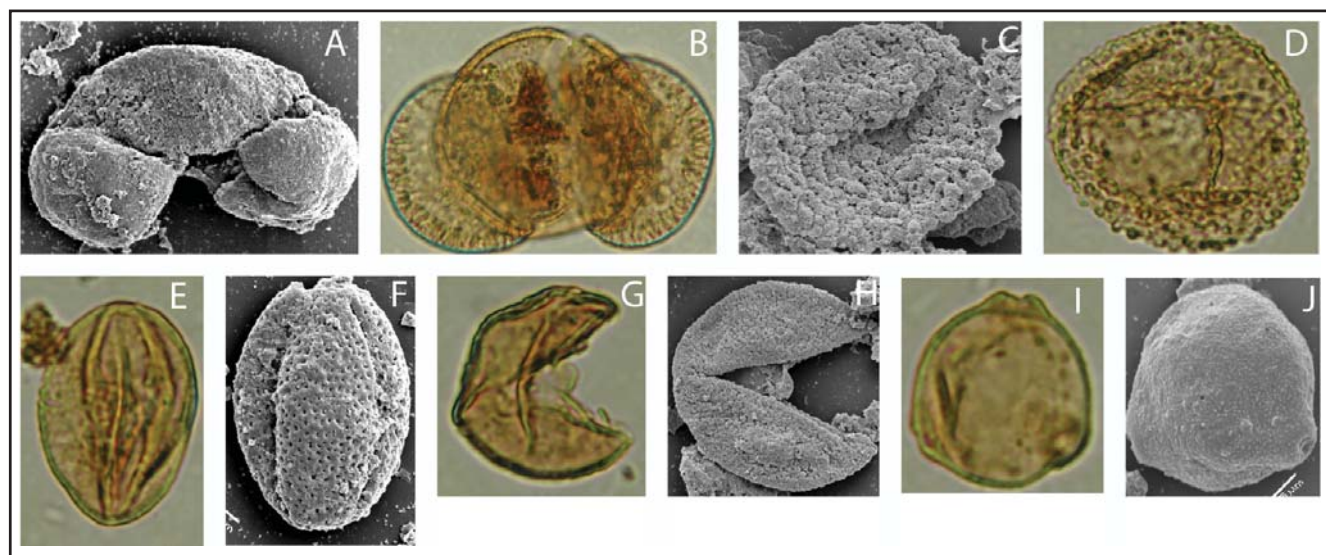
Figure 5. Light micrographs (LM) and SEM-images of A) *Pinus* sp. SEM. B) *Pinus* sp. LM. C) *Sciadopitys* sp. SEM. D) *Sciadopitys* sp. LM. E) *Quercus* sp. LM. F) *Quercus* sp. SEM G) *Taxodium* sp. LM. H) *Taxodium* sp. SEM. I) *Betula* sp. LM. J) *Betula* sp. SEM. All photos are taken at x500.

Dybkjær 2004; Rasmussen & Dybkjær 2005). In order to tie the terrestrial vegetational data to the chronostratigraphic framework, the sampling was performed at the same levels as those studied by Rasmussen & Dybkjær (2005).

The Dykær exposure presents a succession that has stratigraphically been referred to the latest Chattian (latest late Oligocene) to the early Aquitanian (earliest Miocene) and is referable to the upper part of Sequence A and most of Sequence B (Figs. 2, 5). Sequence A, consists of glauconite-rich marine clay from an open marine setting, based on the high glauconite content and a high relative abundance and diversity of dinocysts (Rasmussen & Dybkjær 2005). A shallowing trend in the upper part of Sequence A is interpreted as having resulted from a combination of the topography of the Ringkøbing-Fyn High and a eustatic sea-level fall. Sequence boundary B, seen as a distinct gravel layer in the lower part of the Dykær exposure, was suggested to correlate with the Oligocene–Miocene boundary and with the Mi-1 glaciation event of Miller et al. (1991), (Rasmussen 2004a,b; Rasmussen & Dybkjær 2005; Dybkjær & Rasmussen 2007).The Hindsgavl exposure represents a lower Aquitanian succession referable to the dinocyst zones *Chiropteridium galea* and *Homotryblium* spp., (earliest Miocene) (Dybkjær 2004). This section represents a part of Sequence B with a more distal setting than Dykær. Consequently, the two exposures partly overlap geochronologically but represent different environmental settings, with the Hindsgavl outcrop being more distal than Dykær.

