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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 15.5–21.1º 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 ($\delta^{18}O/\delta^{16}O$) curves have revealed significant changes throughout the Miocene (Kocsis et al. 2009). Miller et al. (1991) described several major oxygen isotope excursions based on measurments 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-

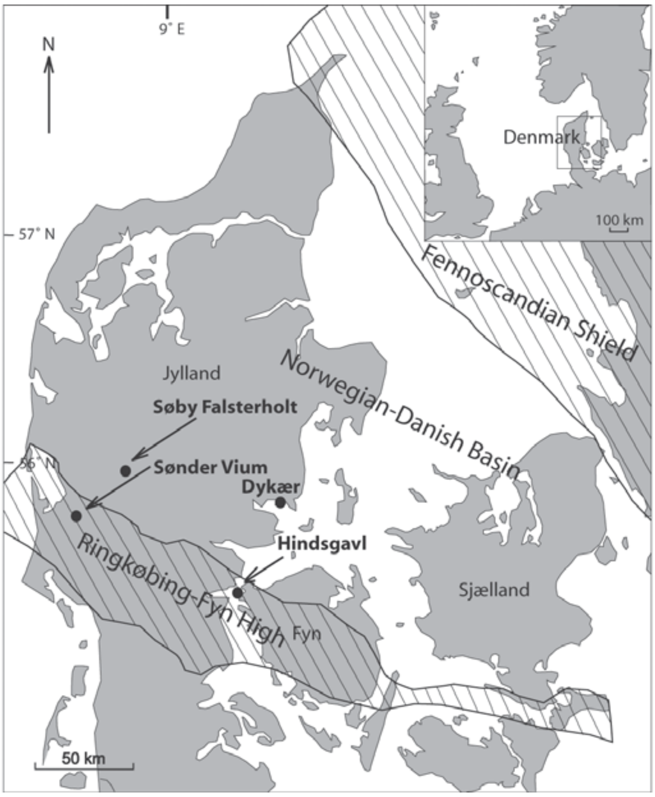

Figure 1. Location of the the Sdr. Vium drill and the outcrop sections in Dykær och Hindsgavl, which have been studied for this PhD-thesis. Included in the figure is also the location of the Søby Falsterholt section, which has previously been comprehensively studied by e.g., Ingwersen (1954), Koch et 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-

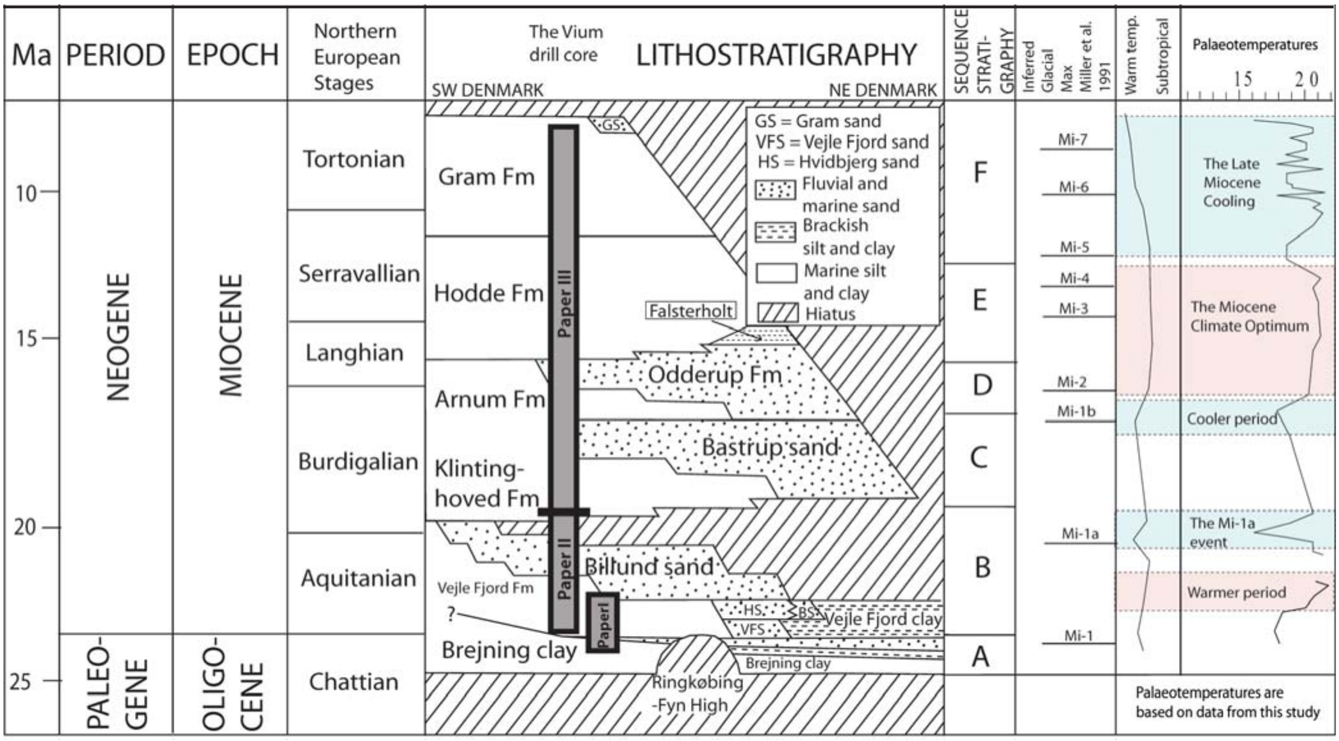

Figure 2. Diagram presenting the Miocene stratigraphy (modified from Rasmussen 2005) in Denmark and the lithostratigrapic extension of the studied sections in this thesis. Included are also the Miocene isotop excursions in comparison with the the mean annual temperatures calculated herein.

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.

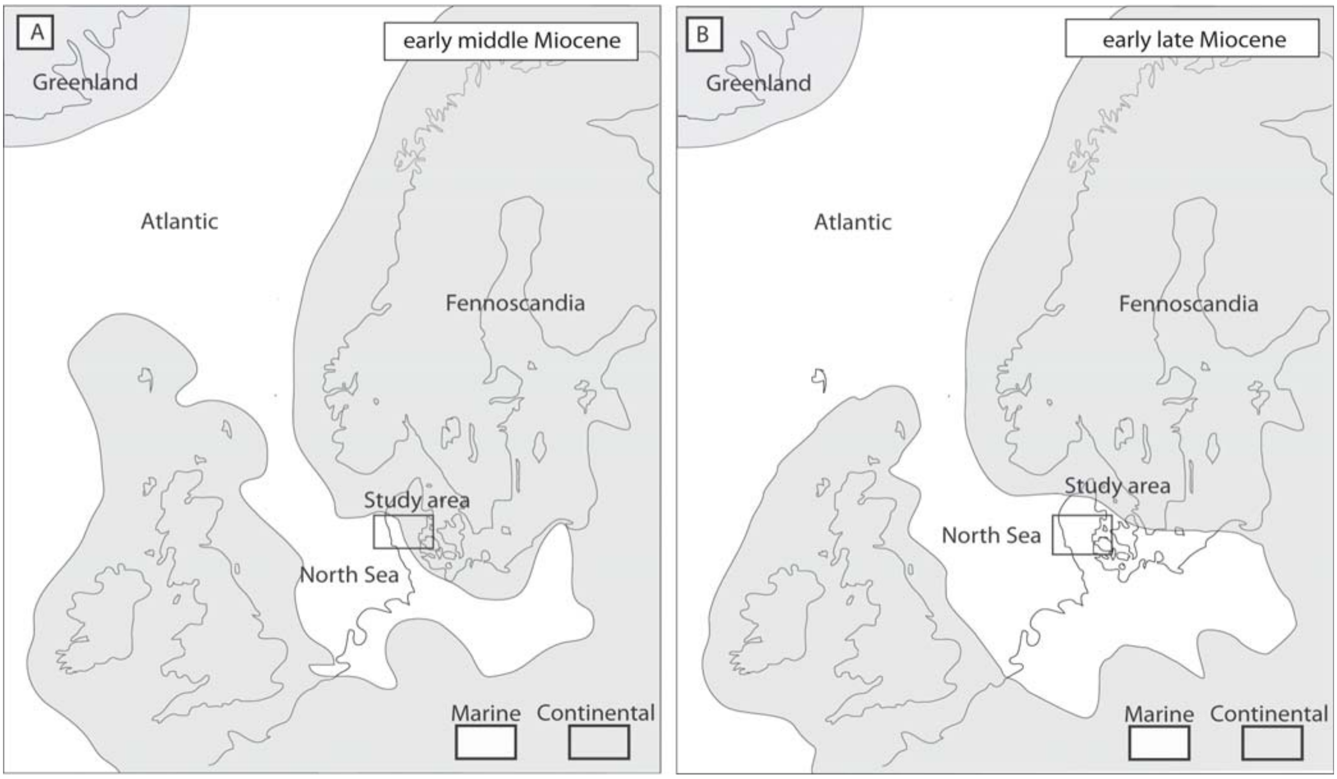

Figure 3. Palaeogeographic maps of A) early middle Miocene (15 Ma) and B) early late Miocene (11 Ma) based on Ziegler (1991) and Rasmussen (2005).

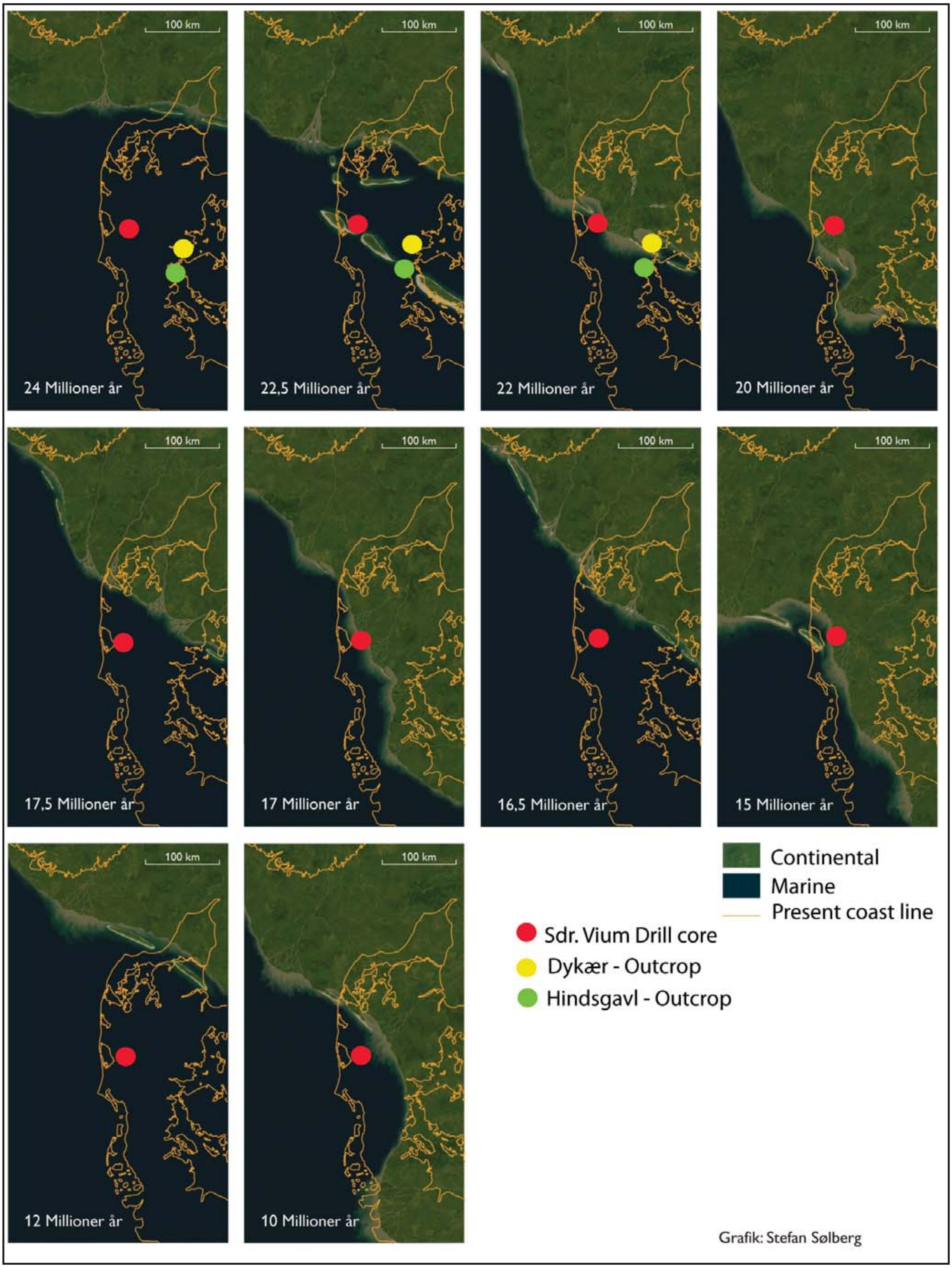

Figure 4. The dynamics of the coast line during the Miocene and the locations of the studied sections in this thesis after Rasmussen (2005). The text in the figures is in Danish and the translation of ”Millioner år” is million years (Ma).

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 charactenized 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 mesophytic 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;

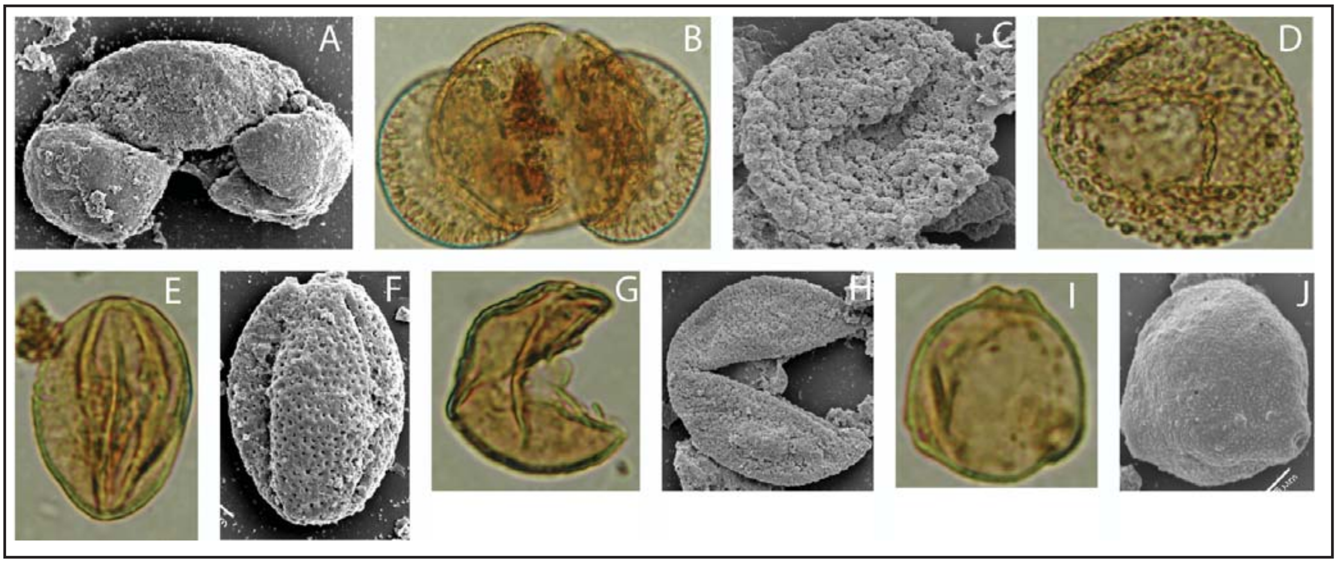

Figure 5. Light micrographs (LM) and SEM-images of A) *Pinus* sp. SEM. B) *Pinus* sp. LM. C) *Sciadopitys* sp. SEM. D) *Sciadopitys* sp. LM. E) *Quercus* sp. LM. F) *Quercus* sp. SEM G) *Taxodium* sp. LM. H) *Taxodium* sp. SEM. I) *Betula* sp. LM. J) *Betula* sp. SEM. All photos are taken at x500.

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 Sachenhofer (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 ”arcto-tertiary” 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 assemblages 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 15.5–20º 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

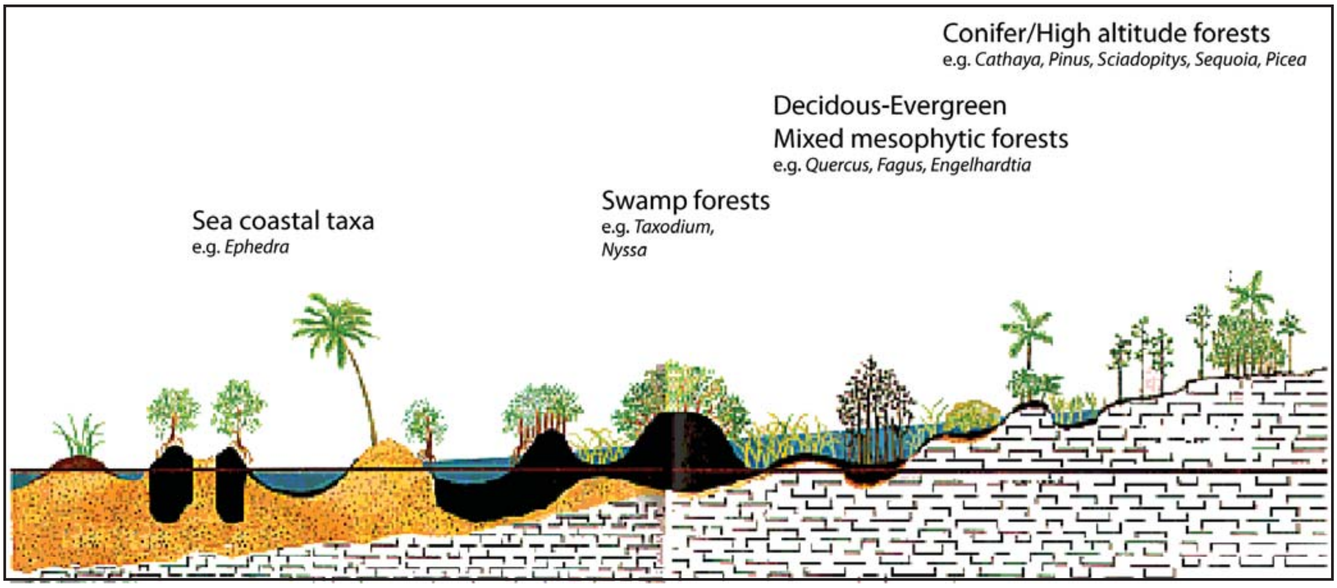

Figure 6. Overview of different palynological palaeoenvironmental assemblages in relationship to the coastline.

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 palaeovegetation 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 15.6–16.6ºC to 16.5–21.1ºC at Dykær, and at Hindsgavl between 13.3–16.6ºC and 16.5–16.6ºC (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 15–17ºC.

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 ºC 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 ºC to 15.5 ºC, 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 ºC to 16 ºC 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 ºC and 27–24 ºC 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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Paper I

Vegetation and climate in the latest Oligocene – earliest Miocene in Jutland, Denmark

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Abstract

Two exposures in Jutland, Denmark, encompassing beds of latest Oligocene to earliest Miocene age (latest Chattian – early Aquitanian) yielded well-preserved palynofloras. The assemblages indicate that Jylland was most probably covered by extensive Taxodaceae 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. Vegetation composition indicates that a warm-temperate climate prevailed in Denmark during the Oligocene–Miocene transition. According to calculations using the Coexistance Approach mean annual temperatures in this timespan were between 15.6–16.6^{o}C. An increase to 16.5–21.1^{o}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 change in palynoflora probably reflects 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.

Keywords: Palaeobotany, palynoflora, climate change, Oligocene, Miocene, pollen, miospores, Denmark

1. Introduction

Climatic variation in the late Oligocene-Miocene have previously been described from the marine realm, via oxygen isotope ($\delta^{18}O/\delta^{16}O$) curves that reveal significant changes in the late Oligocene and early Miocene (20–25.5 Ma). The most prominent of the 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 epoch boundary and major turnovers in both terrestrial and marine taxa (Miller, 1987) and these ecosystem changes were probably the result of global cooling coinciding with the (rapid?) appearance of a full-scale ice sheet on Antarctica (Zachos et al., 2001).

Climate-related changes in the Miocene vegetation in Europe have previously been described, for example, by Mai (1965), Mosbrugger et al. (1994), Ashraf and Mosbrugger (1995), Ashraf and Mosbrugger (1996), Figueiral et al. (1999), Kolcon and Sachsenhofer (1999), and Utescher et al. (2007). However, tying the pollen and spore data from terrestrial environments to international chronostratigraphy has remained problematic. In this study we have been able to correlate our pollen data to the dinoflagellate chronostratigraphy of Dybkjær (2004) and Dybkjær and Rasmussen (2007), thus achieving a better fit between climate change effects and floristic response.

The uppermost Oligocene–Miocene succession in Jutland, (western Denmark) (Fig.1) is represented by a virtually complete sedimentary succession with a well-established chronostratigraphic framework, based primarily on dinoflagellate cyst (dinocyst) studies (e.g., Dybkjær, 2004; Piasecki, 2005; Dybkjær and Rasmussen, 2007; Dybkjær and Piasecki, 2008) and sequence stratigraphy (e.g. Rasmussen, 2004a; Rasmussen and Dybkjær, 2005). Previous investigations of the miospore assemblage and the terrestrial vegetation comprise e.g. Christensen, 1975, 1976, 1978; Friis, 1977, 1979, 1985; Koch, 1989. However, these studies were concentrated on the brown-coal bearing Middle Miocene deposits in the central parts of Jutland (the ”Søby-Fasterholt flora”).

‘Terrestrial’ palynology is a valuable tool for assessing past vegetation and palaeoclimatic patterns but the stratigraphical value of miospore assemblages for the Miocene is limited essentially because all recognized plant genera are long-ranging (since the Eocene: Moreno et al., 2005). As a consequence, quantitative variation might also be taphonomically induced. Therefore, it is of great importance to link the terrestrial palynomorph signal to the marine counterpart, by detailed correlation of terrestrial palynoflora with the dinocyst stratigraphy.

The aims of this study are to:

1) separate the variations in miospore assemblages into those related to climatic change and those related to changes in depositional facies;

2) identify the quantitative shifts in miospore assemblages corresponding to global climatic changes (e.g., Mi-1 glaciation event) across the Oligocene–Miocene boundary;

3) interpret the composition and structure of the latest Oligocene–earliest Miocene vegetation patterns of modern Jutland;

4) interpret the broader floristic responses to climate change through the latest Oligocene–earliest Miocene.

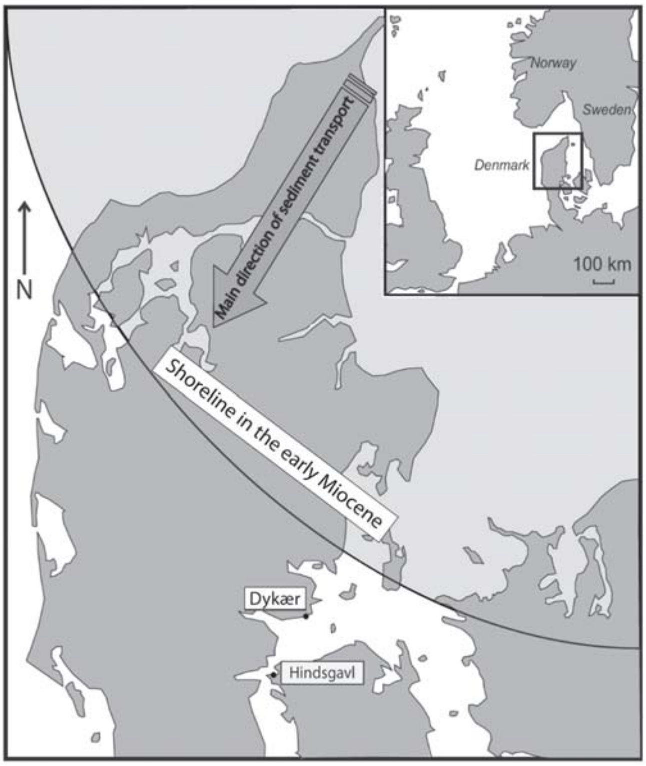


Figure 1. Locations of the studied outcrops in southern Denmark and the approximate trend of the shoreline in the early Miocene.

2. Geological setting

The study area is situated in the eastern part of Jutland, Denmark, which in uppermost Oligocene–lowermost Miocene times was near the eastern border of the North Sea Basin (Fig. 1). The basin has been subjected to several phases of tectonism since the Permian (Ziegler, 1990) and during this time the basin has filled with voluminous sediments of various ages, generating a complex stratigraphic architecture. However, the geological history of the uppermost Oligocene-Miocene sedimentary succession in Jutland is relatively well known. Several studies (e.g. Larsen and Dinesen, 1957; Rasmussen, 1961; Friis et al., 1998, Rasmussen, 1998, 2004a, b; Rasmussen and Dybkjær, 2005) have revealed a complicated interplay between climatic and eustatic sea-level changes and regional and local tectonics in the development of the sedimentary sequences representing this time period.

The uppermost Oligocene–lower Middle Miocene succession in Jutland is characterized by three time intervals with prograding fluvio-deltaic sand wedges, separated by shallow marine mud. The succession dips towards the southwest and has been partially removed by Neogene uplift and erosion (Rasmussen et al., 2006). Consequently, only deposits time-equivalent to the oldest of these sand wedges (the lower Aquitanian Billund sand) are present in the eastern part of the study area.

The complex uppermost Oligocene–lowermost Miocene

Mega-mesothermic elements
- Araliaceae
- Arecaceae
  - *Arecepites*
  - *Monocolpopollenites* sp.
- Potonié, 1934
  - *Sabal*
- *Engelhardtia*
- *Ilex*
- *Myrica*
- *Nyssa*
- *Platycarya*
- *Podocarpus*
- Sapotaceae
- Taxodiaceae-Cupressaceae

Mesothermic elements
- *Acer*
- *Alnus*
- *Betula*
- *Carpinus*
- *Carya*
- *Celtis*
- *Corylus*
- *Fagus*
- *Liquidambar*
- *Liriodendron*
- *Pterocarya*
- *Quercus*
- *Salix*
- *Sciadopitys*
- *Sequoia*
- *Tilia*
- *Ulmus*

Cool temperate plants
- *Abies*
- *Cedrus*
- *Larix*
- *Picea*
- *Pinus*
- *Tsuga*

Herbs and shrubs
- Asteraceae
- *Chenopodipollis* sp.
- *Cyrilla*
- *Ephedra*
- Ericaceae
- Graminae
- *Laevigatisporites* sp.
- *Leiotriletes* sp.
- Lycopodiaceae
- *Osmunda*
- *Plantaginaceae*
- *Retitriletes* sp.
- *Sparganium*
- *Stereisporites* sp.

Freshwater plants
- *Nuphar*
- Nymphaeaceae

Algae
- *Sigmopollis* sp.
- *Botryococcus* sp.

Table 1. The pollen and spore taxa identified in the Dykær and Hindsgavl sections, Jutland, presented as botanical taxa.

succession exposed in eastern Jutland, in the area around Vejle Fjord and Lillebælt, incorporates sediments deposited in an inner neritic setting, comprising marine mud and storm sand layers deposited on the lower and upper shelf, sand deposited in spit systems and tidal inlets, and organic-rich mud and washover sand layers deposited in back-barrier environments. The Ringkøbing Fyn High formed a positive structural element that was very important for the development of the study area (see Rasmussen, 2004a, fig. 7, A to D).

The Dykær and Hindsgavl exposures (Fig. 1) have been studied in detail by Dybkjær (2004) and Rasmussen and Dybkjær (2005). The former study documented dinocyst assemblages that dated the exposures and allowed correlation with a series of other exposures and with beds in several boreholes in Jutland. The latter was a combined sedimentological and palynofacies study that formed the basis for a detailed sequence-stratigraphic interpretation.

The Dykær exposure presents a succession referable to the dinocyst zones *D. phosphoritica*, *Chiropteridium galea* and *Homotryblium* spp. (Dybkjær and Piasecki, 2008). The first zone is referred to the latest Chattian (latest late Oligocene) and the two latter to the early Aquitanian (earliest Miocene). Within the sequence stratigraphic framework for the Danish uppermost Oligocene–Miocene (Rasmussen, 2004; Rasmussen and Dybkjær, 2005) the Dykær exposure is referable to the upper part of Sequence A and most of Sequence B.

The lowermost part of the studied succession, the lower part of Sequence A, 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 and Dybkjær, 2005).

Changes in foraminiferal- and palyno-facies indicate a shallowing trend in the upper part of Sequence A. Cessation of glauconite formation indicates an increase in sediment supply and a high siderite and goethite content might indicate a brackish water environment or even subaerial exposure. The development of brackish conditions is interpreted as having resulted from a combination of the topography of the Ringkøbing-Fyn High and a eustatic sea-level fall. The increase in sediment supply seen in the upper part of the sequence represents a phase of major sedimentary wedges prograding from the Fennoscandian Shield during the early to early middle Miocene.

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 and Dybkjær, 2005; Dybkjær and Rasmussen, 2007). The Hindsgavl exposure represents a lower Aquitanian succession referable to dinocyst zones *Chiropteridium galea* and *Homotryblium* spp., both referred to the early Aquitanian (earliest Miocene) (Dybkjær, 2004). This section represents a part of Sequence B with a more distal setting than Dykær. A distinct increase in the relative abundance of dinocysts in the samples from 3.23 to 5.00 metres has been interpreted as reflecting a maximum flooding surface, which is also present in Dykær from samples at 10.80 to 15.35 metres (Dybkjær, 2004) (also see Fig 4 herein).

The two exposures thus partly overlap but represent different environmental settings, with Hindsgavl being more distal than Dykær.

3. Methodology and approach

3.1 Sampling, preparation, counting and identification

The samples were collected in 2004 at the Dykær and Hindsgavl exposures (Fig. 1). These sedimentary sequences have been dated based on dinocyst stratigraphy (Dybkjær and Rasmussen, 2000; Dybkjær, 2004; Rasmussen and Dybkjær, 2005) and in order to tie our terrestrial vegetation data to the chronostratigraphic framework, the sampling was performed at the same levels as that previous study. All the samples were processed at the Geological Survey of Denmark and Greenland (GEUS). The samples were prepared using standard palynological methods with HCl, HF, HNO_3 then sieved through a 11

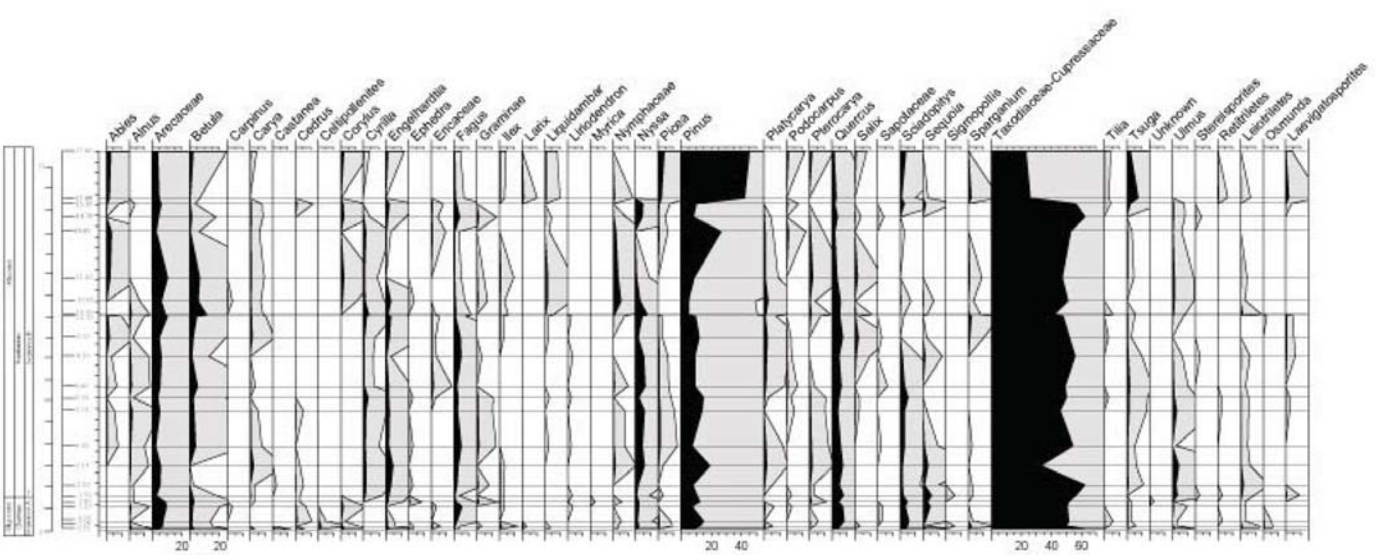


Figure 2. Detailed pollen diagram from the studied outcrop at Dykær.

µm mesh (Poulsen et al., 1990). At Dykær, 23 samples were collected from an interval of 17.65 metres long and at Hindsgavl eight samples were collected covering 3.55 metres of the profile. Strew slides were made in glycerin gelantine and approximately 300 pollen and spore specimens from each sample were counted in a light microscope. In addition, the ratio between marine and terrestrial palynomorphs (dinocysts versus spores and pollen) was counted separately to provide information regarding the depositional environment and in order to interpret whether observed palynological changes are related

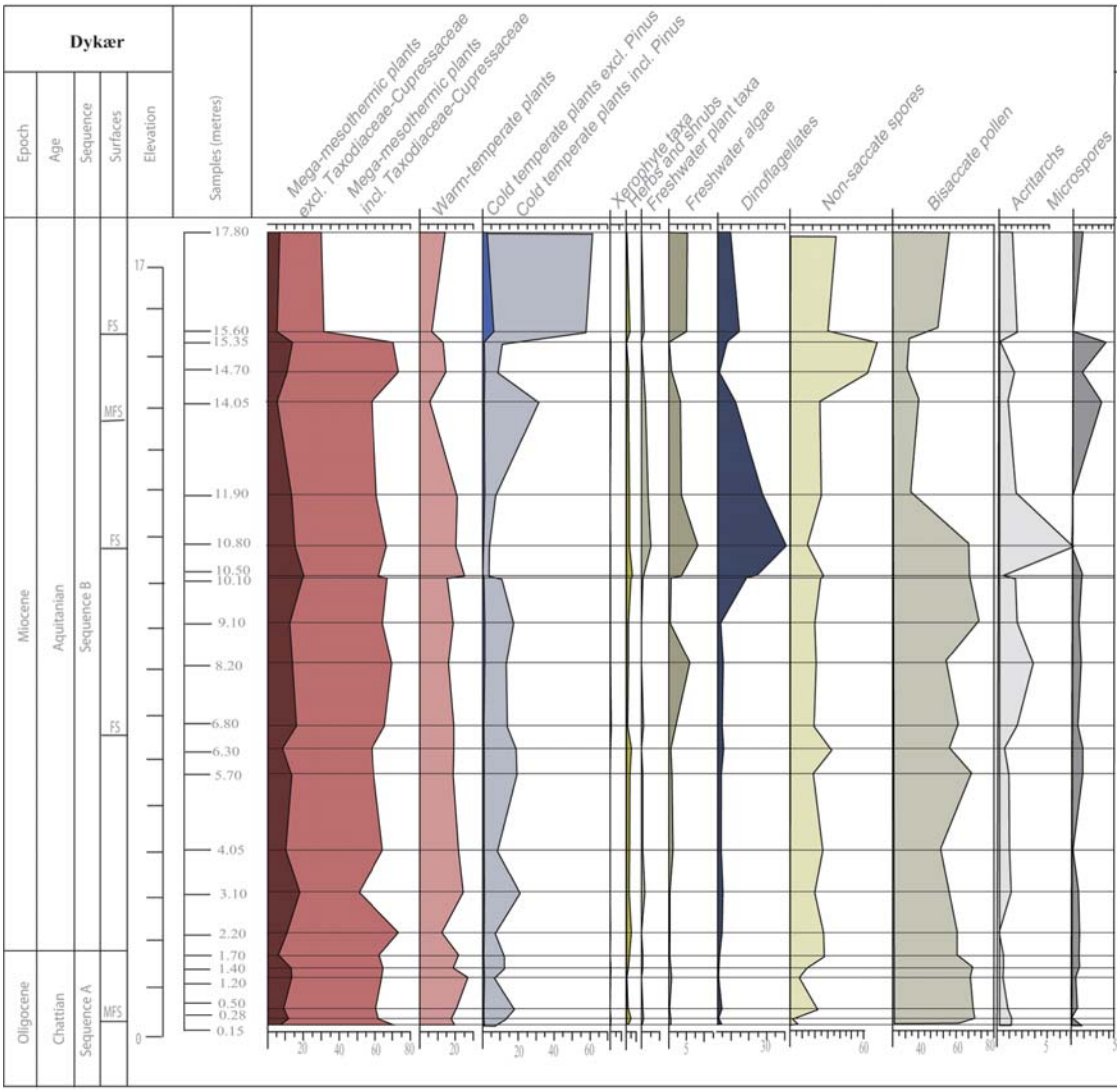


Figure 4. Diagram presenting the percentages of the eco-climatological groups at Dykær and Hindsgavl. The mean annual temperatures (MAT) in Denmark during the latest Oligocene to early Miocene calculated by the Coexistence Approach (Mosbrugger and Utescher, 1997).

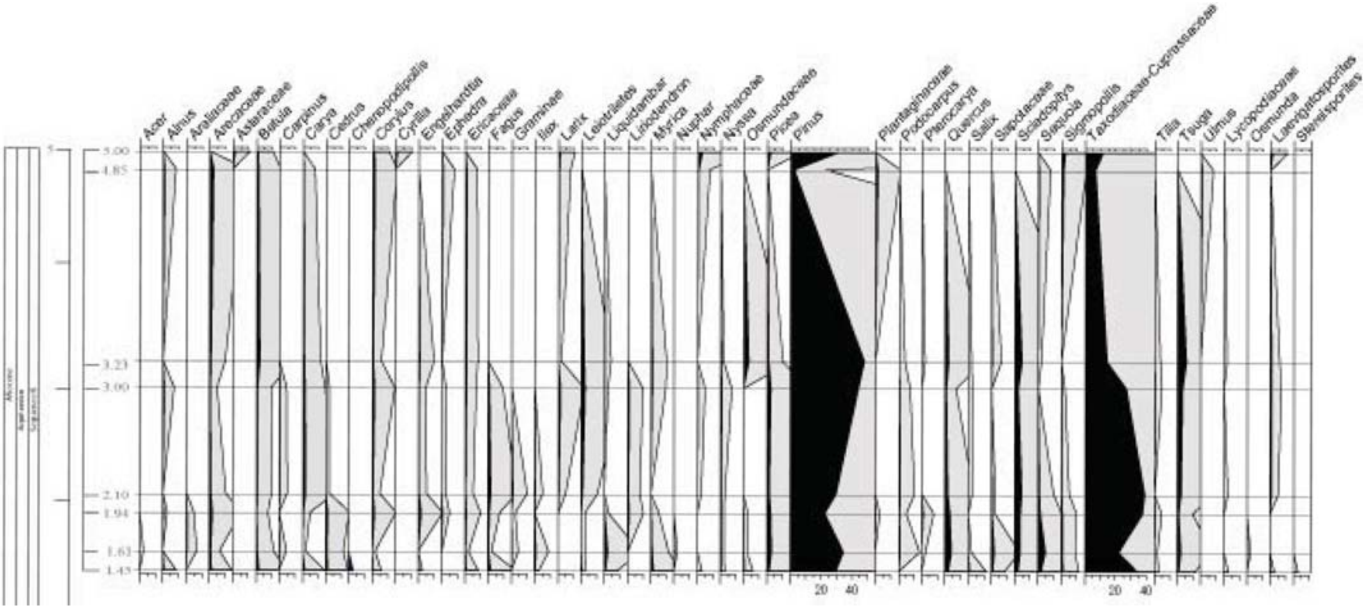
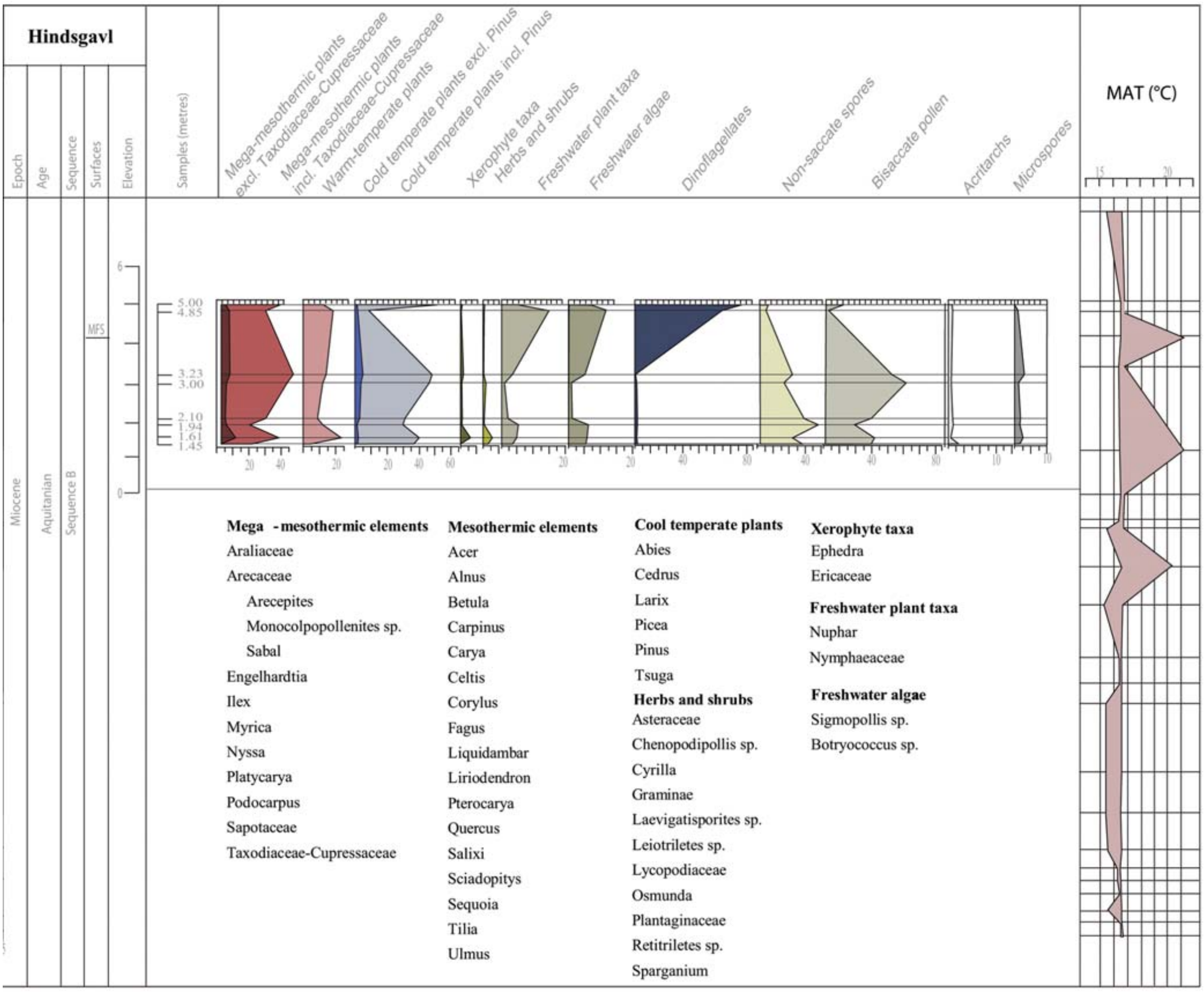


Figure 3. Detailed pollen diagram from the studied outcrop at Hindsgavl.

to climate, or induced by sea level changes. Counts of dinoflagellate cysts and the freshwater algae *Botryococcus* have been used primarily as a tool to assess marine or freshwater influence. Dinocysts have not been taxonomically identified in this study. As a complementary tool some pollen grains were also studied and photographed in a scanning electron microscope (SEM).