The Vium drill core was taken on western Jutland and represents a sedimentary succession spanning the lower to upper Miocene. Paper II is based on the lowermost interval (288–183 m), representing sequence B, with marine clayey prodelta sediments of the Vejle Fjord and Klintinghoved formations (Figs. 2, 4, 5). Sequence B commences with dark silty clays interbedded with sandy layers. At the193 m level, a medium- to coarse-grained sand is initiated. The interval between 183–160 metres was a sandy interval that was lost at the time of drill core recovery. It is, therefore, not studied herein. This sand-

rich fluvio-deltaic deposit is interpreted as the Ribe Formation (sequence B; Sorgenfrei 1958; Rasmussen 2004a, b).

The succeeding and final 160 metre interval of the Vium drillcore has been examined in Paper III (Fig. 2). Forty-one samples were studied palynologically and represent a time span from the early to late Miocene and the sequences C-F (Fig. 2, 5). Sequence C represents a minor transgression and resulted in the accumulation of the marine Arnum Formation. This was followed by the Bastrup Sand representing the progradation of a delta complex in the early Miocene (sequence C) (Figs. 4, 5). This unit is overlain by the upper part of the marine, clay-rich Arnum Formation. A final deltaic progradation, caused by tectonic uplift of the hinterland, occurred at the early to middle Miocene transition and is represented by the coal-bearing Odderup Formation (sequence D; Rasmussen 1961; Koch 1989). Major parts of the North Sea Basin subsided during the late Langhian to Tortonian, which led to deposition of the fully marine clays of the Hodde and Gram formations, representing sequences E and F (Rasmussen 1961; Piasecki 1980).

3.3 Palynological preparation

Totally 114 samples were anlysed for this study. All samples studied were processed at the palynological laboratory located at the Geological Survey of Denmark and Greenland in Copenhagen. Standard palynological preparation techniques including treatment with HCl, HF, HNO_3 and sieving with 11 μm nylon filters (Poulsen et al. 1990). Strew slides were made in glycerin gelantine and approximately 300 pollen and spore specimens from each sample were counted using a light microscope.

3.4 Light microscopy and Scanning Electron Microscopy

The majority of the palynological examinations in this study

Palaeoclimate indicators	Palaeoenvironmental indicators	
Mega-mesothermic taxa	**Sea-coastal taxa**	**Decidous-Evergreen mixed forest**
Arecaceae	*Ephedra*	*Acer*
Sabal	**Swamp forest plants**	*Arecepites*
Tricolporopollenites pusillus	*Alnus*	*Artemisia*
Tricolporopollenites cingulum	*Betula*	*Baculatisporites*
Tricolporopollenites fusus	*Cyrilla*	*Carpinus*
Tricolpororpollenites villensis	*Inaperturopollenites* sp.	*Carya*
T. edmundii	*Myrica*	*Cistarearumpollenties*
Engelhardtia	*Nyssa*	*Corrugatosporites*
Podocarpus	*Salix*	*Corylus*
Platycarya	Sapotaceae	*Engelhardtia*
T. henrici	Symplocaceae	Ericaceae
T. microhenrici	Taxodiaceae-Cupressaceae	*Fagus*
Taxodiaceae-Cupressaceae	**Conifer-forest group**	Graminae
Inaperturopollenites sp.	*Cathaya*	*Guylussacia dumosa*
Mesothermic taxa	*Cedripites*	*Ilex*
Pterocarya	*Pinus*	*Illicum floridanum*
Myrica	*Sciadopitys*	*Laevigatosporites*
Ilex	*Sequoia*	*Leiotriletes*
Corylus	*Tsuga*	*Liquidambar*
Nyssa	**High-altitude forest**	*Liriodendron*
T. libraensis	*Abies*	*Lycopodium*
Carya	*Larix*	*Monocolpopollenites* sp.
Fagus	*Picea*	*Platycarya*
Zelkova	**Freshwater taxa**	*Podocarpus*
Liriodendron	*Botryococcus*	*Pterocarya*
Salix	*Nuphar*	*Quercus*
Liquidambar	Nymphae	*Retitriletes*
Tilia	*Pediastrum*	*Sabal*
Ulmus	*Sigmopollis*	*Sparganium*
		Stereisporites
Meso-microthermic taxa		*T. edmundii*
Quercus		cf. *T. edmundii*
Larix		*T. henrici*
Carpinus		*T. libraensis*
Acer		*T. microhenrici*
Alnus		*Tilia*
Betula		*Tricolporopollenites cingulum*
Tsuga		*Tricolporopollenites fusus*
Abies		*Tricolporopollenites pusillus*
Picea		*Tricolporopollenites villensis*
Pinus		*Ulmus*
		Umbelliferoipollenites
		Zelkova

Table 1. Examples of the pollen and spore taxa recovered in the Sønder (Sdr.) Vium drill core section, presented in their palaeoenvironmental context and as palaeoclimatical indicators.