3.2 Palaeoenvironmental analysis

In order to interpret the palaeoenvironment, the pollen and spores have been assigned to botanical groups (Table 1, Figs 2, 3) based on their extant genera. The groups are modified after Moreno (2005), Kolcon and Sachenhofer (1999), and Larsson et al. (2006) (Table 1, Fig. 4). All pollen and spores recorded in this study have been assigned to plant groups that are based on modern eco-climatologically tolerances in order to reconstruct the Oligocene–Miocene vegetation. However, it must be remembered that these groups are artificial and some of the taxa included might have originally been present in several different ecological environments.

Some assemblages are strongly dominated by families Taxodiaceae-Cupressaceae (T-C). Additionally *Pinus* pollen might have been influenced by exceptional transport and dispersal mechanisms depending on the morphology of the pollen grains. In any case, the high proportion of these groups in some samples masks other significant taxa and their importance in the pollen spectra. Thus, the Taxodiaceae-Cupressaceae and *Pinus* spp. have been excluded in alternative data sets (Fig. 4) in order to illustrate the quantitative changes within the other taxa.

Due to the difficulties in distinguishing between *Taxodium* and *Glyptostrobus* and certain other Cupressaceae in a light microscope these taxa are both counted as Taxodiaceae-Cupressaceae (Kunzmann et al., 2009). However, we also examined samples in the SEM in an attempt to discover the differences which were not visible in the light microscope.

Sequoia is not included in counts of the Taxodiaceae-Cupressaceae because they are more easily distinguished from other taxa in the family and the genus thrives in well-drained or elevated environments, in contrast to *Taxodium*. In the results we included *Monocolpopollenites* sp. to Arecaceae.

3.3 Palaeoclimate and palaeotemperature analysis

In order to interpret the latest Oligocene and early Miocene climates of Denmark, we have applied the Coexistence Approach (Mosbrugger and Utescher, 1997). This method is based on the assumption that the fossil plant taxa found in Neogene sediments have similar climatic requirements as their nearest living relatives. The analysis aims to find the climatic interval in which all fossil taxa could exist. In this study we have only focused on the variation in mean annual temperature (MAT) (Fig. 4).

4. Results

4.1 Palynology Dykær

All 23 samples from the Dykær section contain pollen, spores, freshwater algae and dinocysts (Fig. 2, Appendix 1, Plate 1). Of these, 52 mostly well-preserved pollen, spore and freshwater algae taxa are identified (Appendix 1). Reworked palynomorphs are rare. Spores constitute at most 2.5 % of the total miospore sum and are represented by four taxa, *Baculatisporites* sp., *Retitriletes* sp., *Leiotriletes* sp. and *Stereisporites* sp. The assemblages are overwhelmingly dominated by gymnosperm pollen, comprising 57–80% of the total miospore sum, and particularly by Taxodiaceae-Cupressaceae, varying between 26% and 63% in relative abundance. Other conifers that are also present in all samples include: *Pinus* (2–19%), *Pinuspollenites microalatus* (up to 32%), *Sciadopitys* (up to 6%) and *Picea* (up to 4%). Angiosperm pollen constitutes a relatively large portion of the assemblages 14–37%. Palm pollen (family Arecaceae) are encountered in all samples and constitutes up to 10% in some samples (e.g. *Monocolpopollenites* spp. 1–7%, *Sabal* up to 4% and *Arecepites* up to 3%). *Betula* (1–11%), *Quercus* (1-7 %), *Fagus* (up to 5%) and *Nyssa* (up to 8%) are other angiosperms represented in all samples. Finally, the freshwater algae *Botryococcus* has a relative abundance reaching up to 8%. The ratio between marine and terrestrial palynomorphs reveals that the assemblages in all samples are dominated by terrestrial elements and that the relative abundance of dinoflagellates varies considerably (1–35%).

4.2 Palynology Hindsgavl

The eight samples collected in Hindsgavl contain 43 pollen, spore and freshwater algae taxa (Fig. 3, Appendix 2). The spores make at most 2% of the total miospore sum and are represented by *Baculatisporites* spp., Lycopodiaceae, Osmundaceae and *Stereisporites* spp. All samples are dominated by gymnosperms (41–81%). These are mostly Taxodiaceae-Cupressaceae (15–43%) and *Pinus* (9–54%). Other relatively common taxa are *Sciadopitys* (up to 5%) and *Tsuga* (up to 6%). In nearly all samples the angiosperms constitute approximately 20% and are represented by e.g. *Alnus, Quercus* and *Fagus*. Taxa representing the family Arecaceae are present in all samples except in the sample at 5.0 metres. The freshwater algae *Botryococcus* is present in all samples and has a relative abundance between 2–17%.

5. Palaeoenvironmental and climatic interpretations

5.1 Palaeoenvironment

The pollen and spores can be divided into different groups depending on their eco-climatical preferences. Seven groups, mega-mesothermic taxa, warm-temperate plants, cool-temperate plants, aquatic/freshwater plants, herbs and shrubs, xerophytes and freshwater algae (*Botryococcus)*, are modified after Moreno (2005), Kolcon and Sachenhofer (1999), and Larsson et al. (2006) (Table 1, Fig. 4).

The Mega-mesothermic group consists of taxa that have recent distributions in subtropical climates being evergreen species well adapted to a humid climate with high mean annual temperatures, in the range 14–27°C.

The mesothermic (warm-temperate) taxa mainly consist of deciduous trees, such as *Quercus*, that are typical in mixed forests for example, in central Europe. The mean annual temperature range of these taxa varies markedly but most have ecolo-

Plate 1. 1. *Alnus,* 2. *Betula,* 3. *Betula,* 4. *Engelhardtia,* 5. *Corylus,* 6. *Carya,* 7. *Pterocarya,* 8. *Quercus* sp. 1, 9. *Quercus* sp. 2, 10. *Quercus* sp. 3, 11. *Monocolpopollenites* sp.1, 12. *Monocolpopollenites* sp.2, 13. *Taxodium*, 14. *Monocolpopollenites* sp.3, 15. *Fagus,* 16. *Tilia,* 17. cf. *Nyssa,* 18. *Sequoiapollenites* sp., 19. *a Lycopodium*. 19b. *Stereisporites* sp., 20. Taxodiaceae-Cupressaceae, 21. *Salix,* 22. *Botryococcus,* 23. *Botryococcus,* 24. Taxodiaceae-Cupressaceae , 25. *Sciadopitys,* 26. *Pinuspollenites microalatus,* 27. *Pinus* and 28. *Tsuga*

gical preferences today spanning 4–23°C.

The group consisting of cool-temperate plants have temperature tolerances from several degrees below 0° to 27.4°C. Their broad temperature range complicates their use as climate indicators. Most of the taxa within this group are gymnospermous bisaccates that prefer living in drained and/or upland areas. The morphology of the bisaccate pollen grains makes them difficult to use as climate indicators since they 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 seaward distance to the coast (Moreno, 2005).This phenomenon is also known as the Neves effect (MacDonald, 1996). Consequently, these microfossils commonly reflect eustatic changes rather than climatic cooling. The aquatic/freshwater plant group indicates the existence of freshwater environments and has no significance for climatic interpretation.

Herbs and shrubs include pollen and spore taxa from plants

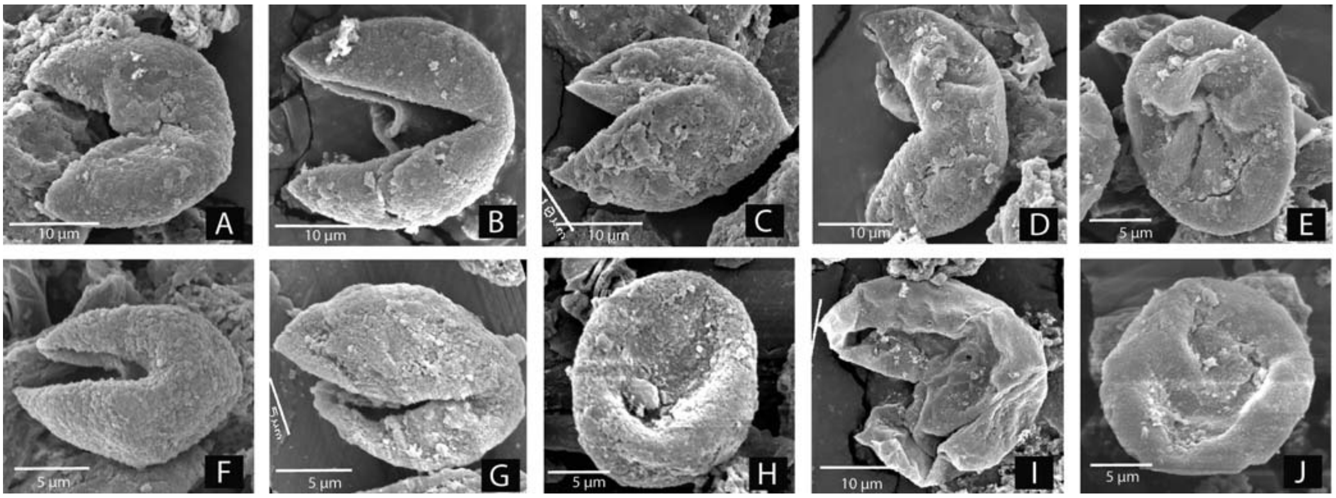


Plate 2. A. Taxodiaceae, B. Taxodiaceae, C. Taxodiaceae, D. Taxodiaceae, E. *Taxodium*, F. *Taxodium*, G. Taxodiaceae, H. Taxodiaceae, I. cf. *Juglans* and J. cf. Juglandaceae

representing the understory vegetation at the depositional site. Present in this group are both pteridophytes and grasses. Nevertheless, they are not used as temperature indicators since they are known to have wide ecological preferences.

The last parameter for interpreting the palaeoenvironment and climate is freshwater algae. The only taxon of the latter recorded in this study is *Botryococcus,* which is used as an indication of freshwater influx in marine environments (Guy-Ohlson, 1992). *Botryococcus* has the ability to live under both brackish and marine conditions, although not as successfully as in lacustrine freshwater environments. Here, we use it as an indication of freshwater influx and not as a temperature indicator since the algae occur in tropical to subarctic climates (Guy-Ohlson, 1992).

5.2 The Coexistence Approach and palaeotemperatures

The coexistence approach (CA), based on the nearest living relative philosophy, was introduced by Mosbrugger and Utescher (1997). It aims to reconstruct ranges, which are tolerated by all of the nearest living relatives of the fossil plant taxa found in the samples. In this work the CA is used partly as an additional input on climate, and partly as a controlling method because of the uncertainties in the grouping based on the ecology of extant taxa. For the samples taken from Dykær, mean annual temperature from 15.6 to16.6°C and 16.5 to 21.1°C, and at Hindsgavl from 13.3 to 16.6 and 16.5 to 16.6°C (Fig. 4). Only minor changes in the miospore assemblage are evident across the Oligocene–Miocene boundary. The sampled interval indicates increased mean annual temperatures up section.

6. Discussion

6.1 *The Oligocene-Miocene vegetation of Jutland, Denmark*

The palynological records from the Dykær and Hindsgavl exposures imply that the Jutland region of Denmark was covered by widespread Taxodiaceae swamp forests in latest Oligocene to earliest Miocene times. Beside Taxodiaceae-Cupressaceae, which are overwhelmingly dominant, other plants common in these swamps were *Alnus*, *Nyssa*, *Betula*, *Salix*, *Cyrilla* and *Myrica*. All these trees and shrubs are well adapted to swamps and grow well under more or less flooded conditions in the bald cypress swamps in the southeastern parts of present day North America (Zetter, 1998). Since identification with the light microscope did not establish the difference between *Glyptostrobus* and *Taxodium* several specimens from the T-C family were examined in the SEM (Plate 2). However, only *Taxodium* and pollen referable to Taxodiaceae-Cupressaceae were present.

The abundance of swamp forest taxa stay relatively stable throughout the Dykær section (42–69% Taxodiaceae-Cupressaceae, Fig 4). However, an abrupt decrease occurs in the two uppermost samples where the swamp forest taxa constitute no more than 26% of the registered taxa. The change in the palynological assemblage can be correlated to the more distal setting of Hindsgavl, where the swamp forest taxa drop from 30% to 19% (Fig.4).

Taxodiaceae pollen are also abundant in samples from contemporaneous sediments from Greenland and Ellesmere Island where taxoidiacean macrofossils were also identified (Manum, 1962). However, Manum (op. cit) also concluded that difficulties exist in classifying pollen within this family, representatives of which live in different ecological habitats. *Taxodium* grows in swampy, seasonally flooded environments, whereas many Cupressaceae species grow in elevated, well-drained habitats. The absence of *Glyptostrobu*s may be due to differences which were not visible in the light microscope. Nevertheless no certain *Glyptostrobus* were identified in the SEM either.

Deltaic swamp forests are commonly subjected to mixing of freshwater from fluvial systems and sea water from tidal or intertidal processes (Kunzmann et al., 2009). Thus, brackish water often prevails in these swamps. In the deltaic ponds and lakes brackish-tolerating algae, such as *Botryococcus*, are common. Pollen from *Nymphaea* implies that there were extensive quiet freshwater habitats in the region and the Danish Miocene Taxodiaceae swamp forests were probably an analogue to the modern River Mississippi deltaic forests.

The zonal vegetation further inland obviously consisted of a mixed forest. Most common in these forests were warm to temperate angiosperms such as *Fagus* and *Quercus* associated with thermophilic taxa such as *Engelhardtia* and Arecaceae. In elevated and/or better drained areas conifers such as *Pinus, Sequoia, Abies* and *Picea* dominated the vegetation, evident from the pollen record.

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), Germany (Mai, 1965, 1995; Zetter, 1998; Kolcon and Sachsenhofer, 1999; Kovar-Eder et al., 2001; Kunzmann et al. 2009), Austria (Zetter, 1998) and Slovakia (Kovacova and Sitar, 2007) but there are subtle differences. In central Europe the Taxodium-Nyssa vegetation was also flourishing in lowland riparian environments during Oligocene and Miocene (Kunzmann et al., 2009). However, the presence of diverse dinoflagellate cyst assemblages, and tidal sediments, in all samples from both Dykær and Hindsgavl confirms a near marine environment.

A majority of the samples from Greenland and Svalbard are dominated by pollen derived from conifers, especially Taxodiaceae-Cupressaceae (Manum, 1962), which agrees with the Danish assemblages studied herein. *Pinus* pollen were also common at all localities examined by Manum (1962). He interpreted the coniferous forests as an hinterland flora. Similar coniferous assemblages are present in this study. However, most of the coniferous taxa probably grew in better drained lowland areas further in land. Manum's results from Svalbard and Greenland indicate temperate conditions in contrast to the palynofloras from Denmark (this study), which instead indicate warm temperate to mesothermal vegetation.

Palynological results from Germany indicate a warm temperate to subtropical climate during the Miocene (Zetter, 1998; Kolcon and Sachsenhofer, 1999; Kovar-Eder et al., 2001). The Miocene pollen assemblages from Slovakia, like Germany, are more southerly and continental compared to Denmark, Iceland, Svalbard and Greenland and are dominated by taxa derived from mixed broad-leafed 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* are recorded frequently, which indicates less expressed seasonality (Kunzmann, 2009), which is indicated by also indicated by several taxa from Denmark (e.g. Cathaya, Engelhardtia).

Pollen originating from Pinaceae are not restricted to upland vegetation only, and most of the taxa found in our present study are probably derived from mixed hardwood swamp forests. However, pollen from conifers that grew in elevated areas are also present, both in Denmark (e.g. *Tsuga*), Slovakia (Kovacova and Sitar, 2007) and Bulgaria (Ivanov et al., 2002). These taxa probably grew in the area of modern day Sweden and Norway, according to palaeogeography and direction of sediment transport (Fig 1). No information regarding the palaeolatitudes in the hinterland areas has been found but the elevation was probably less than 500 m above sea level (Anders Lindh, pers comm.).Consequently, Dykær and Hindsgavl preserve a flora from a warm temperate climate incorporating a mix of zonal mixed forests with a minor percentage of evergreens and azonal vegetation and components from more distant stands. Several other parameters have influenced the composition of the Danish assemblages apart from climate. The deltaic setting of the Danish strata has led to a significant marine influence and greater taphonomic sorting compared to the more continental setting and local vegetation sources of the German assemblages.

6.2 Miospore assemblages compared to depositional facies

An abrupt change in composition in the uppermost samples at Dykær (14.05 m and above) and Hindsgavl (4.85 m and 5.00 m) is probably due to a greater marine influence associated with a maximum flooding surface (MFS), indicated by sequence stratigraphy (Dybkjær, 2004) and changes in palynofacies (Dybkjær, 2004; Rasmussen and Dybkjær, 2005). The MFS has been correlated between the two exposures and occurs below sample 14.05 m in Dykær, and below sample 4.85 m in Hindsgavl (Fig. 4). Near and above the MFS the predominance of Taxodiaceae-Cupressaceae is replaced by an abrupt increase in gymnospermous bisaccates such as *Pinus*. This level also indicates the highest MAT throughout the sampled interval.
If pollen abundances alone are considered, this might be interpreted as an indication of a rapid cooling event or a better drained and more elevated depositional environment. However, these samples are strongly enriched in dinoflagellates and *Botryococcus* (Fig. 4) reflecting a shift towards a more distal (marine) facies, which might be the result of a global warming followed by a rising sea level. As the transgression proceeded large and dense palynomorphs, which are more difficult to transport, become scarcer in these increasingly marine-influenced strata. Consequently, there is an over-representation of those palynomorphs that can travel large distances such as bisaccate pollen grains (MacDonald, 1996). The decrease in taxodiacean pollen at these levels does not exclude the possibility of *Taxodium* forests still existing further inland, only that their pollen was deposited closer to the shoreline.

6.3. Palaeoclimate proxies and correlation to the Mi-1 event (Oligocene/Miocene boundary)

In the samples taken from Dykær, the mean annual temperature estimates vary between 15.6–16.6°C to 16.5–21.1°C, and in Hindsgavl between 13.3–16.6°C and 16.5–16.6°C based on the pollen associations (Fig. 4). These temperature estimates 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.
Mosbrugger et al. (2005) proposed a cooling connected to the Mi-1 event based on megafloral change in central Europe. Surprisingly, our study revealed minor changes in the miospore assemblages across the Oligocene–Miocene boundary and the Mi-1 event and a slight drop in MAT (Fig. 4). However, we interpret the lower part of the studied succession in Dykær to

represent sediments deposited *within* the cold time-interval of the Mi-1 period and the temperature drop connected with the deterioration at the beginning of Mi-1 had probably already begun. At the same time, the stable temperatures discerned across the Oligocene–Miocene boundary in this study might reflect a dampening of the change signal induced by the ameliorating effects of the maritime setting.

The results point towards an amplified mean annual temperature in the upper parts of the sampled sections at Dykær and Hindsgavl from the level at 8.20 metres in the Dykær section. This warmth seems to be stepwise and is expressed in the palynofloras by both vegetation and facies changes. The first increase in temperature coincides with higher abundances of dinoflagellate cysts and a minor increase in mega-mesothermic plant taxa. The following step at 14.95 metres is marked by a more abrupt increase of mega-mesothermical plant taxa (Fig. 4). The temperature increase estimated in the top of the sampled interval coincides with the abruptly higher abundances of dinoflagellates in Hindsgavl (4.85m) and an influx of bisaccate pollen in Dykær (15.35–15.60m).

The first warming is interpreted as a response to the beginning of a transgressional phase, which explains the sudden pulse of dinoflagellate cysts (Fig. 4). This is followed by a high sea level stand marked by the MFS visible in both Dykær and Hindsgavl. At this time the most seaward depositional settings are expressed in the sampled sections. Consequently, the dominant pollen are those prone to travel great distances by wind or water. In this case the change is reflected by the unexpected predominance of bisaccate pollen in sample 15.6 m in Dykær and sample 3.00 m in Hindsgavl. Despite the influx of what would normally be considered cool temperate plants, this time interval is the warmest in the sampled section, at least in Dykær. This contradiction would have been difficult to interpret without the detailed sequence stratigraphic framework and temporal controls provided by dinoflagellates, which underpin this study.

7. Conclusions

When separating the palynological results into groups, based on their preferences in temperature, the results from Dykær strikingly reveal dominance by plants that are mega-mesothermic. In contrast to Dykær, the Hindsgavl pollen spectrum generally indicates a predominance of cool temperate plants (when including bisaccates). This distinct difference between the miospore assemblages from the two localities (with higher relative abundances of bisaccate cool temperate pollen) from Hindsgavl, is probably due to different depositional environments, with Hindsgavl being the most distal. Excluding bisaccates from the datasets reveals that dominant groups remain the mega-mesothermic and warm temperate plants.

The pollen spectra indicate a warm-temperate climate with Taxodiaceae swamp forests covering the coastal areas of Denmark during the latest Oligocene and earliest Miocene. Further inland, mixed forests with angiosperms such as *Fagus* and *Quercus* prevailed, and thermophilic elements such as *Engelhardtia* and Arecaceae were also common.