were carried out using an Olympus light microscope. Taxonomic identifications were made using 100x and 40x magnification, and the counting of pollen grains was undertaken at 40x magnification. In paper I, scanning electron microscopy (SEM) was included. The scanning electron microscope (SEM) is a type of electron microscope that constructs images of the sample surface by scanning it with a high-energy beam of electrons. The SEM can produce very high-resolution images of a sample surface, revealing details well below the typical miospore ornament size of 1 to 5 μm. Due to the way these images are created, SEM micrographs have a very large depth of field yielding a characteristic three-dimensional appearance useful for understanding the surface structure of a sample. I

primarily used the SEM in order to identify smaller structures on the outer surface in certain taxa, which in the light microscope would be easy to miss (Fig. 5). However, the most convenient way to undertake quantitative palynology is by using the light microscope. The latter also has the advantage of viewing the specimens in color, an important advantage in judging, for example wall thickness and thermal maturity, when compared with electron microscopes.

3.5 Taxonomic identification

The most important part of palynological studies concerns the

identification of morphotypes. However, besides morphological identification, biological identification is crucial for vegetation analysis of Cenozoic assemblages. To accomplish the main aims of this thesis, e.g. interpret the palaeoenvironments as well as climate, I have striven to use the botanical determination of pollen grains. This is achievable in the Miocene since the majority of the living plant genera have been represented since the Eocene (Suc 1981). However, some fossil taxa have as yet unknown biological affiliations and in those cases I have used a combination of natural taxa and parataxa. The approaches of the papers have also differed as in Paper II, an attempt was made to determine the age of the Danish samples by comparing our results with older studies from Europe, which also used parataxonomy. In all other cases we used taxonomy according to botanical affinities, in most cases to family or genus level by adapting the systematics of e.g., Thomson & Pflug (1953), Krutzsch (1971), Thiele-Pfeiffer (1980), Nagy (1985), Traverse (1988), and Kolcon & Sachsenhofer (1999).

3.6 Approaches in palynological grouping

3.6.1 Palaeoenvironment

All pollen and spores recorded in this study have been assigned to vegetational/environmental categories that are based on the ecology of extant genera (see Paper I, II, and III) (Table 1). The groups are modified from those given by e.g. Moreno (2005) and Kolcon and Sachsenhofer (1999). Thus, one must keep in mind when doing any interpretations that the groups are artificial and some of the taxa recorded might be represented in multiple ecological associations or in unique communities no longer represented in the modern flora.

Additionally, dinoflagellate cysts have been noted when spores and pollen were counted in order to gain information regarding the depositional environment. In papers I and II the dinocysts were counted separately, but in paper III the dinocysts were only registered as present or absent.

3.6.2 Palaeoclimate and palaeotemperature

In order to interpret the climate the Coexistence Approach (CA) as introduced by Mosbrugger and Utescher (1997) was applied. This method is based on the assumption that the fossil plant taxa identified in Neogene sediments have similar climatic requirements as their nearest living relatives. The analysis aims to find the climatic zone in which all fossil taxa could coexist. In this study I have focused on the variation of mean annual temperature (Fig. 2). The results from the CA-analysis have been compared to results from previous investigations performed by e.g., Kolcon & Sachsenhofer (1999); Figueiral et al. (1999); Ivanov et al. (2002); Mosbrugger et al. (2005), Utescher et al. (2007, 2009). In Paper II, taxa are assigned to "arctotertiary" and "palaeotropic" associations. However, as previously mentioned, the ecological requirements of these categories may diverge (Kolcon & Sachsenhofer 1999). Therefore, it was found to be more appropriate to interpret palaeotemperature by the CA.

4. Summary of papers

Paper I

Larsson, L.M., Vajda, V., Dybkjær, K. 2009. Vegetation and climate in the latest Oligocene–earliest Miocene in Jutland, Denmark. Submitted. Review of Palaeobotany and Palynology.

This study focuses on the Oligocene-Miocene boundary with the objective of separating variations in miospore assemblages into those induced by climatic change and those related to changes in depositional facies. The study further aims to interpret the composition and structure of the latest Oligocene–earliest Miocene vegetation patterns and whether the miospore assemblages are modified in correspondence with the global climatic changes (e.g., Mi-1 event) identified across the Oligocene–Miocene boundary. Thus, two sedimentary exposures were examined in Jutland (Jylland) Denmark, encompassing the uppermost Oligocene-lowermost Miocene (latest Chattian – early Aquitanian).

The pollen and spores can be divided into groups depending on their eco-climatic preferences. Seven groups; mega-mesothermic taxa, warm-temperate plants, cool-temperate plants, aquatic/freshwater plants, herbs and shrubs, and xerophytes and freshwater algae (*Botryococcus)*, were utilized in a modified sense from Mosbrugger et al. (1994), Moreno (2005), Kolcon & Sachenhofer (1999), and Larsson *et al.* (2006) (Table 1, Fig. 4). The presence of diverse dinoflagellate cyst assemblages and tidal sediments in all samples from both Dykær and Hindsgavl confirms a deposition environment which altered between shallow marine, and a coastal plain with marine influence. The pollen assemblages indicate that Jutland was most probably covered by extensive Taxodiaceae swamp forests in the mid-Cenozoic. Besides a Taxodiaceae-Cupressaceae association, which was overwhelmingly dominant, other common plants in this habitat were *Alnus*, *Nyssa*, *Betula*, *Salix*, *Cyrilla* and *Myrica*. Most of the trees and shrubs are well adapted to swamps and thrive under more or less flooded conditions in modern bald cypress swamps of the southeastern North America.

The floral pattern documented in this study strongly resembles assemblages identified from earlier studies conducted on the early and middle Miocene of Europe and the Arctic e.g., Svalbard, Iceland and Greenland (Manum 1962), Denmark (Friis 1975, 1978; Larsson et al. 2006; Grímsson & Denk 2007), Germany (Mai 1965 1995; Zetter 1998; Kolcon & Sachsenhofer 1999; Kovar-Eder et al. 2001; Kunzmann et al. 2009), Austria (Zetter 1998) and Slovakia (Kovacova & Sitar 2007) but there are subtle differences.

In central Europe, the *Taxodium-Nyssa* vegetation also flourished in lowland riparian environments during the Oligocene and Miocene (Kunzmann et al. 2009). Vegetation composition indicates that a warm-temperate climate prevailed in Denmark during the Oligocene–Miocene transition. Palynological results from Germany indicate a warm temperate to subtropical climate during the Miocene (Zetter 1998; Kolcon & Sachsenhofer 1999; Kovar-Eder et al. 2001). The Miocene pollen as-

semblages from Slovakia, like Germany, are more southerly and continental compared to Denmark, Iceland, Svalbard and Greenland and are dominated by taxa derived from mixed broadleafed forest with both evergreen and deciduous trees (Kovacova and Sitar 2007). The Slovakian palynoflora in general corresponds to the Danish mixed mesophytic forest association with elements indicating a humid, subtropical climate. In the Slovakian area *Glyptostrobus* is recorded frequently, suggesting less expressed seasonality (Kunzmann et al. 2009), a conclusion corroborated by several taxa from Denmark (e.g., *Cathaya*, *Engelhardtia*).

According to calculations using the Coexistence Approach, mean annual temperatures during this interval were between 15.6–16.6°C. An increase to 16.5–21.1°C is inferred from the palynoflora in the upper part of the section. The earlier, cooler period possibly reflects global cooling associated with the Mi-1 glaciation event at the Oligocene–Miocene boundary. Correlation with the well-established chronostratigraphic and sequence-stratigraphic framework for the studied succession reveals that the most distinctive palynofloral changes probably reflect a shift in depositional facies (due to an increase in sea level) rather than direct climatic change. The sea-level rise is interpreted here to be eustatic and related to melting of Antarctic ice-caps at the end of the Mi-1 glaciation event.

Paper II

Larsson, L. M., Vajda, V., Rasmussen, E. S. 2006. Early Miocene pollen and spores from western Jylland, Denmark – environmental and climatic implications. GFF 128, 261–272.

A cored section from Vium in western Jylland (Jutland), Denmark, provided new data regarding the vegetation and climate in the early Miocene. The miospore assemblages are well preserved and diverse by means of 95 terrestrial taxa. An apparent dominance by pollen and spores, and lesser proportions of dinoflagellates and freshwater algae indicate an inner-neritic setting. A level containing comparatively abundant dinoflagellate cysts probably represents a transgressional event. Five distinct terrestrial plant associations were recognised (1) Swamp forest canopy association, (2) Cool temperate "mixed mesophytic" forest canopy association, (3) Warm temperate plant association, (4) Mesophytic understorey plant association, and (5) Aquatic plants and algal association. The pollen record is dominated by swamp forest taxa such as Taxodiaceae-Cupressaceae suggesting that swamp forests dominated the onshore region. Besides *Taxodium,* the swamp forest also contained angiosperm taxa such as Myricaceae, *Nyssa*, *Betula* and *Alnus*. Previous work in Europe by e.g. Kolcon & Sachsenhofer (1999) has shown that *Taxodium* swamp forests dominated central Europe. Consequently, this study extends the northern limit of this swamp forest vegetation, at least as far as present Denmark. Better drained areas further inland hosted diverse mesophytic forests with a ground cover of reeds, sedges and pteridophytes. Abundant pollen taxa derived from mesophytic forests indicates the presence of evergreen conifers, such as *Pinus, Sequoia* and *Sciadopitys*, and deciduous

angiosperms, including *Fagus* and *Quercus*.