The Arecaceae was also confirmed by Mosbrugger et al. (1994) as a common element in peat-forming vegetation in Germany during the Miocene. Conifers such as *Pinus, Sequoia, Abies* and *Picea* probably dominated the vegetation in elevated and/or better-drained areas.

Mean annual temperatures in late Oligocene and early Miocene were between 15.6–16.6°C to 16.5–21.1°C based on the quantitative palaeoclimate reconstruction using the Coexistence Approach. The first temperature interval probably reflects global cooling associated with climate change at the Oligocene–Miocene boundary followed by a warmer period, as indicated by the warmer interval. The latter is possibly reflecting a warmer global climate which may also have resulted in melting ice caps on Antarctica and a global sea level rise. This sea level rise is also responsible for the increase in dinoflagellate cysts and bisaccate pollen grains that coincides with the increased MAT in Denmark during the early Aquitanian.

The present study is an example of how immediate changes in local depositional setting can influence the miospore-assemblage much more than global climatic changes. The distinct increases in cold-temperate pollen seen at both exposures are related to a transgression (actually interpreted to result from a global warming) rather than a general climatic change towards colder conditions.

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Dykaer Elevation (m)	0.15	0.28	0.50	1.20	1.40	1.70	2.20	3.10	4.04	5.70	6.30
Swamp forest											
Taxodiaceae-Cupressaceae	63,1	50,2	51,4	50,5	51,6	56,4	62,2	33,2	54,3	45,8	49,9
Nyssa	0,9	2,2	1,1	2,3	2,0	0,9	1,9	6,0	4,3	5,8	2,2
Betula	3,0	1,5	1,4	2,0	3,1	1,8	0,3		3,8	2,9	2,4
Alnus	1,8	0,9		1,3	0,3	0,3	0,3	1,3	1,0	2,1	0,3
Salix		0,3								0,3	0,3
Cyrilla						1,2	1,9	1,9	1,0	1,6	3,0
Myrica			0,0		0,3						
Total percentage	68,8	55,1	53,9	56,1	57,2	60,6	66,5	42,4	64,4	58,4	58,1
Cool temperate forest ass.											
Abies									0,8	0,5	
Larix		0,3									
Tsuga				0,3	0,3		1,1	0,6	0,5	1,3	1,3
Tsuga (Zonalapollis)		0,6	0,3								
Pinus	5,4	8,3	8,3	2,3	4,5	2,7	5,1	12,3	3,8	5,2	6,2
Pinuspollenites microalatus		1,8	4,3	6,4	5,2	8,2	7,9	2,7	6,6	3,5	8,6
Carya	0,3				0,3	0,3	0,3	2,2	0,8	0,5	
Picea		0,9	0,8			0,3		0,3	1,3	1,0	0,8
Pterocarya		0,3	0,6		1,1	0,3	0,3	1,6	1,3	1,0	1,1
Quercus	3,6	2,5	5,6	5,9	4,0	7,3	4,3	7,0	5,6	3,7	4,0
Corylus	2,1	1,2	0,3	1,6	0,8						
Fagus	0,3	0,3	1,7	5,2	1,4	0,3	1,9	2,8	4,5	2,1	3,0
Ulmus	0,9	0,3	0,3	0,3		3,3	2,4	4,1	0,3	2,9	1,6
Tilia		0,3	0,6								0,3
Sequoia	1,8		1,7	4,9	2,8	5,8	1,1	3,5	1,0	0,3	
Liquidambar	0,3	0,3							0,3		0,3
Cf. *Fagus*					0,3						
T. microhenrici	0,3										
Carpinus				0,3							
Total percentage	16,8	19,7	26,4	26,2	23,8	28,2	18,9	41,1	23,5	27,2	27,2
Warm-temperate plants											
Arecaceae		2,2	2,8	2,6	1,7	0,3	0,5		0,5	0,3	
Engelhardtia	2,4	0,6	0,6		1,1	1,5	2,9	4,4	1,5	2,1	1,6
Cedrus	0,6		1,1	0,7	0,3	0,3	0,5	0,3		0,5	
Ilex		1,2		0,3	0,3	0,3	0,3	0,3			
Monocolpopollenites sp.	3,6	3,7	4,4	6,6	6,8	2,7	4,8	5,7	2,3	3,9	3,0
Podocarpus				0,3		0,3				0,5	0,3
Platycarya		0,6		0,7			0,5	1,6	1,3		0,3
Tricolporopollenites cingulum		1,2						0,3			
Tricolporopollenites fusus				0,7							
Tricolporopollenites pusillus			0,9	0,8	0,3		0,3	0,3			0,3
Sabal	0,3	1,2		0,3	0,8					1,0	1,1
Sapotaceae			0,3	0,3					0,3		
Zelkovaepollenites	0,6			0,7				0,3			
Liriodendron				0,3		0,3			0,3		0,3
Sciadopitys	3,3	4,6	5,6	3,3	4,8	1,8	1,3	1,6	3,0	2,9	5,1
Ephedra	0,3	0,3			0,8		0,3		0,3		0,3
Total percentage	12,3	15,4	15,6	17,0	16,7	7,9	11,7	14,2	9,3	11,5	12,4
Mesophytic understorey plant ass.											
Ericaceae		0,6		0,3							0,3
Leiotriletes sp.	1,2	1,2	0,3	0,3	0,3	0,9	1,9	0,6	0,5	0,5	0,5
Stereisporites sp.						0,3					
Retitriletes sp.			0,3			0,3				0,3	0,3
Baculatisporites sp.	0,6	0,6	0,6								
Total percentage	1,8	2,5	1,1	0,7	0,3	1,5	1,9	0,6	0,5	0,8	1,1
Aquatic plants											
Graminae		0,3			1,4		0,8		1,3	1,0	1,1
Sparganium		2,2	0,3			0,3	0,3		0,3		
Nuphar											
Nymphhaeae	0,3	0,3	0,6		0,6			1,6	0,8	0,8	
Sigmopollis		0,6				0,6					
Total percentage	0,3	3,4	0,8	0,0	2,0	0,9	1,1	1,6	2,3	1,8	1,1
Non-terrestrial palynomorphs											
Botryococcus	0,6	0,6	0,5	1,2	0,6	0,3	0,3	1,8	1,5	0,9	2,1
Totalt percentage of freshwater algae	0,6	0,6	0,5	1,2	0,6	0,3	0,3	1,8	1,5	0,9	2,1
Marine palynomorphs											
Dinoflagellate cysts	2,3	1,8	3,4	0,2	0,6	1,4	3,4	3,8	3,7	4,0	3,7

Appendix 1. Percentage of palynomorphs counted in the Dykær section. Note that the dinoflagellate cysts and freshwater algae were retracted before the individual spore percentages were calculated.

Dykaer Elevation (m)	6.80	8.20	9.10	10.10	10.15	10.80	11.90	14.05	14.70	15.35	15.60	17.80
Swamp forest												
Taxodiaceae-Cupressaceae	49,1	55,7	51,9	47,6	42,0	51,1	47,4	53,1	62,2	56,2	26,1	23,2
Nyssa	6,1	5,5	1,9	4,6	7,6	3,2	0,9		4,3	4,8		
Betula	5,1	1,3	2,4	4,9	11,2	6,0	6,5	0,6	1,7	0,4	0,7	2,4
Alnus	1,4	1,3	0,3	1,0	1,4	0,7				0,4		
Salix		1,0	2,4	0,3	1,1		1,9		0,4			0,8
Cyrilla	0,7	0,6	0,8	2,0	3,6	1,4	0,9	1,9	0,4			0,4
Myrica												
Total percentage	62,5	65,4	59,6	60,4	66,9	62,3	57,7	55,6	69,1	61,8	26,8	26,8
Cool temperate forest ass.												
Abies	0,7	0,3	1,9	1,0			2,3	3,4		0,8	2,0	2,8
Larix											1,0	
Tsuga	1,7	1,0	0,3	0,5	0,6		0,5	0,3		2,4	7,7	2,4
Tsuga (Zonalapollis)												
Pinus	2,7	2,9	5,6	5,1	2,2	3,5	4,2	19,8	3,5	6,8	13,4	13,0
Piceae	6,5	6,5	6,4	4,6	2,8	1,4	4,7	7,1	4,8	3,2	28,8	32,5
Carya	0,3		1,6	1,0	0,8	0,7	0,9	0,6	0,9	0,8		0,4
Picea	0,7	0,6	0,3	0,3				0,6	0,4	0,8	2,0	4,1
Pterocarya	0,3			0,8	1,4	0,4	2,3	0,9	0,4			1,6
Quercus	5,8	3,9	6,6	4,6	5,3	5,3	3,3	1,9	2,6	2,0	2,7	1,2
Corylus						1,1	2,3		2,2	1,6		2,0
Fagus	2,0	4,5	4,0	0,8	1,1	0,7	0,5	0,3	3,9	2,0	0,7	0,4
Ulmus	0,7	0,6		0,8	0,8	1,1	1,4	0,3	0,9	0,8		
Tilia			0,3		0,6					0,4	0,3	0,4
Sequoia		1,3	0,3		0,3	0,7				2,0	0,3	
Liquidambar			0,3	0,3	0,6	1,8	1,9	0,3	0,4		1,0	0,8
Cf. *Fagus*												
T. microhenrici												
Carpinus						0,4						
Total percentage	21,5	21,7	27,4	19,7	16,5	16,9	24,2	35,5	20,0	23,7	59,9	61,8
Warm-temperate plants												
Arecaceae	0,3		0,5	2,6	2,8	1,4	1,9		0,4		1,7	
Engelhardtia	1,7	0,3	2,4	3,3	1,4	3,2		0,3	1,3	2,0		1,2
Cedrus										1,2		
Ilex			0,3	0,3	0,6	0,4	0,9				0,3	0,4
Monocolpopollenites sp.	5,1	5,8	4,5	4,1	3,9	2,8	5,6	0,3	3,9	6,0	2,3	4,1
Podocarpus	0,7	0,3	0,3					1,2		0,8		1,2
Platycarya	1,4	1,6	2,4	0,8	1,4	2,5	0,9	0,6	0,4			
Tricolporopollenites cingulum												
Tricolporopollenites fusus												
Tricolporopollenites pusillus	0,3	0,6	0,5	0,5		0,4			1,3			
Sabal		0,3		3,8	2,5	2,1	3,3	2,8		0,4	1,0	
Sapotaceae	0,7		0,3						0,4			
Zelkovaepollenites	0,3					0,4		0,3				
Liriodendron		0,3		0,3								
Sciadopitys	2,7	1,3		0,3	0,3	0,7		0,3		2,8	1,0	4,1
Ephedra						0,4						
Total percentage	13,3	10,7	11,2	15,9	12,9	14,1	12,6	5,9	7,8	13,3	6,4	11,0
Mesophytic understorey plant ass.												
Ericaceae	1,4	0,3	0,3	0,5	0,3			0,9	0,4	0,8		
Leiotriletes sp.	0,3	0,6			1,4	0,4	0,5				0,7	
Stereisporites sp.		0,3							0,4			
Retitriletes sp.											0,7	
Baculatisporites sp.				0,3								
Total percentage	1,7	1,3	0,3	0,8	1,7	0,4	0,5	0,9	0,9	0,8	1,3	0,0
Aquatic plants												
Graminae		0,3				0,7	0,5		1,3			
Sparganium			1,1	2,0	0,8	0,4	0,9				2,0	
Nuphar												
Nymphhaeae	1,0			0,8	1,1	5,3	3,7	2,2	0,9		1,3	
Sigmopollis					0,0							
Total percentage	1,0	0,3	1,1	2,8	2,0	6,3	5,1	2,2	2,2	0,0	3,3	0,0
Non-terrestrial palynomorphs												
Botryococcus	5,9	0,5	0,8	3,7	6,6	3,0	4,0	1,1	0,2	0,0	8,1	6,9
Totalt percentage of freshwater algae	5,9	0,5	0,8	3,7	6,6	3,0	4,0	1,1	0,2	0,0	8,1	6,9
Marine palynomorphs												
Dinoflagellate cysts	3,8	3,7	2,0	15,7	20,3	35,4	22,9	10,5	1,7	5,8	13,6	6,1

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Hindsgavl								
Elevation(m)	1.45	1.61	1.94	2.10	3.0	3.23	4.85	5.0
Swamp forest								
Taxodiaceae-Cupressaceae	37,0	24,7	42,7	40,8	27,6	15,7	29,0	20,8
Nyssa	0,3	0,3	0,3	0,3	0,7	0,2		
Betula	2,2	1,3	0,9	1,1	1,0	2,8	6,5	1,9
Alnus	0,9		0,3		0,7		3,2	
Cyrilla								1,9
Total percentage	40,4	26,2	44,1	42,2	30,0	18,7	38,7	24,5
Cool temperate forest								
Tsuga	1,2	2,5	1,2	2,4	3,4	6,4		
Ulmus							3,2	
Quercus	1,9	4,5	3,5	1,9	0,7	2,6		
Pterocarya		0,3	0,9	0,0		0,2		
Corylus	0,6	0,3	1,7	0,5	1,5	0,6	6,5	1,9
Picea	1,6	3,3	2,6	1,6	2,7	1,1		3,8
Pinuspollenites microalatus	1,2	3,8	3,2	7,0	3,7	5,4		
Sequoia	2,2	5,3	1,7	1,1		0,2	3,2	
Pinus	30,7	34,3	21,9	24,1	41,2	45,9	9,7	54,7
Carya	1,6	0,3	0,6	2,2	1,5	1,3	3,2	
Carpinus		0,5		0,5	0,5			
Total percentage	41,0	54,9	37,2	41,4	55,1	63,7	25,8	60,4
Warm-temperate plants								
Arecaceae		0,3	0,3					
Araliaceae		0,8	0,6					
Engelhardtia	0,3		1,7	0,5	0,5	1,1		
Monocolpopollenites sp.	1,6	0,5	2,0	1,1	0,5	1,1	3,2	
Sabal							6,5	
Podocarpus		1,5	0,6	1,1	0,7	0,4		
Tricolporopollenites pusillus	0,3		0,0	0,0				
Sapotaceae	0,9	2,0	0,3	0,3		0,6		
Tilia	0,3	0,3	0,6	0,0	0,5	0,4		
Acer		0,3						
Ilex	0,3	1,0		0,5				
Liriodendron			1,2	0,8	1,0			
Sciadopitys	2,5	4,0	4,0	4,6	2,2	4,9		
Cedrus	1,6	1,3	1,7	0,3	0,2			
Ephedra			0,6	0,3	0,2		3,2	
Total percentage	7,8	11,8	13,5	9,5	5,9	8,6	12,9	0,0
Mesophytic understorey plant ass								
Ericaceae	0,9	0,3	1,2	0,5	0,7	0,9	3,2	
Baculatisporites sp.		0,3						
Chenopodipollis sp.	0,3							
Plantago			0,3				6,5	
Asteraceae								1,9
Graminae		0,5	0,3	1,1				
Stereisporites sp.	0,3							
Laevigatosporites sp.	0,3			0,5	0,7	0,6		1,9
Lycopodiaceae	0,3			0,3		0,2		
Total percentage	2,2	1,0	1,7	2,4	1,5	1,7	9,7	3,8
Aquatic plants								
Nymphaea	0,3			0,3	0,5		3,2	5,7
Sigmopollis	1,2	1,0	1,2	0,5	0,2		6,5	3,8
Nuphar		0,3						
Total percentage	1,6	1,3	1,2	0,8	0,7	0,0	9,7	9,4
Non-terrestrial palynomorphs								
Botryococcus sp.	7,1	10,1	11,0	4,3	1,8	7,3	17,3	10,4
Totalt percentage of freshwater algae	7,1	10,1	11,0	4,3	1,8	7,3	17,3	10,4
Marine palynomorphs								
Dinoflagellate cysts	0,3	0,9	1,0	1,0	1,2	0,2	58,0	76,0
Totalt percentage	0,3	0,9	1,0	1,0	1,2	0,2	58,0	76,0

Appendix 2. Percentage of palynomorphs counted in the Hindsgavl section. Note that the dinoflagellate cysts and freshwater algae were retracted before the individual spore percentages were calculated.

Paper II

GFF volume 128 (2006), pp. 261–272. Article

Early Miocene pollen and spores from western Jylland, Denmark – environmental and climatic implications

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Abstract: A palynological analysis of a Lower Miocene cored section from Sønder Vium in western Jylland, Denmark, provides new data regarding the vegetation and climate during the earliest Neogene. Most samples yielded well-preserved palynomorphs. Terrestrial pollen and spores dominate, with lesser proportions of dinoflagellates. A fluvial input into the marine setting is corroborated by the presence of freshwater algae, indicating an inner-neritic setting. A level containing comparatively abundant dinoflagellate cysts probably represents a transgressional event. The late Aquitanian age of the sequence as suggested by previous studies is supported by the composition of the palynoflora, e.g., by the presence of *Ephedripites*, *Platycarya*, and the relatively frequent occurrence of *Engelhardtia*. The pollen record is dominated by Taxodiaceae-Cupressaceae suggesting that swamp forests dominated the onshore region, which is consistent with previous results from central and northern Europe. Besides *Taxodium,* the swamp forest also contained angiosperm taxa such as Myricaceae*, Nyssa*, *Betula*, and *Alnus*. Elevated or better drained hinterland areas hosted a diverse mesophytic forest, 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*. A decrease in relative abundances of thermophilous elements such as Arecaceae (palms), *Ilex,* Mastixiaceae and *Engelhardtia,* in the middle part of the studied succession indicates a possible correlation to the late Aquitanian climatic deterioration. The composition of the palynological assemblages including widely distributed *Taxodium* swamps, suggests a warm, frost-free temperate climate during the Aquitanian in Denmark.

Keywords: Sønder Vium, Miocene, Denmark, palynology, paleoclimate, Taxodiaceae, Cupressaceae, swamp forest.

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Introduction

The Neogene has a complex history of global climate evolution and one of the most remarkable episodes was the Miocene Climatic Optimum, which peaked 17–15 million years ago. In Danish sediments this is reflected in the mid-Miocene Falsterholt flora indicating warm temperate to subtropical climatic conditions (Friis 1975). However, this interval was preceded by an earliest Miocene cooling event, and global climate oscillations are characteristic for the whole epoch (Kashiwagi & Shikazono 2003). As Antarctica became isolated, the circulation patterns in the oceans changed to "modern" configurations and the south circum-polar ocean current became established. This significantly inhibited the mixing of cold polar water with warmer tropical water, which led to the buildup of the Antarctic polar cap (e.g., Lear et al. 2003; Roberts et al. 2003). In central Europe, the climate changed from subtropical to cool temperate during the transition from Late Oligocene to Miocene. During the Late Aquitanian and Early Burdigalian a severe temperature decrease is evident from central European sediments, which is correlated to a glacial maximum (Miller et al. 1991; Rasmussen 2004b).

Palynology is an excellent tool for interpreting paleoclimate variations as the world's climatic zones are closely reflected by the distribution of vegetation types. Despite comprehensive Neogene vegetation and climate records from west-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), few data have been forthcoming from Scandinavia. So far, paleobotanical investigations of the Danish Miocene have been based mainly upon plant macrofossils collected from lignite-bearing

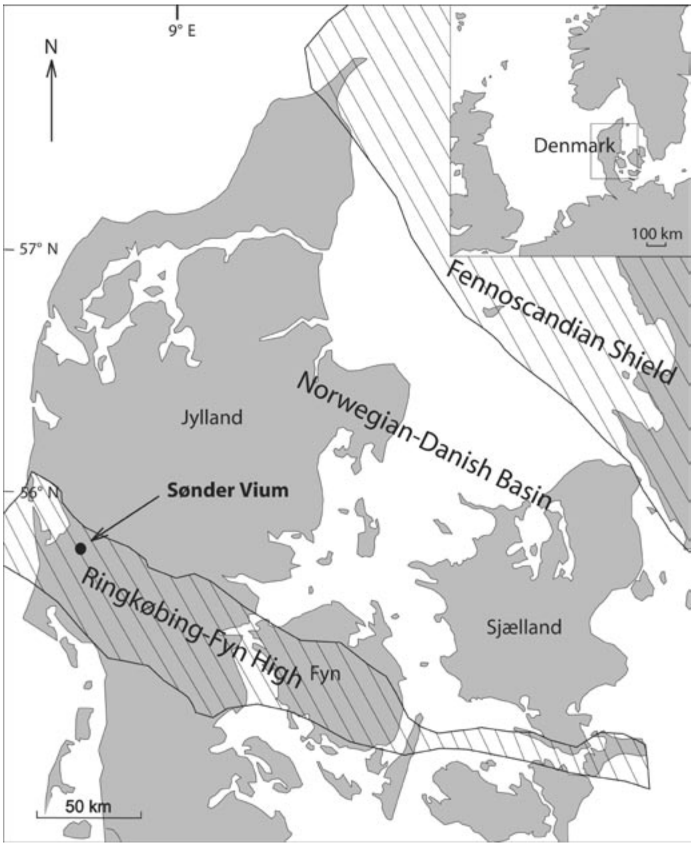

Fig. 1. Location of the Sønder Vium borehole in Denmark, with the structural elements mentioned in the text (mainly after Dybkjaer 2004).

Middle Miocene deposits in central Denmark (e.g., Ingwersen 1954; Koch et al. 1973; Christensen 1974, 1976; Friis 1975, 1977a, 1977b, 1978).

The extensive palynological material investigated in this study is derived from a cored section in the Sønder Vium borehole (Fig. 1) penetrating a pro-deltaic unit. Rasmussen (2003) interpreted the predominantly silty sediments to have been deposited during a relatively short interval in the early part of the Miocene. This study aims to reconstruct the vegetation, paleoenvironment and climate for the earliest part of the Neogene.

Geological setting

Tectonic evolution

During the Cenozoic the North Sea area was developed as an epicontinental basin with periodic connections to the Tethys Sea towards the south and east and the North Atlantic through a narrow strait between present-day Norway and Scotland (Ziegler 1990). The basin was bounded towards the north and north-east by the Fennoscandian Shield. The southern limit was located within the area of northern Poland, Germany, and northern France and the western border was probably located in the British Isles. The shape of the basin was influenced by several tectonic events associated with the Alpine Orogeny (Vejbæk & Andersen 1987; Ziegler 1990; Rasmussen 2004a). Most distinctive was the Early Paleocene inversion tectonism, which reshaped the basin along older fault zones such as the Sorgenfrei-Tornquist Zone and Coffee Soil Fault. Uplift of the Fennoscandian Shield took place in the Late Eocene (Michelsen & Nielsen 1993). Mid-Oligocene rejuvenation of older faults resulted in the formation of a topographic relief especially on the Ringkøbing-Fyn High and within the Norwegian-Danish Basin where older salt structures were reactivated. The relief formed prior to the Miocene strongly controlled the deposition of Miocene sediments (Rasmussen 2004a). Tectonic movements and initial subsidence of the central North Sea area occurred during the late Early–Middle Miocene (Koch 1989; Rasmussen 2004a). This phase resulted in a minor shift in sediment transport direction towards a more easterly source area. In addition, thicker coal-rich deposits were concentrated along reactivated older fault trends. The overall subsidence of the North Sea area resulted in a major flooding of the Danish and southern Scandinavian area in the Late Miocene. Strong tilting of the eastern North Sea area occurred around the Pliocene to Pleistocene transition (Japsen 1993; Rasmussen 2005).

Sedimentation

Cold-water carbonates dominated sedimentation in the basin during the Danian (Surlyk 1997) and the area adjacent to the Fennoscandian Shield was dominated by accumulation of bryozoan banks and coral reefs. This pattern changed dramatically in the Selandian to a predominance of fine-grained siliciclastic sedimentation (Heilmann-Clausen et al. 1985). Paleocene and Eocene clay-rich deposits where laid down in deep marine environments that probably covered major parts of the Fennoscandian Shield as evidenced by relictual outliers in southern Finland (Fenner 1988). The uplift of the Fennoscandian Shield during the Late Eocene (Michelsen & Nielsen 1993; Michelsen et al. 1998) resulted in progradation of major deltas in the Oligocene. In the Early Miocene, three phases of delta progradation occurred, reaching the area of modern Denmark. The progradation of deltas occurred from the north and north-east towards the south and south-west and consequently a northwest–southeast trend on the shoreline. The large fetch across the North Sea resulted in wave-dominated deltas with barrier/lagoonal complexes located on the eastern side on the main delta lobes. Development of this Lower Miocene succession was controlled by a combination of sea-level changes and tectonism (Rasmussen 2004a). A major transgression in the Middle Miocene resulted in deposition of the clayey deposits in the North Sea area and persistence of high-stand deposits for the remainder of the epoch. At the termination of the Miocene a distinct progradation of deltas from the Fennoscandian Shield and Central Europe reached the central part of the North Sea area. Infilling of the central part of the North Sea area continued from the Pliocene to the Holocene and was punctuated only by minor transgressions.

Stratigraphy of the Danish Miocene succession

The Miocene succession, the focus of this study, is characterised by several transgressive-regressive cycles that generated five distinct depositional sequences named B to F in ascending order by Rasmussen (2004b) and Rasmussen & Dybkjaer (2005). An approximate correlation of these sequences to the lithostratigraphy of Denmark (Rasmussen 1961; Rasmussen 2004b) is presented here (Fig. 2).

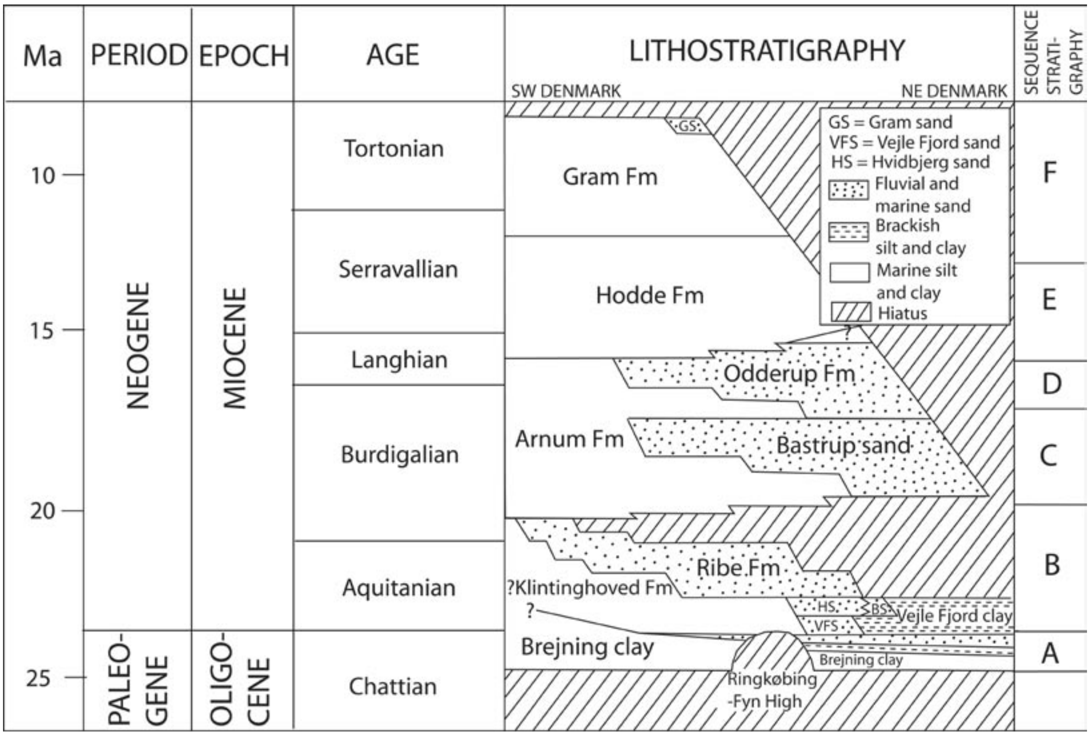

Fig. 2. Upper Oligocene and Miocene lithostratigraphy of Denmark (modified from Dybkjaer 2004; Rasmussen & Dybkjaer 2004).

The earliest Miocene transgression resulted in the deposition of marine clayey prodelta sediments of the Vejle Fjord and Klintinghoved formations (Sorgenfrei 1958; Larsen & Dinesen 1959; Rasmussen 1961; Rasmussen 2004b) and sand-rich fluvio-deltaic deposits of the Ribe Formation (sequence B; Sorgenfrei 1958; Rasmussen 2004b). Subsequently, a minor transgression resulted in the accumulation of the marine Arnum 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 in the Early Miocene (sequence C). This unit was overlain by the upper part of the marine, clay-rich Arnum Formation. The third and final deltaic progradation occurred at the Early to Middle Miocene transition and is represented by the coal-bearing Odderup Formation (sequence D; Rasmussen 1961; Koch 1989). A warming phase in the early part of the Middle Miocene corresponded to a major transgression and deposition of the marine Hodde and Gram formations (sequences E and F; Rasmussen 1961; Piasecki 1980).

Material and methods

This study is based on palynomorphs extracted from the succession referred to as sequence B in the Sønder Vium bore hole (DGU 102.948; Piasecki et al. 2004). The lowermost interval (288–193 m), is characterised by dark, silty clays in some cases interbedded with sandy layers. The succeeding interval (193–183 m) is a medium to coarse-grained sand (Fig. 3). All samples were processed at the Geological Survey of Denmark and Greenland in Copenhagen using standard palynological preparation techniques including treatment with HCl, HF, HNO_3 and sieving on 11 μm nylon filters (Poulsen et al. 1990). Forty-one samples collected from the 288 to 183 metre interval were examined. Only two samples were examined from the arenitic 192 to 183 metre interval of the studied succession (Fig. 3) as these were the only ones recovered from the drilling.

The taxa used herein represent a combination of natural taxa and parataxa, and the taxonomy is primarily based on the works of Thomson and Pflug (1953), Krutzsch (1971), Thiele-Pfeiffer 1980), Nagy (1985), Traverse (1988), Koch (1989), and Kolcon and Sachsenhofer (1999). Between 340 and 600 terrestrial palynomorphs and additional marine palynomorphs were counted in each sample to interpret the depositional environment.

Because the assemblages are strongly dominated by the conifers Taxodiaceae-Cupressaceae they mask the perturbation in the pollen spectra of other groups (Fig. 4A, B). Therefore, we have excluded Taxodiaceae-Cupressaceae in one of the data sets (Fig. 4B) in order to better illustrate the quantitative variations in the other taxa. Paleoenvironmental and vegetation analyses involved grouping taxa into distinctive plant associations, which are modified from Kohlman-Adamska (1993) and Kolcon & Sachsenhofer (1999). In addition, the quantitative relationship between marine and terrestrial palynomorphs is calculated for paleoenvironmental purposes (Fig. 3).

The botanical affinities of pollen and spores from recent plant taxa can be used to aid interpretation of the structure of paleovegetation and ecological tolerances of individual ancient plant taxa. This can further be used to interpret the ancient climatic conditions. All taxa were categorized according to botanical affinities, in most cases to family or generic level (Table 1), by using palynological works by, e.g., Thomson & Pflug (1953), Thiele-Pfeiffer (1980), and Kolcon & Sachsenhofer (1999).

Palynology

All samples contain well-preserved marine and terrestrial palynomorphs. A total of 95 terrestrial palynomorph taxa were identified and assigned to 54 botanical groups (Table 1, Fig. 4A,

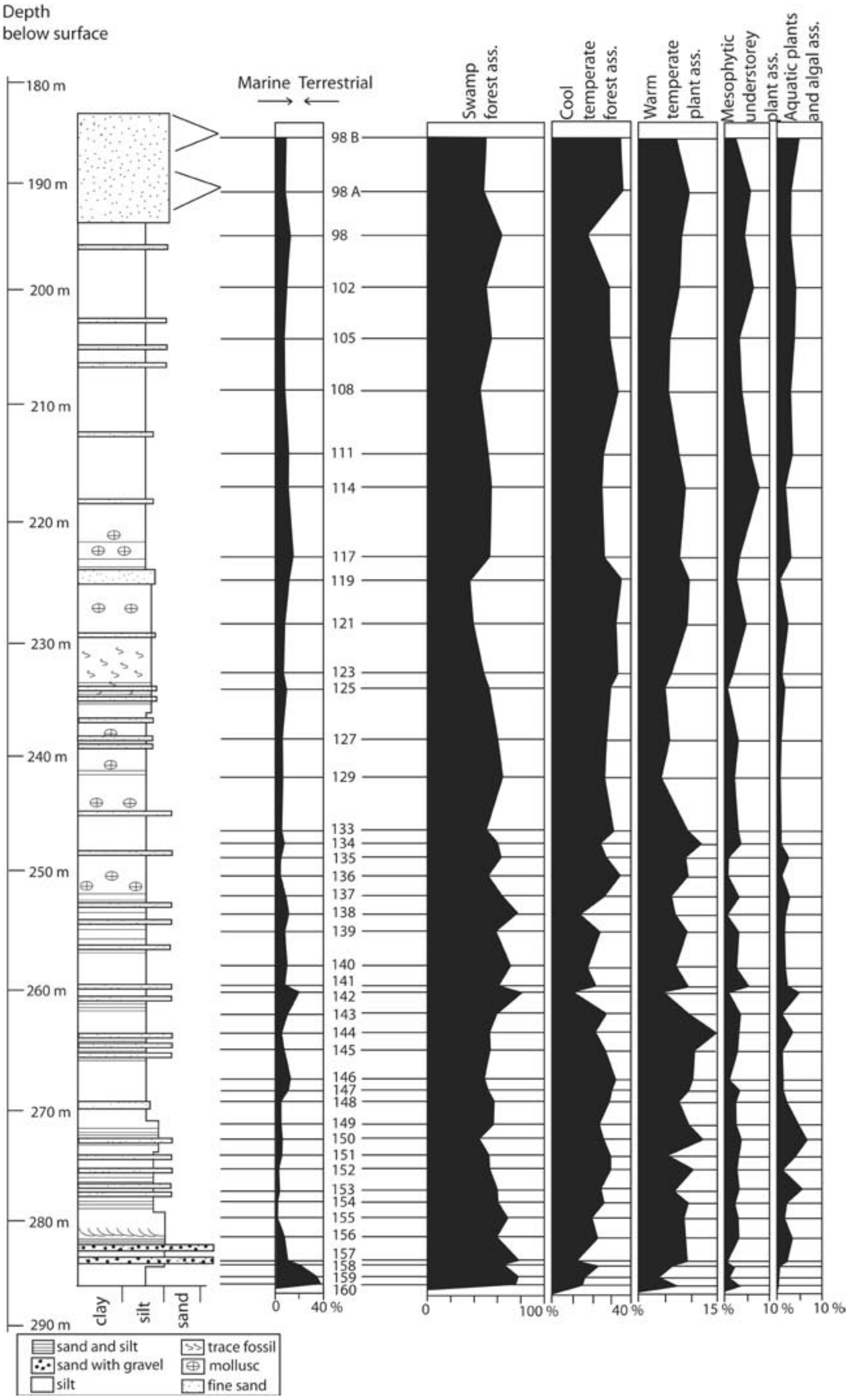

Fig. 3. Simplified sedimentary log of the studied succession (Sequence B) in the Sønder Vium borehole, showing the relationships between marine and terrestrial palynomorphs, and between the different plant associations mentioned in the text.

B). The marine palynomorphs are mainly dinoflagellate cysts, but algae, such as *Tasmanites,* and acritarchs also occur. Marine palynomorphs comprise 20–39% of the palynomorphs in the three lowermost assemblages, (286–284 m) and 22% at the 260 m level, but the relative abundances of marine palynomorphs decrease markedly upsection. The present study focuses on the terrestrial palynomorphs. The dinoflagellate cyst assemblages in the studied section were studied by Piasecki et al. (2004).

Although vegetation types certainly interact with each other, five distinct plant associations are recognized here based on their growth habits and ecology (Fig. 4). Naturally, there will be overlap in ecological requirements for several taxa and in order to interpret climate we have been obliged to segregate taxa that have traditionally been assigned to "arctotertiary" and "paleotropic" associations (Kolcon & Sachsenhofer 1999).

Plants have been grouped into following associations; (1) *Swamp forest association,* (2) *Cool temperate" mixed mesophytic" forest canopy association,* (3) *Warm temperate plant association,* (4) *Mesophytic understorey plant association*, and (5) *Aquatic plant and algal association* (modified from Kolcon & Sachsenhofer 1999).

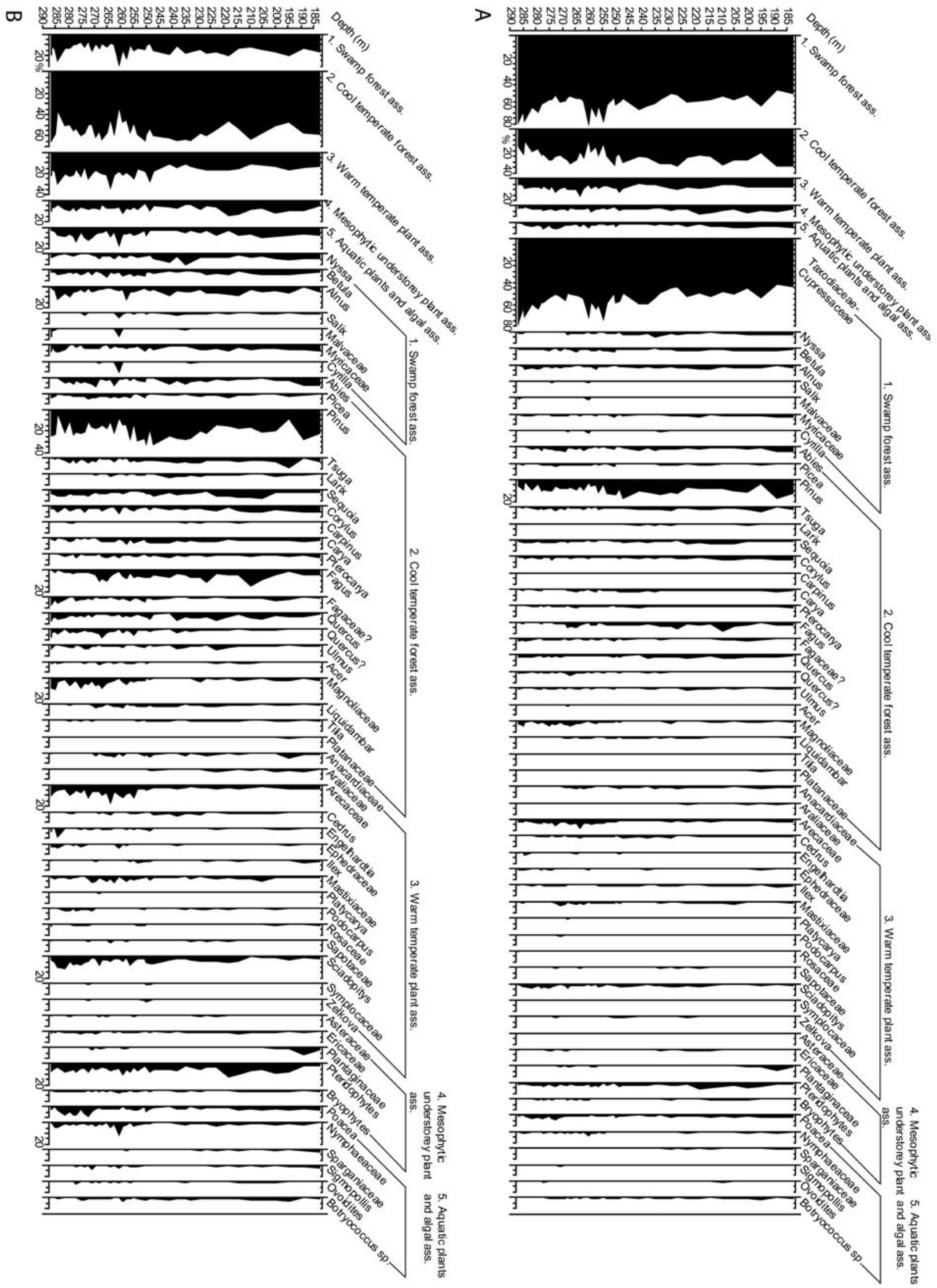

Fig. 4. **A.** Relative abundance diagram of pollen and spores recorded in the studied succession. **B.** Relative abundance diagram of pollen and spores recorded in the lowermost part of the Vium drill core with the Taxodiaceae-Cupressaceae group exluded.

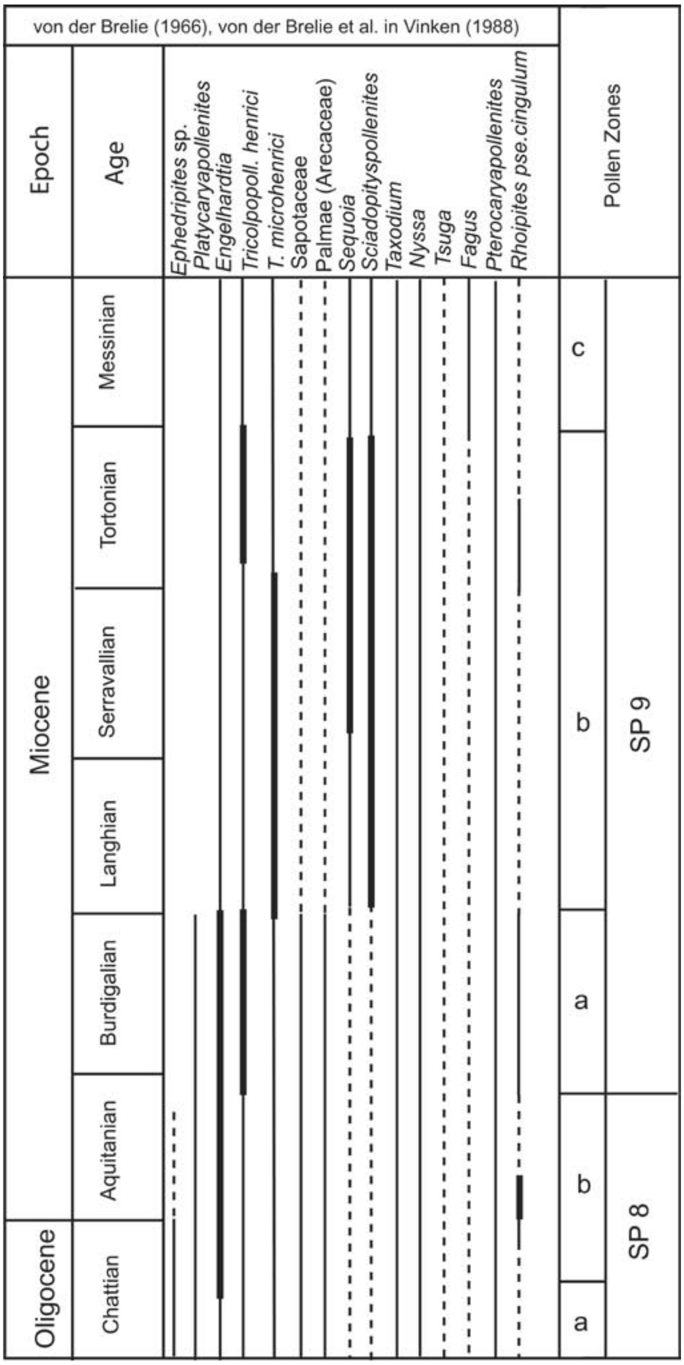

Fig. 5. Stratigraphically important pollen taxa and zones in the uppermost Oligocene and Miocene of central Europe (from von der Brelie 1966; von der Brelie et al. 1988). Line thickness indicates relative abudance but this has not been defined quantitatively.