There are difficulties in correlating the pollen spectra at different locations (Traverse 1988; Sadowska 1995). For this objective, the palynological results from the Sønder Vium succession have been compared with the quantitative results of von der Brelie (1967) in order to assess the applicability of the central European zonation to Denmark. Results from the studied succession indicate that early Miocene key taxa such as *Ephedripites, Platycarya* and *Engelhardtia* are consistent, but subsidiary, elements throughout the sampled succession. The presence of Arecaceae (palms), *Ilex* and *Engelhardtia* suggest a warm temperate climate. According to Mai (1995), the climate in Europe was warm temperate to humid subtropical, with slight climate deterioration at the end of the Aquitanian. Climate change is reflected in the studied succession by a general reduction in warm temperate taxon palynomorphs up section. A pronounced reduction in warm temperate taxa in this upper part is revealed when excluding Taxodiaceae-Cupressaceae from the pollen signal. We contend that this climatic deterioration may indicate a late Aquitanian age for this part of the succession.

Paper III

Larsson, L.M. 2009. North European climate evolution during the Miocene based on Danish palynological assemblages. In manuscript.

The upper part of a drill core taken in Sønder Vium on Jutland was examined palynologically. The drill core sediments correspond to the lower–upper Miocene i.e., between 20 and 8 Myrs before present. A marine environment is indicated by the relatively high abundances of dinoflagellate cysts in all samples. The pollen assemblages are rich and diverse and reveal that coastal areas were dominated by *Taxodium* swamp forests during the Miocene in present day Denmark. Additional elements in the swamp forest were Myricaceae, *Nyssa*, *Betula* and *Alnus*. Further inland, a mixed deciduous-evergreen forest prevailed with taxa such as *Fagus, Carya, Ulmus* and thermophilic components such as *Engelhardtia* and *Ilex*. In areas with better drained soils, or on elevated areas, conifer-forests including taxa such as *Pinus*, *Sequoia* and *Sciadopitys* prevailed. The palynological assemblages in this study are strikingly similar to the "Søby-Fasterholt flora" (Koch 1989), which was investigated from the lignite-bearing middle Miocene deposits in the central parts of Jutland. A work conducted on the identical drill core as this present study (Larsson et al. 2006) reveals a similar palaeoenvironmental setting and vegetation structure. Thus, despite climate changes, the dominance of swamp forests persisted throughout the Miocene.

The climate was warm temperate during major parts of the studied period with mean annual temperatures of 15.5–20°C. By employing the Coexistence Approach (Mosbrugger & Utesher 1997) combined with grouping taxa in eco-climatic groups, new information has been provided regarding the Miocene climate in Denmark and northwestern Europe. Four different climatic events are detected within the studied succession. The oldest event identified, I, is a cooling at the beginning of the Burdigalian, approximately 20 Ma, which coincides with
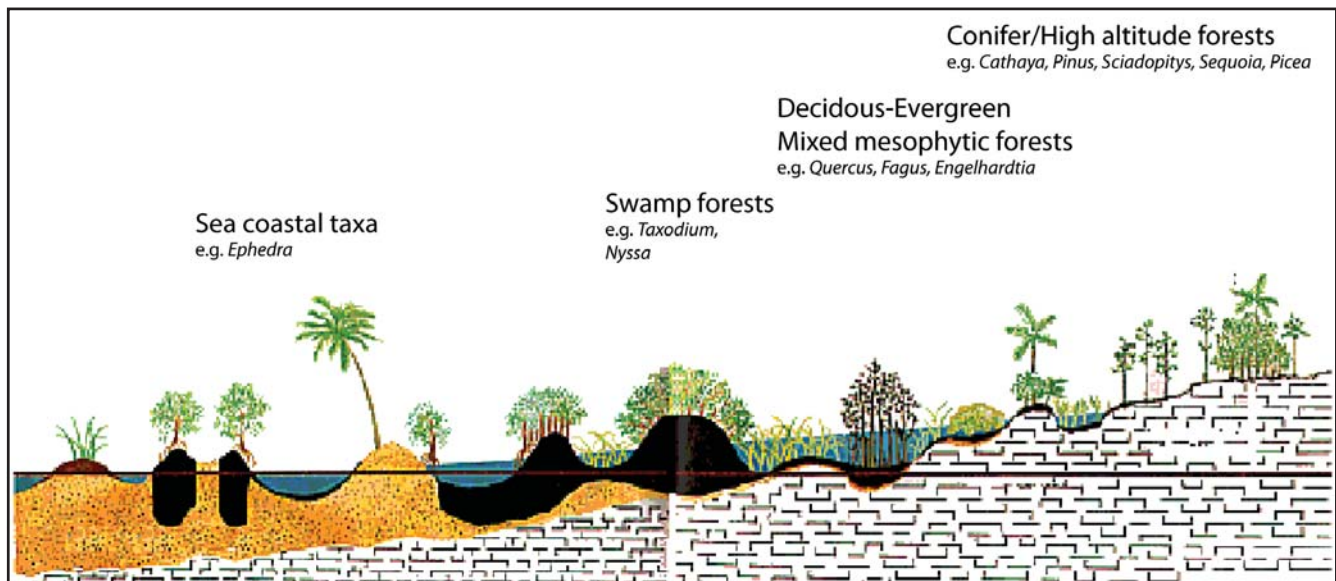
Figure 6. Overview of different palynological palaeoenvironmental assemblages in relationship to the coastline.