Swamp forest association (Figs. 3, 4A,B)

Pollen from plants that predominantly grow in mire habitats are by far the dominant palynomorphs in the studied succession (Figs. 3, 4A). Eight pollen taxa are assigned to this association, which mainly includes pollen derived from Taxodiaceae-Cupressaceae and *Nyssa*. Although Taxodiaceae is considered to be nested within Cupressaceae according to some molecular and morphological studies (Gadek et al. 2000) it is not always appropriate to group these traditionally separate families, because their representatives may have different environmental tolerances. However, they are grouped here because the preservation of these palynomorphs is poor in some cases and they are not always distinguishable at a generic level (Zetter 1998). Note that *Sequoia*, which is well preserved, is segregated from this grouping. Taxodiaceae-Cupressaceae are the most abundant taxa in this association comprising 42–76% of all identified pollen grains. The highest relative abundances of Taxodiaceae-Cupres-

Table 1. Recorded palynomorph taxa in the lowermost interval of the Vium drillcore, placed within their known plant affinity (mainly after Thomson & Pflug 1953; Tschudy & Scott 1969; Krutzsch 1971; Figueiral et al. 1999).

Gymnosperms
Abies
- *Abiespollenites* sp

Cedrus
- *Cedripites* sp.

Larix
- *Laricipollenites gerceensis* Nagy, 1985

Picea
- *Piceaepollis* sp. (Fig. 7P)
- *Piceaepollis planoides* Krutzsch, 1971
- *Pityosporites alatus* (Potonié, 1931) Thomson & Pflug, 1953

Pinus
- *Pinuspollenites* sp.
- *Pinuspollenites labdacus* Potonié, 1958 (Fig. 6O)
- *Pityosporites microalatus* (Potonié, 1931) Thomson & Pflug, 1953, (Fig. 6 P)

Podocarpus
- *Podocarpidites* sp. (Fig. 7O)

Sciadopitys
- *Sciadopityspollenites serratus* (Potonié & Venitz, 1934) Raatz, 1937 (Fig. 6J)
- *Sciadopityspollenites* sp.

Sequoia
- *Sequoiapollenites* sp.
- *Sequoiapollenites polyformosus* Thiergart, 1937 (Fig. 6L)

Taxodiaceae-Cupressaceae
- *Inaperturopollenites* sp. (Fig. 6K)
- *Inaperturopollenites hiatus* Thomson & Pflug, 1953 (Fig. 6N)
- *Inaperturopollenites dubius* Potonié & Venitz, 1934
- *Inaperturopollenites concepidites* Wodehouse, 1933
- *Inaperturopollenites verrupapillatus* Trevisan, 1967
- *Inaperturopollenites incertus* Thomson & Pflug, 1953
- *Cupressacites* sp.
- *Cupressacites bockwitsensis* Krutzsch, 1971 (Fig. 6M)

Tsuga
- *Tsugaepollenites* sp.
- *Tsugaepollenites robustus* Krutzsch, 1971
- *Zonalapollis* sp. (Fig 7Q)

Angiosperms
Acer
- *Aceripollenites* sp.

Alnus
- *Alnipollenites* sp. (Fig. 6F)
- *Alnipollenites verus* Potonié, 1934
- *Polyvestibulopollenites* sp.

Anacardiaceae
- *Rhoipites pseudocingulum* Potonié, 1960 (Fig. 7G)

Araliaceae
- *Araliaceoipollenites* sp.

Arecaceae
- *"Arecaceaepollenites"*
- *Arecipites* sp.
- *Sabalpollenites papillosus* Nagy, 1969
- *Monocolpopollenites* sp.
- *Monocolpopollenites tranquillus* Thomson & Pflug, 1953 (Fig. 7B)

saceae were found in the basal interval between 286–284 m, although three additional peaks occur at the levels of 260, 257 and 254 metres (Fig. 4A). The occurrence of *Nyssa* is generally low, (below 4.5%); however, it should be pointed out that its representation in this association increases up-section (Fig. 4A). Also included in this association are small trees and shrubs, such as *Betula, Alnus*, Myricaceae, *Salix*, Malvaceae (other than *Tilia*), and *Cyrilla*, which grow in periodically flooded riparian environments. These palynomorphs are present in low quantities and show no significant variation in abundance throughout the investigated succession (Fig. 4A).

When the Taxodiaceae-Cupressaceae group is excluded, the other elements of the swamp forest association reach a relative abundance of 6–28% (Fig. 4B). The palynological signals are enhanced by this procedure and spikes of taxa that previously where hidden by the overwhelming abundance of Taxodiaceae-Cupressaceae are now amplified. Most significantly, important peaks in the typical swamp genera *Alnus*, *Salix*, *Malvaceae* and *Cyrilla* are revealed around the 260 m level.

Cool temperate” mixed mesophytic” forest canopy association, (Figs. 3, 4A, B)

This association comprises 20 identified taxa and constitutes between 9 and 34% of the total miospore assemblage. Pollen in this association is derived from conifers and other evergreen plants but also deciduous angiosperm trees and shrubs, often referred to as “arctotertiary taxa” (Kolcon & Sachsenhofer

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- *Monocolpopollenites areolatus* Potonié, 1934
- *Betula*
  - *Trivestibulopollenites betuloides* Pflug, 1953
  - *Betulaepollenites betuloides* Nagy, 1953 (Fig. 6E)
- *Carpinus*
  - *Carpinipites* sp.
- *Carya*
  - *Caryapollenites* sp. (Fig. 6C)
- *Corylus*
  - *Triporopollenites coryloides* Pflug, 1953
- Asteraceae
  - *Artemiseaepollenites* sp.
- *Cyrilla*
  - *Cyrillacaepollenites exactus* Potonié, 1960
- *Engelhardtia*
  - *Engelhardtioidites* sp. (Fig. 7J)
- Ephedraceae
  - *Ephedripites* sp.
- Ericaceae
  - *Ericipites* sp. (Fig. 7M)
- Fagaceae?
  - *Tricolporopollenites pusillus* (Potonié, 1931) Thomson & Pflug, 1953 (Fig. 6G)
  - *Tricolporopollenites fusus* Potonié, 1934
- Fagus
  - *Faguspollenites* sp. (Fig. 6I)
- Poaceae
  - *Graminidites* sp. (Fig. 7L)
  - *Triatriopollenites coryloides* Pflug, 1953 (Fig. 7K)
- *Ilex*
  - *Ilexpollenites* sp.
  - *Tricolpopollenites iliacus* (Thiergart, 1937) Potonié, 1960
- *Liquidambar*
  - *Liquidambarpollenites* sp.
- Magnoliaceae
  - *Liriodendroipollis semiverrucatus* Krutzsch, 1971
  - *Magnolipollis neogenicus minor* Krutzsch, 1971
- Malvaceae
  - *Malvacearumpollis* sp.
- Mastixiaceae?
  - *Tricolporopollenites edmundii* (Potonié, 1931) Thomson & Plug, 1953 (Fig. 7C)
- Myricaceae
  - *Triatriopollenites myricoides* Kremp, 1949
  - *Triatriopollenites bituitus* (Potonié, 1931) Thomson & Pflug, 1953 (Fig. 6D)
  - *Triatriopollenites rurensis* Thomson & Pflug, 1953
- Nymphaeaceae
  - *Nupharipollenites kedvesi* Nagy, 1969
  - *Nymphaeaepollis minor* Nagy, 1985
- Nyssa
  - *Nyssapollenites* sp. 1960 (Fig. 6H)
- Plantaginaceae
  - *Plantaginacearumpollis miocaenicus* Nagy, 1963
- Platanaceae
  - *Platanus* sp.
- *Platycarya*
  - *Platycarypollenites* sp. (Fig. 7I)
- *Pterocarya*
  - *Pterocaryapollenites* sp.
- Quercus
  - *Quercopollenites* sp. (Fig. 7D)
- Quercus?
  - *Tricolpopollenites henrici* (Potonié, 1931) Thomson & Pflug, 1953 (Fig. 7H)
  - *Tricolpopollenites microhenrici* (Potonié, 1931) Thomson & Pflug, 1953 (Fig. 7F)
- Rosaceae
  - Rosaceae-type
- *Salix*
  - *Salixipollenites* sp.
- Sapotaceae
  - *Sapotaceoidaepollenites* sp. (Fig. 7E)
- Sparganiaceae
  - *Sparganiaceaepollenites* sp.
- Symplocaceae
  - *Porocolpopollenites* sp.
- *Tilia*
  - *Tilia* sp. (Fig. 7N)
- Ulmus
  - *Ulmipollenites* sp.
- Zelkova
  - *Zelkovaepollenites potoniei* Nagy, 1969
- Pteridophytes
  - Lycopodiaceae
  - Polypodiaceae
  - *Polypodiisporites* sp.
  - *Foveotriletes* sp.
  - *Baculatisporites* sp.
  - *Gleicheniidites senonicus* Ross, 1949
  - *Laevigatosporites* sp. (Fig. 6B)
  - *Laevigatosporites hardtii* Thomson & Pflug, 1953
  - *Leiotriletes* sp.
  - Osmundaceae
  - *Triplanosporites* sp.
- Bryophytes
  - *Stereisporites* sp. (Fig. 6A)

Algae
- *Sigmopollis* sp.
- *Ovoidites* sp.
- *Botryococcus braunii* Kützing, 1849
- *Tasmanites* sp.

Acritarchs

Dinoflagellates

Fungal spores

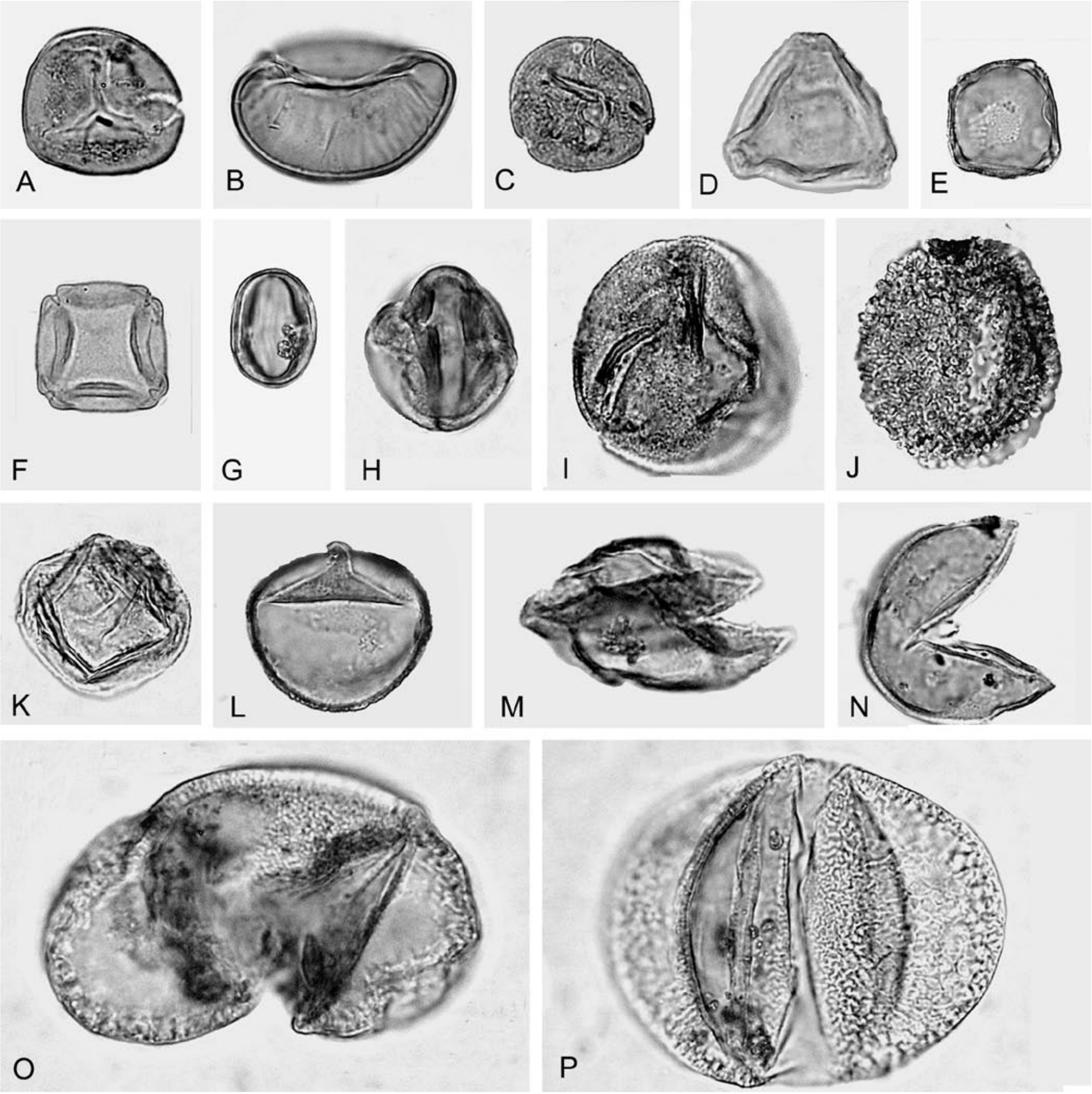

Fig. 6. Photomicrographs of selected palynomorph taxa from the studied succession, magnification ×700. **A.** *Stereisporites* sp. **B.** *Laevigatosporites* sp. **C.** *Caryapollenites* sp. **D.** *Triatriopollenites bituitus* (Potonié 1931) Thomson & Plug, 1953. **E.** *Betulaepollenites betuloides* Nagy, 1969. **F.** *Alnipollenites* sp. **G.** *Tricolporopollenites pusillus* (Potonié, 1931) Thomson & Pflug, 1953. **H.** *Nyssapollenites* sp. **I.** *Faguspollenites* sp. **J.** *Sciadopityspollenites serratus* (Potonié &Venitz, 1934) Raatz, 1937. **K.** *Inaperturopollenites* sp. **L.** *Sequoiapollenites polyformosus* Thiergart, 1937 **M.** *Cupressacites bockwitzensis* Krutzsch, 1971. **N.** *Inaperturopollenites hiatus* Thomson & Pflug, 1953. **O.** *Pinuspollenites labdacus* Potonié, 1958. **P.** *Pityosporites microalatus* (Potonié, 1931) Thomson & Pflug, 1953.

1999). The association is dominated by conifer pollen such as *Pinus* (1–16%), *Abies* (0–4%), *Picea* (0–2%), *Tsuga* (0–4%), and *Sequoia* (0.3–4%); (Fig. 4). Pollen from deciduous trees such as *Fagus* (0–8%) and *Quercus* (up to 3%) are also relatively frequent. Minor constituents include, among others, *Carpinus, Ulmus, Corylus,* Magnoliaceae, and *Tilia*. Other significant taxa include Araliaceae and Rosaceae. Where the Taxodiaceae-Cupressaceae is omitted (Fig. 4B) a more pronounced but basically identical palynological signal is recorded.

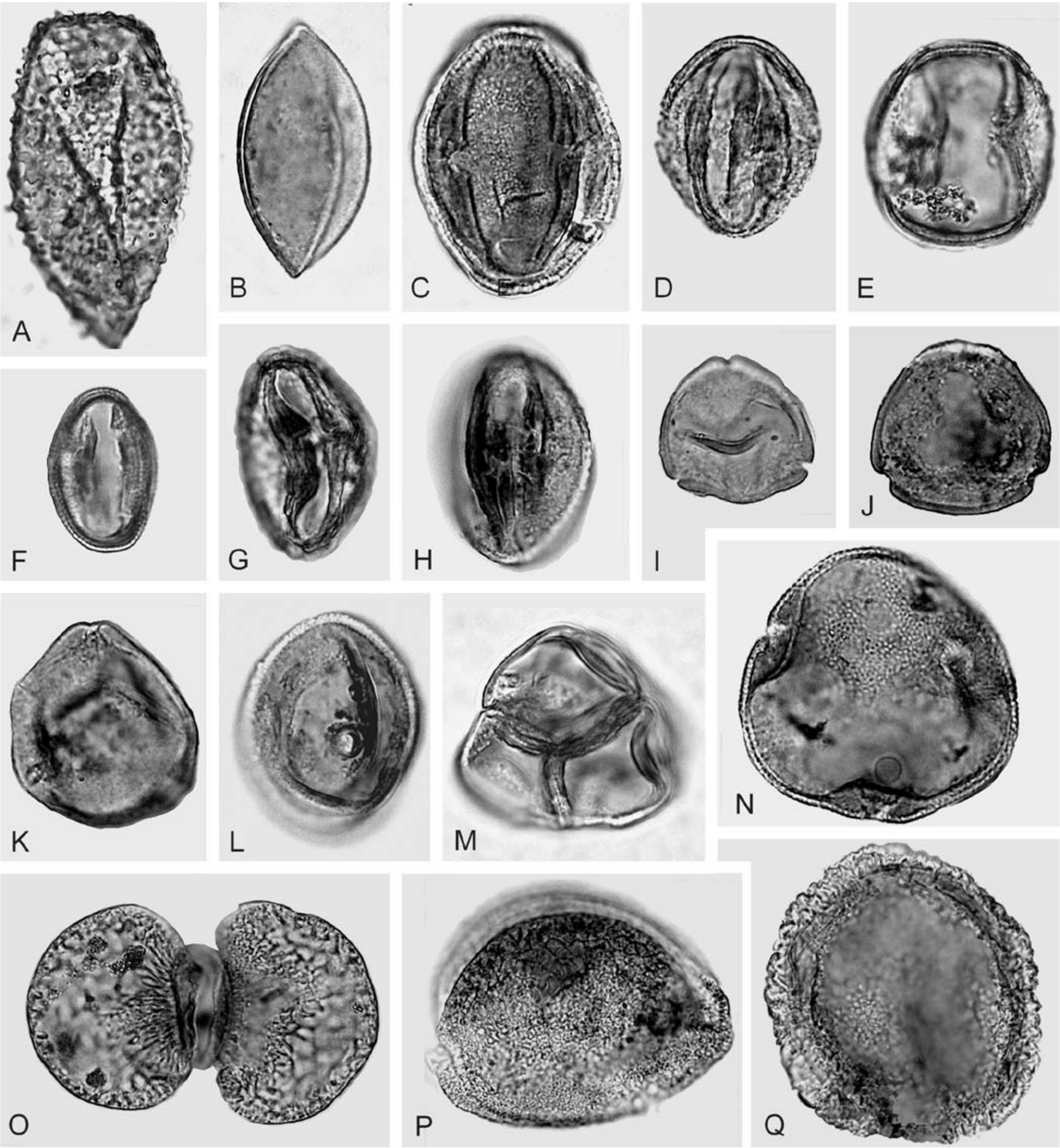

Fig. 7. Photomicrographs of selected palynomorph taxa from the studied succession, magnification ×700. **A.** *Liriodendroipollis semiverricatus* Krutzsch, 1971. **B.** *Monocolpopollenites tranquillus* Thomson & Pflug, 1953. **C.** *Tricolporopollenites edmundii* (Potonié, 1931) Thomson & Pflug, 1953. **D.** *Quercopollenites* sp. **E.** *Sapotaceoidaepollenites* sp. **F.** *Tricolpopollenites microhenrici* (Potonié, 1931) Thomson & Pflug, 1953. **G.** *Rhoipites pseudocingulum* Potonié, 1960. **H.** *Tricolpopollenites henrici* (Potonié, 1931) Thomson & Pflug, 1953. **I.** *Platycaryapollenites* sp. **J.** *Engelhardtioidites* sp. Potonié, 1960. **K.** *Triatriopollenites coryloides* Pflug, 1953. **L.** *Graminidites* sp. Cookson, 1947. **M.** *Ericipites* sp. Wodehouse, 1933. **N.** *Tilia* sp. **O.** *Podocarpidites* sp. **P.** *Piceapollis* sp. **Q.** *Zonalapollis* sp.

Warm temperate plant association (Figs. 3, 4A, B)

This association comprises 15 thermophilous taxa, representing the "palaeotropic flora" (Kolcon & Sachsenhofer 1999), and 4–16% of the total miospore assemblage. The main constituents are angiosperm taxa, among others, *Arecaceae* (1–8%), *Mastixiaceae* (0–3%), *Engelhardtia* (0–3%), *Ilex* (0–1%) and *Platycarya* (0–1%). Gymnosperms are represented by the presence of conifer pollen such as *Sciadopitys* (0.2–4.5%), *Cedrus* (0–1.5) and *Podocarpus* (0–1%). The warm temperate taxa included in this group grew in different habitats. Thus, the quantitative variations mainly serve to interpret the paleoclimate. After excluding the Taxodiaceae-Cupressaceae, a significant decrease in the relative abundance of the warm temperate plant association is revealed above the 247 m level (Fig. 4B).

Mesophytic understorey plant association (Figs. 3, 4A, B)

This association consists of five taxa that constituted ground-cover vegetation in the mesophytic forests. This group makes the smallest contribution to the total palynoflora comprising only 1–7% of the total miospore assemblage. Pteridophytes are the dominant group in this association, comprising up to 6% of total terrestrial palynomorphs (Fig. 4A). Other taxa contributing to the association are bryophytes, Asteraceae, Ericaceae, and Plantaginaceae. When excluding Taxodiaceae-Cupressaceae, the same general trend in relative abundance is evident for this association (Fig. 4B).

Aquatic plants and algal association (Figs. 3, 4A, B)

This association includes palynomorphs from plants that prefer mainly moist environments (although Poaceae frequently occur as undergrowth plants in other communities). In the studied succession this association varies between 1 and 6% (Figs. 3, 4A). Taxa included are Poaceae, Sparganiaceae, and Nymphaeaceae. Poaceae occur in almost every sample, comprising up to 4% of the total miospore assemblage (Fig. 4A), although it is most abundant in the lowermost samples. The aquatic taxon Nymphaeaceae is present in almost every sample although it peaks at the 260 m level where it comprises 3% of the total miospore assemblage (Fig. 4A).

Since this study deals primarily with paleovegetational reconstruction, freshwater taxa, such as *Sigmopollis, Ovoidites*, and *Botryococcus* are included in this association. Freshwater taxa are present in almost every sample, except in those from the basal part of the succession (Fig. 4A). After excluding Taxodiaceae-Cupressaceae the previously mentioned spike of Nymphaeaceae is enhanced and an additional spike of *Sigmopollis* occurs at the 260 m level (Fig. 4B).

Discussion

Age of the succession

Palynological subdivision of the northern European Miocene is difficult for several reasons. Firstly, most species range throughout the epoch (von der Brelie 1967). Secondly, major differences in phytogeographic distributions and depositional environments occurred in Europe during this time, hence there are difficulties in correlating the pollen spectra at different locations (Traverse 1988; Sadowska 1995).

Based on quantitative differences in the pollen spectra of central Europe, von der Brelie (1967) established five pollen zones for the Miocene, which was enhanced by the more general study of von der Brelie et al. (1988; Fig. 5). The palynological results from the Sønder Vium succession have been compared with the quantitative results of von der Brelie (1967) and von der Brelie et al. (1988) in order to assess the applicability of the central European zonation to Denmark (Fig. 5). Von der Brelie (1967) indicated that the ranges and relative abundance of certain pollen taxa such as *Tricolpopollenites henrici* and *T. microhenrici* were stratigraphically significant as they show a slight increase in abundance at the Aquitanian–Burdigalian boundary. Results from the studied succession indicate that these species represent consistent but subsidiary elements throughout the sampled succession. In addition, Paleogene key pollen, such as *Ephedripites,* disappear by the end of the Aquitanian whereas *Engelhardtia* occurs throughout the Miocene, but is most common during the Early Miocene (Fig. 5; von der Brelie 1967; von der Brelie et al. 1988). These taxa were consistently recorded throughout the sampled portion of the Sønder Vium core.

An Early Miocene age is indicated by the presence of *Ephedripites, Platycarya*, and the consistent occurrence of *Engelhardtia.* Based on the known range of *Ephedripites* (von der Brelie 1967), the studied section should be assigned to the Aquitanian. In addition, the increasing level of *Rhoipites pseudocingulum* (Anacardiaceae), accompanied by successively decreasing amounts of palm pollen suggest that the studied succession is possibly of late Aquitanian age.

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 taxa starting at the level of 262 metres. However, a more pronounced reduction in warm temperate taxa above 247 metres (sample 133) is revealed when excluding Taxodiaceae-Cupressaceae from the pollen signal (Fig. 4B). We contend that this climatic deterioration may indicate a late Aquitanian age for this part of the succession.

The new spore-pollen data supports a late Aquitanian age for the studied succession in the Sønder Vium bore core (sequence B), as proposed by previous authors (Dybkjaer 2004; Piasecki et al. 2004) based on dinoflagellate cyst assemblages.

Depositional environment, vegetation and climatic conditions

The consistent occurrence of marine dinoflagellate cysts in all the studied samples, combined with the strong dominance of terrestrial palynomorphs implies that deposition occurred in an inner-neritic setting. This interpretation agrees well with seismic data from the studied area. Here southwards dipping clinoforms indicate an Early Miocene delta progradation (Rasmussen 2004a). Samples showing increased relative abundances of dinoflagellate cysts, e.g., the level of 286–284 m, probably reflect a minor transgressional phase resulting in less terrestrial influence in the studied area (Fig. 3).

The Sønder Vium terrestrial palynomorph assemblages indicate no major change in diversity as most taxa persist through the investigated succession. However, the relative abundance of taxa varies. All five palynological associations show pronounced fluctuations in relative abundance in the lower one-third of the studied succession compared to the more stable composition in the upper two-thirds (Fig. 4A, B). This signal is enhanced when the Taxodiaceae-Cupressaceae are excluded. The transition from variable to more uniform assemblages occurs at the 247 m level and is coincident with the vegetational signal of climatic deterioration. We contend that the relatively uniform palynofloras from the upper part of the succession reflect a more stable climate during the time of deposition, but their homogeneity could also indicate a higher sedimentation rate (i.e., shorter period of deposition).

A warm and humid climate during the Early Miocene favoured the widespread development of herbaceous mires and peat-forming *Taxodium* swamp forests in adjacent coastal lowlands of central Europe and northwestern Germany (Ziegler 1990; Figueiral et al. 1999; Kolcon & Sachsenhofer 1999; Bechtel et al. 2002). 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; Bechtel et al. 2002). The Sønder Vium assemblages extend the distribution of this paleovegetation type and imply swamp forests in coastal Denmark in the earliest Miocene. Modern analogues for these are the river swamp forests of the Mississippi delta, where the canopy is co-dominated by *Taxodium* and *Nyssa*.

Mesophytic forests dominated the vegetation in moderately wet areas further inland. The pollen spectra indicate that these were rather diverse forests incorporating both warm and cool temperate elements, although the latter dominate the assemblage. The most abundant warm temperate taxa in the mesophytic assemblage, besides Arecaceae, are Mastixiaceae, *Ilex* and *Engelhardtia*. *Pinus,* which is the most abundant taxon in the mesophytic forest, might also have been quite common in the better drained, sandy parts of the swampy forest (Zetter 1998).

The ground vegetation of the mesophytic forests and open areas of swamp forests was probably dominated by reed, sedges and pteridophytes. These groups maintain stable relative abundances and do not appear to have been influenced by transgressive/regressive events. This category of plants undoubtedly includes taxa derived from many habitats with varied characteristics.

In the lower part of the succession dinoflagellates are abundant, whereas fresh and brackish water algae are absent. An increase in fluvial input up-section is corroborated by higher percentages of *Botryococcus* (Fig. 4A, B). Higher in the studied succession freshwater palynomorphs such as *Sigmopollis* become more abundant, together with pollen derived from aquatic plants, such as Nymphaeaceae, indicating the occurrence of open freshwater ponds in the *Taxodium* swamp forests (Zetter 1998; Masselter & Hofmann 2005).

The individual elements of the family Poaceae are difficult to identify as the pollen grains of different genera do not show significant morphological differences. However, comparisons with the floristic composition of extant riparian swamp forests provide clues to the likely representatives of this family in the Miocene flora. In the palynological assemblages from Sønder Vium, it is most likely that the Poaceae would have been represented mostly by reeds and other hydrophilous graminoids rather than xeric grasses. As the relatively high abundance of Poaceae coincides with the strong representation of warm temperate taxa and Nymphaeaceae, it is possible that bamboo was a constituent of this swamp forest community. Bamboo has previously been recorded from several Neogene localities in Europe, both as macro and microfossils and coexisting with typical swamp forest taxa, such as Taxodiaceae-Cupresseace, *Alnus* and *Salix* (Worobiec & Worobiec 2005). In addition, the entomophilous pollen taxon Mastixiaceae, an autochthonous element, common in warm and humid climates (Masselter & Hofmann 2005), is also relatively abundant in the Sønder Vium assemblages. We contend that the palynological signal reflects a transition to a slightly cooler climate at the end of the Aquitanian.

The ratio between warm and cool-temperate taxa in the Lower Miocene of central Europe is typically 1:1 (Kolcon & Sachsenhofer 1999). This is not the case for the palynofloras in the succession studied here, which show a slight dominance of cool temperate elements. This is probably due to the higher paleolatitude of the studied area compared to previous studies carried out on sediments from central Europe.

The increased abundances of swamp forest pollen (Taxodiaceae-Cupressaceae group) at the levels of 286–284 m, 260 m, 257 m, and 254 m correlates well with increased relative abundances of dinoflagellates. Taxodiaceae-Cupressaceae pollen probably derives from swamp forest communities that dominated the lower delta plain. Interestingly, around the 260 m level the palynofloras contain relatively high percentages of hydrophilous taxa (Nymphaeaceae, Arecaceae, *Alnus*, *Salix*, Malvaceae and *Cyrilla*) presumably derived from riparian and coastal settings. This reinforces our interpretation that the lower portion of the studied succession was deposited in an inner-neritic environment during a transgressional event. In contrast, samples with abundant pollen of mesophytic forest plants above the 247 m level have low levels of dinoflagellates and swamp forest pollen, and these intervals may correspond to delta progradation.

Conclusions

The miospore assemblages from the studied succession of Sønder Vium are mainly well preserved and incorporate 95 terrestrial taxa. A near-shore pro-deltaic environment is suggested by dinoflagellates in all samples. The lowermost samples in the succession include abundant dinoflagellate cysts and probably represent a transgressional event. A late Aquitanian age is indicated by the presence of *Ephedripites*, *Platycarya*, and relatively frequent occurrences of *Engelhardtia*, together with the increasing levels of *Rhoipites pseudocingulum* (Anacardiaceae), and coeval decreasing amounts of Arecaceae.

Five distinct terrestrial plant associations, can be 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*. Previous work in Europe by Bechtel et al. (2002) and Kolcon & Sachsenhofer (1999) have shown that *Taxodium* swamp forests dominated central Europe. 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. They included both warm and cool temperate taxa, with a dominance of the latter. The presence of Arecaceae (palms) and other warm temperate taxa such as *Ilex* and *Engelhardtia,* Mastixiaceae together with the widely distributed *Taxodium* swamps, suggest that a warm temperate climate prevailed with slight climatic deterioration reflected in the upper part of the succession possibly corresponding to the climatic deterioration in the late Aquitanian.

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Paper III

North European climate evolution during the Miocene based on Danish palynological assemblages

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Abstract

A palynological investigation has been conducted on lower–upper Miocene drill core sediments from Jutland, Denmark, which correspond to the time interval between 20 and 8 Ma. The sediments were deposited in marine to marginal-marine environments, as shown by the relatively high abundance of dinoflagellate cysts in all samples. Nevertheless, rich and diverse pollen assemblages occur throughout and analysis reveals that in Denmark during the Miocene coastal areas were dominated by *Taxodium* swamp forests that also hosted terrestrial angiosperms such as *Nyssa*, *Betula*, *Alnus* and elements of the Myricaceae. Further inland, a mixed deciduous-evergreen forest prevailed. In areas with better drained soils, or on elevated areas, gymnospermous conifer-forests prevailed including taxa such as *Pinus*, *Sequoia* and *Sciadopitys*. Overall, the climate in the study area was warm temperate during major parts of the Miocene with mean annual temperatures between 15.5–20 ºC. By employing the Coexistence Approach combined with the method of grouping taxa in ecoclimatical groups, four different climatic events within the Miocene in Denmark and into northwestern Europe are detected within the studied sequence. The oldest, event (I) is a cooling in the beginning of the Burdigalian, at approximately 20 Ma, which coincides with the Mi-1a oxygen isotope excursion of Miller 1987, 1991. Event II is a further cooling period 18.5 Ma ago, which has not previously been described from the European terrestrial record. Next, at approximately 17 Ma, the warmest period occurred, and this event (III) in Denmark lasted from 17–14 Ma, corresponding to the globally recognized middle Miocene Climatic Optimum (MCO). Following this, a marked climate cooling initiating about 11 Ma occurred (event IV), which coincides with the beginning of the globally identified late Miocene Cooling (LMC).

Key words: palynology, Paleoenvironment, pollen, climate change, Miocene, MCO, LMC, Denmark.

1. Introduction

The Neogene has a complex history of global climate evolution, and one of the most interesting episodes was the Miocene. Significant global climate changes have previously been identified based on oxygen isotopes ($\delta^{18}O/\delta^{16}O$)from the marine realm (Miller et al. 1991). A marked oxygen isotope excursion occurs across the Oligocene-Miocene boundary followed by eight other similar excursions during the early to late Miocene. These anomalies in the oxygen isotopic record have been interpreted as sudden events indicating global cooling, the Mi-1 and Mi-4 glaciations, respectively (Miller & Katz 1987, Miller et al. 1991) linked to the expansion of the Antarctic ice sheet (Kocsis et al. 2009).

In Europe the Oligocene-Miocene boundary is characterized by temperate to warm-temperate climate (Utescher et al. 2000). Climate oscillations characterize the whole epoch (Kashiwagi & Shikazono 2003). In the early Miocene, global temperatures were increasing and a warm peak in the Aquitanian in Europe has been reported by Sittler (1967). The most prominent warming during the epoch occurred in the Middle Miocene, approximately 17–15 Ma ago, and this is referred to as the Miocene Climatic Optimum (MCO) (Zachos et al. 2001), which is a globally recognized event (Utescher et al. 2000). Following this at approximately 11 Mya, a distinct ”Late Miocene cooling” (LMC) cooling took place (Utescher et al. 2000; Turco et al. 2001). The decreasing temperatures were an early trend towards a global cooling in the late Miocene, accompanied with more frequent climatic oscillations in the Pliocene, with reports that the climate began to oscillate already in the late Miocene.

The main problem concerning the interpretations of the Miocene climate of Europe has been the difficulty in correlating continental deposits with the marine realm, and linking this to international chronostratigraphy. However, Danish sections with marginal marine deposition and enclosed palaeo- and palynofloras enable correlation between terrestrial and marine ecosystems, allowing links to be made and thus a better understanding of important global climatic changes.

Comprehensive palaeobotanical and palynological studies have been conducted on Miocene assemblages of 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; Ivanov et al. 2002), which show that generally a warm temperate to subtropical vegetation prevailed, with a humid/semihumid character, which influenced the changing floras during the Miocene.

The Miocene vegetation in Europe was more homogenous than at the present time. Broadleaved deciduous forests were most common in the northern parts, whereas mixed mesophytic forests were dominant in the central part. In wet areas, there were swamp forest associations (Utescher et al. 2007). Overall, however, the Broadleaved forests were only a minor component of the Miocene forests in Europe. Evergreen and thermophilous taxa are present in the pollen assemblages and peak during the globally recognized MCO. Subsequently, climate deterioration occurred as the LMC came into effect, which instigated a cooler climate with higher than previous seasonality (Utescher et al. 2000). At the LMC as a consequence of drier seasons and decreasing temperatures, the Broadleaved forests completely disappear from the central parts of Europe (Utescher et al. 2007).

Investigations of the Danish Miocene have mainly been based palaeo- and palynofloras collected from middle Miocene brown coal-bearing deposits in central Denmark (e.g., Ingwersen 1954; Koch et al. 1973; Christensen 1975, 1976; Friis 1975, 1977). An investigation conducted by Koch (1989) includes a comprehensive palynological study of the middle Miocene Søby-Falsterholt Flora, which revealed a diverse palynoflora. Based on his results, Koch (1989) concluded that swamp forests, bottomland hardwood forests, and forests adapted to slopes and well-drained soils were the dominant vegetation types: *Taxodium* was by far the most dominant taxa in the swamp forest; *Alnus*, *Ulmus* and *Acer* were common in the hardwood forest that bordered the swamp; in the more well-drained areas *Magnolia*, *Castanea* and *Juglans* were common. Koch (1989) also considered that the presence of only one tropical taxon and very few palaeotropical taxa indicated that the climate was neither tropical, nor subtropical but that the palaeoenvironment and palynofloral composition was very similar to the present-day flora in the bottomlands forests in SW North America (Alabama, Florida) and the mesophytic forests of what part of SW China. Despite these comprehensive works on the Middle Miocene of Denmark only a diminutive amount is known about the Miocene vegetation and concomitant climate evolution of northwestern Europe, and whether the climatic changes detected in other parts of Europe also include the north-west.

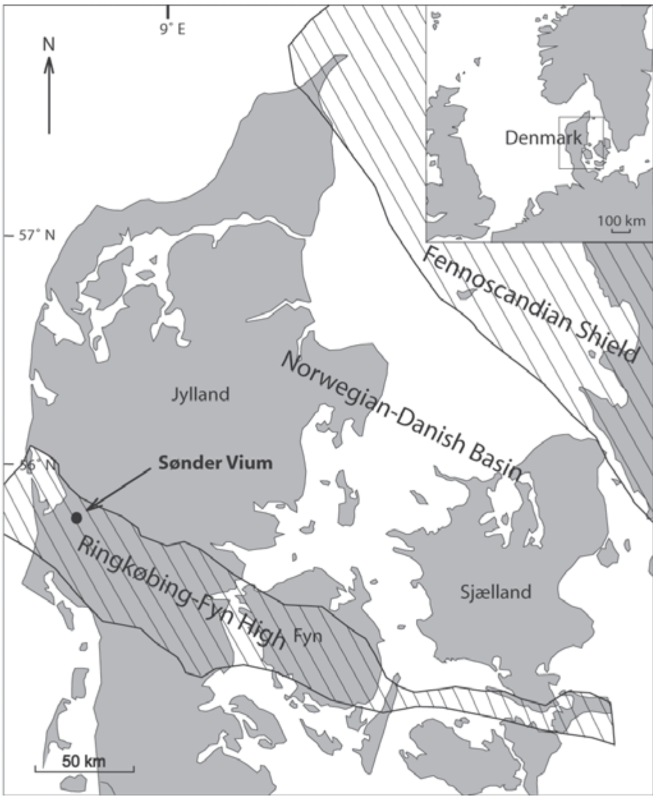


Figure 1. Location of the studied drill core in southern Denmark and the approximate trend of the shoreline in the early Miocene (based on Rasmussen 2005).

The present study is based on terrestrial palynology, which is an excellent tool for interpreting variations in palaeoclimate because the world's climatic zones are closely reflected by the distribution of different vegetation types. The extensive palynological material investigated in this study was derived from a cored section in Sdr. Vium on the Danish peninsula of Jutland (Fig. 1), which penetrates a unit spanning the lower to upper Miocene. Thus, the continuity seen in this drill core provides a unique opportunity to map climatic changes in Europe during the Miocene. A previous pollen analysis was conducted on the lower Miocene strata from the Sdr. Vium drill core (Larsson et al. 2006). However, the present work gives the first pollen analysis to bring continuous palaeovegetational information for the early to late Miocene in Denmark, which allows a reconstruction of vegetation, palaeoenvironment, palaeotemperatures and climate in northwestern Europe during that time. The analysis further aims to put the results into a broader, global context.

2. Geological setting

2.1 Palaeogeography and previous studies

The study area is situated near the eastern border of the North Sea Basin (Fig. 1), which during the Cenozoic was developed

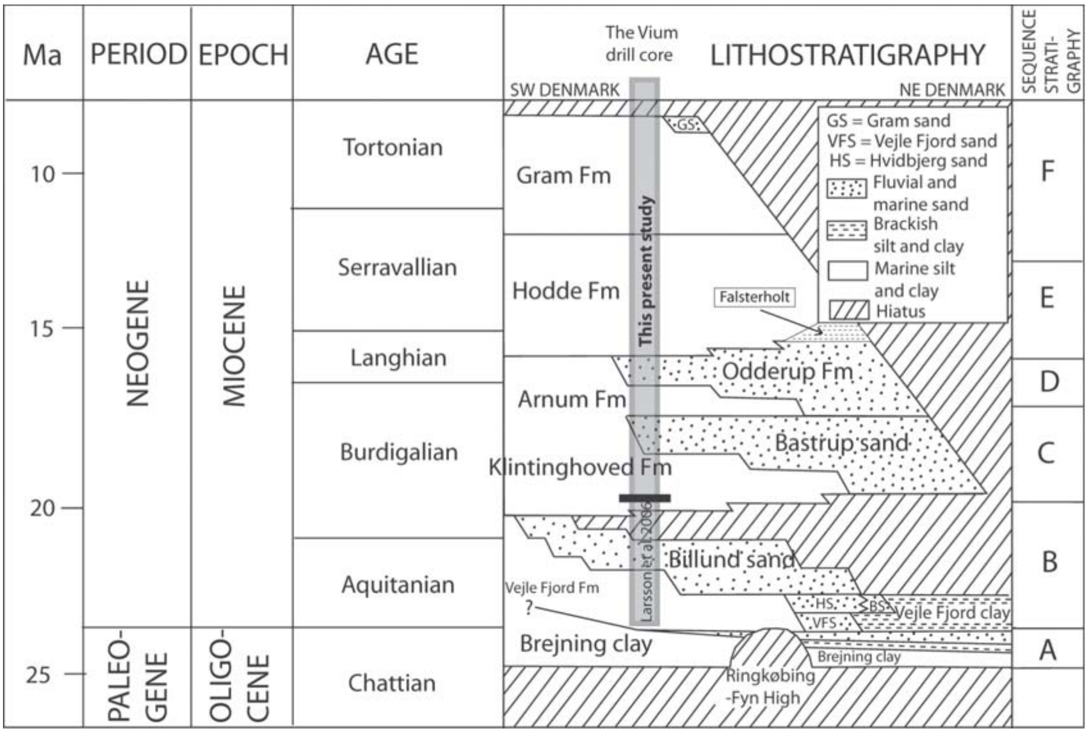


Figure 2. Miocene lithostratigraphy in Denmark and the approximate place of the Sdr. Vium drill core (based on Rasmussen 2005).

as an epicontinental basin with periodic connections to 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 towards the north and north-east by the Fennoscandian Shield; the southern limit was located within what is the area of northern Poland, Germany through northern France and the western border was probably located in what is the British Isles. The shape of the basin was influenced by the Alpine Orogeny (Vejbæk & Andersen 1987; Ziegler 1990) and also subjected to several other phases of tectonism from the Permian to the present (Rasmussen 2004a).

Through time, the basin was filled with voluminous sediments at various times, generating a complex stratigraphic architecture. Nevertheless, the geological history of the Miocene sedimentary succession in Jutland is relatively well known and is represented by a virtually complete sedimentary succession (Fig. 2).

The succession dips towards the southwest and has been partially removed by Neogene uplift and erosion (Rasmussen 2005). Consequently, the most complete Miocene deposits are present in the western part of the Jutland. Several studies (e.g. Larsen & Dinesen, 1957; Rasmussen 1961; Rasmussen, 2004a, b; Rasmussen & Dybkjær 2005) have revealed a complex interplay between climatic and eustatic sea-level changes and regional and local tectonics in the development of these sedimentary sequences.