the Mi-1a oxygen isotope excursion (Miller 1987, 1991). The second event, II, is also a cooling period roughly 18.5 Ma ago, which has not previously been described from the European terrestrial record. Approximately 17 Ma, the warmest period occurred in Denmark, and this event (III) lasted from 17 to 14 Ma and is also recognized globally as the middle Miocene Climatic Optimum (MCO). The warming pattern reflected in the Danish succession perfectly matches the middle Miocene Climatic Optimum (MCO), which is detected all over the Northern Hemisphere (Utescher et al. 2000). Several previous palaeobotanical investigations have detected this warm interval in other areas (e.g., Thomson & Pflug 1953; von der Brelie 1967; Zagwijn & Hager 1987; Mai 1995; Ashraf & Mosbrugger 1995, 1996; Mosbrugger & Utescher 1997; Utescher et al. 2000, 2007; Ivanov et al. 2007; Moreno et al. 2005; Figueral et al. 1999). Following this, a marked climate cooling is noted, event IV, which coincides with the beginning of the globally identified late Miocene Cooling. Further evidence of the latter event is revealed in the results of several studies from elsewhere in Europe (Utescher et al. 2007). Apart from decreasing temperatures, the LMC is also associated with a higher degree of seasonality. The cooling that occurred during the late Miocene continued more or less until the Pliocene (Utescher et al. 2000).

5. Discussion

5.1 Palaeoenvironment

Warm and humid climates during the early Miocene favoured the widespread development of *Taxodium* swamp forests in adjacent coastal lowlands of central Europe and northwestern Germany (Ziegler 1990; Figueiral et al. 1999; Kolcon & Sachsenhofer 1999). These wet lowlands were surrounded by elevated forests incorporating both palaeotropical and arctotertiary elements (e.g. Thiele-Pfeiffer 1980; Sadowska 1995; Zetter 1998; Kovar-Eder et al. 2001). The palynological assemblages

examined in this study extend the distribution of this palaeo-vegetation type and imply the presence of swamp forests in coastal Denmark during the entire Miocene (Fig. 6). Modern analogues for this vegetation type are the riparian swamp forests of the Mississippi delta and the Bald cypress swamp forests of Southeastern United States, where the canopy, as herein interpreted for the Miocene of Denmark, is also dominated by *Taxodium* and *Nyssa*. The Danish Miocene assemblages also include other swamp forest taxa such as Myricaceae, *Nyssa*, *Salix*, *Betula* and *Alnus*, which are relatively abundant and bring substance to this conclusion. Taxodiaceae pollen grains are also abundant in samples from contemporaneous sediments from Greenland and Ellesmere Island where taxoidiacean macrofossils were also identified (Manum 1962).

Deciduous-evergreen mixed forests bordered the swamp forests in Denmark during the Miocene, and grew in areas slightly drier and well-drained than the swamp forests (Moreno et al. 2005) (Fig. 6). These species-rich forests included both deciduous and evergreen trees and shrubs, however the deciduous elements are dominant and the evergreen elements constitute mostly smaller trees and shrubs (Kovar-Eder et al. 2001; Mosbrugger 2009). The pollen spectra indicate that these were rather diverse forests incorporating both "arctotertiary" and "palaeotropic" elements. The most abundant taxa in these forests were temperate taxa such as *Fagus, Carya* and *Querqus* but thermophilic taxa such as Mastixiaceae, *Ilex* and *Engelhardtia* are also present.

This vegetation probably responds to Koch's (1989) hardwood forests of the middle Miocene Søby-Falsterholt Flora. There is also strong resemblance to the assemblages investigated by Manum (1962) on Spitsbergen. Likewise, similar forest associations have been recorded in Europe (Zetter 1998). The conifer forest group is an artificial group that was constructed in order to represent a slightly higher elevation vegetation category including gymnosperms that thrive in well-drained areas such as *Sciadopitys* and *Cathaya*. However, the taxon *Pinus* is not restricted to mid-altitudes but can also grow in well-drained areas closer to the shoreline or in dry patches

in the deciduous-evergreen mixed forest (Fig. 6). The high altitude forests consisting of cool temperate gymnosperms are less common than other vegetation types, which is probably due to the long distance their miospores need travel from the source to the depositional area. This group commonly increases in association with high amounts of aquatic taxa, which might imply that they are more represented in transgressional phases as they have the advantage of travelling longer distances than non-saccate pollen grain. This is further evident as e.g. *Tsuga* and *Abies* occur in larger numbers together with other bisaccate taxa independent of eco-climatologically preferences.

Freshwater taxa are present in all samples in this study, which indicates the proximity to land. They seem to increase in pulses that probably represent transgressional phases, since they seem to coincide with increasing numbers of bisaccates. Nevertheless, it is clear that fluvial systems occurred along the coastline, transporting both terrestrial pollen grains and freshwater algae out to the marine depositional area.

The floristic pattern documented in this study strongly resembles assemblages identified from earlier studies conducted on the early, middle and late Miocene of Europe and the Arctic, e.g., (Svalbard, Iceland and Greenland (Manum 1962), Denmark (Friis 1975, 1978; Larsson et al. 2006) (Grímsson & Denk 2007), Germany (Mai 1965, 1995; Zetter 1998; Kolcon & Sachsenhofer 1999; Kovar-Eder et al. 2001; Kunzmann et al. 2009), Austria (Zetter, 1998) and Slovakia (Kovacova & Sitar 2007) Additionally, the similarities between the palynological assemblages in this study are strikingly similar to the "Søby-Fasterholt flora" (Koch 1989).

5.2 Palaeoclimate

In this thesis I have used two methods for determining palaeoclimate. The first method is employed in the first published paper (Paper II in this thesis) and is based on the ratio between warm and cool-temperate taxa. In the lower Miocene of central Europe this ratio is typically 1:1 (Kolcon & Sachsenhofer 1999). This is not the case for the palynofloras studied in Paper II where the assemblages show a slight dominance of cool temperate elements. This method has proven to be slightly inappropriate for the overall goals of this study, because the palynological assemblages have been subjected to transport and sorting on their way to the depositional site. Therefore, I have used the Coexistence approach (CA) in Papers I and III.

The CA was established as a method for climate analysis by Mosbrugger & Utescher (1997). In Paper I, covering the Oligocene-Miocene boundary, the mean annual temperature estimates vary between 15.6–16.6°C to 16.5–21.1°C at Dykær, and at Hindsgavl between 13.3–16.6°C and 16.5–16.6°C (Fig. 2). These temperatures match previous studies conducted on fossil macrofloras (Uhl et al. 2007) and pollen (Ivanov et al. 2007) in central Europe, which both indicate MATs of 15–17°C.

The Dykær data indicates that the beginning of the late Aquitanian was a warm period (Fig. 2). However, the markedly lower temperatures in Hindsgavl are probably due to the inclusion of taxa that are not appropriate to use in the CA such as *Sequoia* and *Sciadopitys*. Consequently, the climate in early

Miocene was fairly stable and pretty similar to the European record.

Paper III reveals several climatic events in the late early Miocene and onwards. The mean annual temperature (MAT) varies between 15.5–21.1 °C throughout the sampled section. This is consistent with the MAT based on coeval palynological assemblages from Germany (Utesher et al. 2000). Four excursions are detected by the CA-method, which are also visible in the pollen assemblages that were constructed from the eco-climatological preference palaeotemperatures in the pollen assemblages.

The first event occurs where the MAT decreases from 20 °C to 15.5 °C, and this period is correlated with the Mi-1a event (Fig. 2), which is one of seven isotope zones based on benthic foraminifera defined by Miller et al. (1991). This event occurred at the boundary between Aquitanian and Burdigalian and has previously been recorded as a climatic cooling by Lotsch (1968). The second cooling event recorded does not coincide with any change in the sedimentological record, which clearly indicates that it is climatically induced. Nonetheless, this particular event has previously not been detected in NW Europe, which might be due to the lack of sediments of this age.

The third and most prolonged climatic trend occurs in the sample corresponding to an age of 17–14 Ma. The warming that appears in the palynological record perfectly matches the middle Miocene Climatic Optimum (MCO) (Fig. 2), which is detected all over the Northern Hemisphere (Utescher et al. 2000). In the marine realm, a corresponding signal to the MCO of the terrestrial record has been detected in the oxygen isotope signature of foraminifera (e.g. Miller et al. 1991; Zachos et al. 2001). However, earlier palaeobotanical and palynological studies conducted on Miocene sediments of Denmark have not included any method to estimate palaeo-temperatures, hence these are the first numerical records from Denmark. Confusingly, Koch (1989) only identified one tropical, and few subtropical taxa in the "Søby-Fasterholt flora", thus referring it to a climate that was "neither tropical, nor subtropical", even though the assemblages are strikingly similar to this present study. Nevertheless, all studies in Europe identifying the MCO have detected floras with an increase in mega-mesothermic elements and with a related decreased in the microthermic taxa.

The fourth and youngest of the climatic stages detected in this investigation commences at the end of the MCO and is interpreted as a cooling period (Fig. 2). The MAT decreases from 19 °C to 16 °C during the deposition of the sedimentary sequence of the Gram Formation. The age of this event is according to Rasmussen (2005) approximately 11 Ma ago. The cooling is also clearly visible in the CMM and WMM, which drops from 13.5–10 °C and 27–24 °C respectively. The abrupt cooling is indicated, either by an increase or decrease, within all the palaeoclimatical groups. The relative amount of mega-mesothermic taxa decreases from approximately 15 to 5%, whereas the percentage of meso-micothermic taxa increases from 5-15%. The mesothermic taxa are amplified by more than 10%. Consequently, this climatic cooling is substantial. Further evidence of this cooling is revealed by the results of several previous works from Europe and globally (Utescher et al. 2007). The definition of this event is the late Miocene Cooling (LMC),

which was, apart from decreasing temperatures, also associated with a higher seasonality (Moreno et al. 2005). The cooling that occurred during the late Miocene continued more or less until the Pliocene (Utescher et al. 2000). In Europe evidence of the LMC is reported from the Tortonian, whereas the cooling trend seems to have begun slightly earlier in, for example, Siberia (Nikitin 1988) and Japan (Flower & Kennett 1994), where the cooling is registered to have occurred at approximately 14 Ma. Also, Wolfe (1994) set this age as the beginning of the cooling in North America. This early cooling is, therefore, referred to as the middle Miocene Cooling, whereas in this study it is referred to as the LMC.

5.3 Challenges

Bisaccate pollen grains have the ability to travel large distances by wind or water (Traverse 1988; MacDonald 1996). Therefore, in marine environments, the relative abundances of bisaccate pollen grains increase with distance from the coast seawards and commonly reflect eustatic changes rather than climatic cooling (Moreno et al. 2005). This phenomenon is also known as the Neves' effect (Traverse 1988; MacDonald 1996). Consequently, the high proportion of this group might mask other significant taxa and their importance in the pollen spectra. The same dominance is recorded in taxodiacean pollen grains throughout the Miocene record in Denmark. However, although the *Taxodium* swamp forests were the most dominant component of the vegetation, the extreme dominance of their pollen grains may have been enhanced due to their size, shape, and quantity per parent plant. This is clear when removing the taxodiacean pollen grains from the data sets. As they are removed, one can clearly see that the rest of the taxa in the swamp forest community remain relatively stable throughout the sampled interval, whereas *Taxodium* varies. Thus, the abundances of *Taxodium* are probably to some degree linked to facies.

An example of this is the marked decline in *Taxodium* at the beginning of the Gram Formation. There, only *Taxodium* decreases, not the other swamp forest taxa. Hence, this is not a climatic signal. Instead, it is probably due to the subsidence of the North Sea Basin and a related relative rise in sea level (Rasmussen 2005).

Consequently, the Taxodiacean pollen grains are deposited in a more nearshore environment and taxa from different vegetation types have the possibility to outnumber them in more open marine settings. This interpretation is also supported by the increase in bisaccate pollen grains at the same level as the Taxodiaceae-Cuppressaceae decrease, which is consistent with the mentioned Neves' effect.

A good example of the importance of communicating these problems is at the beginning of the Gram Formation, which included a major facies shift to an open marine environment. This level also coincides with the palynological evidence of climatic cooling. The lowermost part of the Gram Formation commences with a glauconite-rich layer and continues with the deposition of fully marine clay (Rasmussen 2005). This would certainly affect the composition of the palynological associations with an increase in bisaccate pollen grains and lesser occurrences of terrestrial pollen could be expected. However, the facies-related problems are already considered and addressed during construction of the palaeoclimatological data sets. Consequently, there is a marked cooling associated with the Gram Formation and the end of the Serravallian and beginning of the Tortonian in Denmark.

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