The Miocene succession in Denmark has a well-established chronostratigraphic framework based primarily on dinoflagellate cyst (dinocyst) studies (e.g., Dybkjær 2004; Piasecki 1980; Dybkjær & Rasmussen 2007; Dybkjær & Piasecki 2008) and sequence stratigraphy (e.g. Rasmussen 2004b; Rasmussen & Dybkjær 2005).

2.2 Depositional history and stratigraphy of the Danish Miocene succession

Palaeocene and Eocene sediments of the eastern North Sea were deposited in an entirely marine setting resulting in clays. Uplift of the Fennoscandian area during the Eocene–Oligocene transition, resulted in deposition of fluvio-deltaic sands north of present day Jutland and fully marine clays in Jutland (Fig. 1). Due to eustatic sea-level fall in the latest Oligocene (Mi-1), a distinct shallowing is evident in the Danish succession, which also marks the beginning of the Miocene succession, the focus of this study.

The Miocene stratigraphic succession is characterized by several transgressive-regressive cycles, which generated five distinct depositional sequences, designated B to F in ascending order by Rasmussen (2004a, b) (Fig. 2).

The earliest Miocene transgression resulted in the deposition of organic-rich, restricted marine clays of the Vejle Fjord Formation (Sorgenfrei 1958; Larsen & Dinesen 1959; Rasmussen 1961; Rasmussen 2004b) and sand-rich fluvio-deltaic deposits of the informal Billund Sand (sequence B; Rasmussen 2004a, b). Subsequently, a minor transgression resulted in the accumulation of the marine, clayey prodelta sediments of the 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 in the Early Miocene (sequence C). This unit was overlain unconformably/disconformably by the upper part of the marine, clay-rich Arnum Fm.

The third and 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 Fm. (sequence D; Rasmussen 1961; Koch 1989). Major

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. The pollen and spore taxa identified in the Sdr. Vium drill core section, presented in palaeoenvironmental context and as palaeoclimatical indicators.

parts of the North Sea Basin was subsided during the late Langhian to Tortonian, which resulted in the deposition of fully marine clays of the Hodde and Gram formations, representing sequences E and F (Rasmussen 1961; Piasecki 1980).

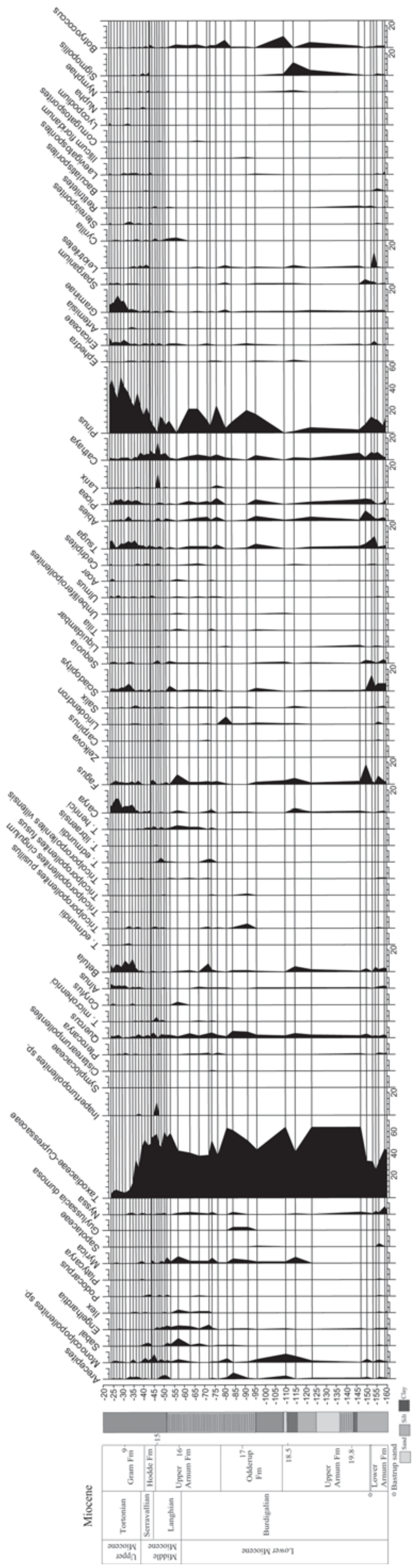
3. Material & Methods

3.1 The Sdr. Vium drill core — sample collection, chemical preparation and counting of palynomorphs

In total, 42 samples from a 160-meter interval of drill core were collected. All samples from the Sdr. Vium drill-core were prepared at the Geological Survey of Denmark and Greenland (GEUS) in Copenhagen using standard palynological methods (Poulsen et al. 1990) with HCl, HF, HNO_3 and then sieved through a 11 um mesh. In order to assess the quantitative composition of the assemblages, approximately 300 specimens were identified from each sample. However, some samples contained few palynomorphs, and in those cases as many specimens as possible were counted.

3.2 Taxonomical determination and palaeoenvironmental analysis

In this study, the botanical determination of pollen grains was used since the majority belonged to living plant genera that



have been represented since the Eocene. This approach allows interpretation of the palaeovegetation, ecology and climate (Moreno et al. 2005).

Owing to the difficulties in distinguishing between *Taxodium* and *Glyptostrobus* and certain other Cupressaceae under a light microscope, these taxa were all counted as Taxodiaceae-Cupressaceae (Kunzmann et al. 2009). *Sequoia* was separated from the Taxodiaceae-Cupressaceae family group because the pollen of the genus are more easily distinguished from other taxa in the family. In the final analysis I included *Monocolpopollenites* sp. within the Arecaceae.

In order to interpret the palaeoenvironment and vegetation, all pollen and spores recorded in this study have been assigned to groups that are based on the modern ecology of extant genera (Table 1), using categories based and modified from e.g. Moreno et al. (2005), Kolcon & Sachenhofer (1999), and Larsson et al. (2006). It must be remembered that the groups are artificial and some of the taxa included might have originally been present in different ecological environments. The groups used for palaeoenvironmental interpretation are (Table 1):

1. *Sea-coastal taxa*: represented by saline bearing elements;
2. *Swamp forest assemblage*: consists of plants that thrive in moist environments; included in this group are also riparian taxa since they are resistant to seasonal flooding;
3. *Deciduous-evergreen mixed forest group*: includes taxa that grew under better-drained conditions compared to the swamp forests. Hard-wood trees, shrubs and herbs are included in this group;
4. *Conifer forest group*: mainly composed of gymnospermous taxa that preferred drained environments and higher altitudes than group 3;
5. *High-altitude forest group*: constitutes a vegetation that preferred high altitudes;
6. *Freshwater taxa*: includes algae and freshwater plants;

Additionally, estimations of dinoflagellate cyst presence has been noted during counting in order to gain information regarding the depositional environment. However, the dinocysts have not been taxonomically identified or counted.

3.3 Palaeoclimate and palaeotemperature analysis

In order to interpret the middle and late Miocene climate of Denmark, the Coexistence Approach (CA) that was first introduced by Mosbrugger & Utescher (1997) was applied. This method is based on the assumption that the fossil plant taxa identified in Neogene sediments have similar climatic requirements to their nearest living relatives. The analysis aims to find the climatic interval in which all fossil taxa could co-exist. In this study I have focused on the variation of mean annual temperature. The taxa *Sequoia*, *Sciadopitys*, and *Cathaya* are not included in the CA-analysis because their nearest relati-

Figure 3. Detailed pollen diagram distributing the percentages of registered taxa from the Sdr. Vium drill core.

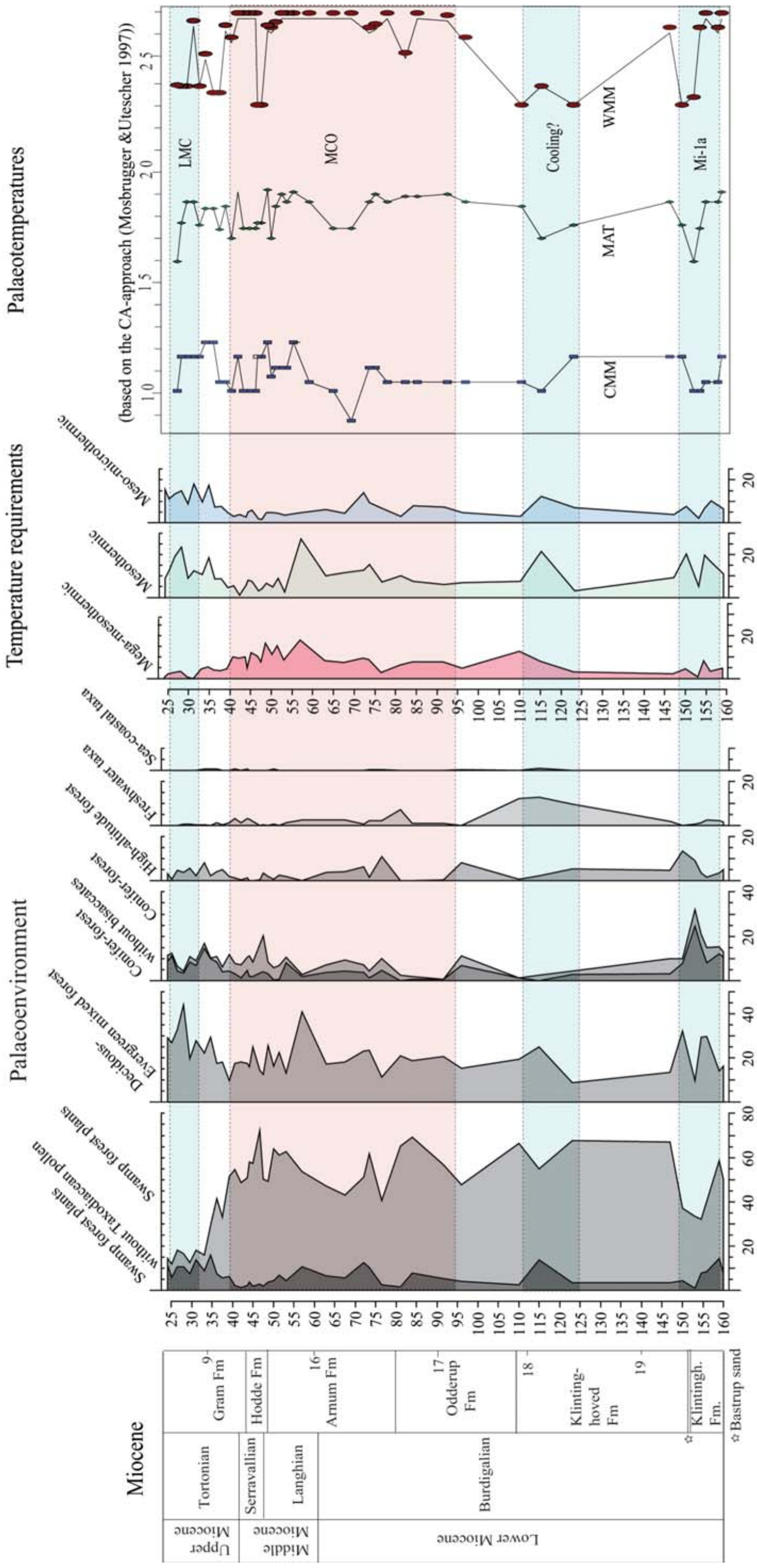


Figure 4. Diagram presenting the percentages of the eco-climatological and palaeoenvironmental groups in the Sdr. Vium drill core. The mean annual temperatures (MAT) in Denmark during the latest Oligocene to early Miocene calculated using the Coexistence Approach of Mosbrugger & Utescher (1997).

ves belong to extinct groups. Thus, assessing their climatic preferences would not provide accurate results in this study. Also, because of the difficulties in identification, I have excluded the Graminae, and the cool temperate taxon, *Larix* since the pollen of this genus is probably transported far distances by wind.

The results from the Sdr. Vium drill core CA-analysis have been compared to those from previous investigations (e.g. Kolcon & Sachsenhofer 1999; Figueiral et al. 1999; Ivanov et al. 2002; Mosbrugger et al. 1994, 2005; Utescher et al. 2009).

4. Results

4.1 Pollen analysis

All 41 samples in this study contained well-preserved palynological assemblages. Pollen and spores of 66 terrestrial taxa have been identified and these are shown in Figure 3. In addition, five freshwater algae and three marine taxa have been recorded. Reworked palynomorphs are rare. The assemblages are overwhelmingly dominated by gymnosperm pollen grains, comprising 45–89% of the total miospore sum, and particularly by Taxodiaceae-Cupressaceae and *Pinus*. Angiosperm pollen grains dominate the rest of the assemblages and only minor portions of spores are registered. Dinoflagellates are present in all samples. Photomicrographs of selected taxa are presented in Plate 1.

4.2 Palaeoenvironmental analysis

The different palaeoenvironmental groups are represented in Figures 3 and 4. Apart from a predominance of Swamp-forest taxa (assemblage 2), the

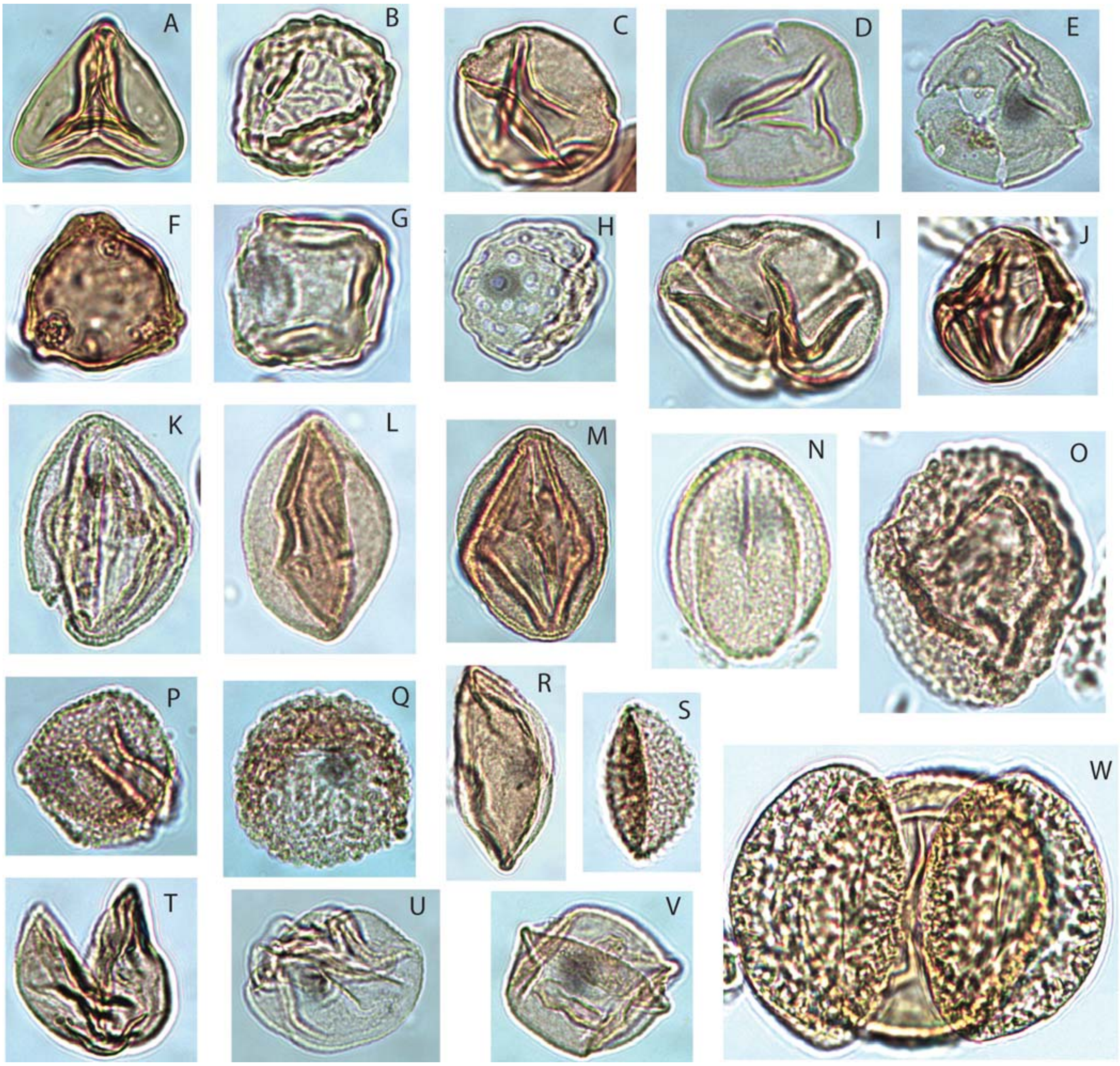


Plate 1. Photographs of abundant palynomorphs in the Sdr. Vium drill core. Photos are taken at x500. A. *Leiotriletes* sp., B. *Zelkova* sp., C. *Carya* sp., D. *Myrica* sp., E. *Engelhardtia* sp., F. *Betula* sp., G. *Alnus* sp., H. *Liquidambar* sp., I. *Fagus* sp., J. Sapotaceae , K. *Tricolporopollenites edmundii* , L. Quercus sp., M. *T. edmundii* , N. *Quercus* sp., O. *Tsuga* sp., P. *Sparganium* sp., Q. *Sciadopitys* sp., R. Arecaceae, S. Sabal sp., T. *Taxodium* sp., U. Taxodiaceae-Cupressaceae, V. Taxodiaceae-Cupressaceae and W. *Pinus* sp.

pollen spectrum shows that the Deciduous-evergreen taxa (assemblage 3) were the most abundant. These two groups comprise up to 72% and 41% respectively. Also the Conifer forest elements (assemblage 4) occur in great numbers, up to 61% in some samples. Less common is the high-altitude forest group (assemblage 5), which is represented by less than 13% in all samples. The group representing freshwater taxa (assemblage 6) varies in abundance between 0–13 %. The Sea-coastal environment group (assemblage 1) is represented by the single taxon *Ephedra*, which is a saline-bearing element. This group reaches 1% at most.

The dominant Swamp-forest plant group is mainly represented by the Taxodiaceae-Cupressaceae families. Common in this group are also riparian elements such as *Betula* and *Alnus*. The diverse deciduous-evergreen mixed-forest group includes trees, shrubs and herbs, most commonly *Fagus* (up to 18%), *Carya* (up to 14 %), and Arecaceae (up to 12%). *Quercus* is also present (up to 6%) as well as *Engelhardtia* (up 5%). The Conifer-forest group is mainly composed of gymnospermous taxa such as *Pinus* (up to 50%), *Cathaya* (up to 10%), and *Tsuga*, together with less abundant *Sequoia* and *Sciadopitys*. The High-altitude forest group is present in all samples represented by 0–12%. Freshwater taxa are mainly represented by the algae of *Botryococcus,* which comprise up to 10% in certain samples. Pollen taxa derived from the water lily Nymphaeae are also present in some samples.

4.3 Palaeoclimate

The coexistence approach (CA), based on the nearest living relative philosophy, as noted above, aims to reconstruct ranges that are tolerated by all of the nearest living relatives of the fossil plant taxa found in the samples. By using this approach on the miospore assemblages of this study, the mean annual temperature (MAT) during the early to late Miocene varied between15.5–20°C (Fig. 4). The coldest month mean (CMM) fluctuated between 8.5–12.5°C and the warmest month mean (WMM) between 22–27°C.

The pollen and spores have been divided into different groups based on their temperature preferences in order to further visualize the changes in the flora as a response to climate. The groups are modified from those defined by Kovar-Eder et al. (2001). The composition and percentages of these three groups are presented in Table 1 and Figure 4. The groups are:

1. *The mega-mesothermic taxa*: plants growing under a MAT between 20–24ºC, which corresponds to subtropical regions.
2. *The mesothermic group*: includes cool temperate plants that grow under a MAT between 14–20ºC in warm temperate regions.
3. *The meso-microthermic group*: consists of plants growing under 10–14ºC, which exist now in cool temperate regions.

The most common group is the group comprising mega-mesothermic plants, which also includes the dominant Taxodiaceae-Cupressaceae group (Fig. 4). The plants belonging to the Cool-temperate group are also strikingly common. Most assemblages in the samples are strongly dominated by either pollen belonging to the Taxodiaceae-Cupressaceae (T-C) or bisaccate pollen such as *Pinus*. Both of these taxa are of gymnospermous origin and known to produce vast amounts of pollen. 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 seaward distance to the coast and commonly reflect eustatic changes rather than climatic cooling (Moreno et al. 2005), a phenomenon known as the Neve's effect (Traverse 1988; MacDonald 1996). Consequently, the high proportion of these groups might mask other significant taxa and their importance in the pollen spectra. Thus, the Taxodiaceae-Cupressaceae and bisaccates have been excluded in the data sets presenting climatological changes (Fig. 4).

5. Discussion

5.1 Palynology

The presence of well-preserved pollen and spores in the Sdr. Vium samples mirrors the relatively short distance to the parent vegetation, and thus the assemblages probably reflect well the local palaeoenvironment. A rather near-shore environment is further indicated by the presence of freshwater algae in the samples. Although not counted, dinoflagellate cysts are present in all samples and bring further evidence of a marine environmental influence. The total dominance of gymnospermous pollen most probably signifies a true dominance of these elements in the nearby vegetation.

5.2 Palaeoenvironment

The dominance of swamp-forest taxa is evident in this study, which surely reflects the presence of extensive swamp forest adjacent to the depositional site. Such a flora inhabits wet environments and a good modern analogue would be the Bald cypress swamp forests of the southwestern USA. Even though *Taxodium* swamp forests were probably the most dominant vegetation, the extreme taphonomic dominance of their pollen grains might have been favored because of their size and shape. This is clear when removing the taxodiacean pollen grains from the data sets; when they are excluded one can clearly see that the rest of the taxa in the swamp-forest community remain relatively stable throughout the sampled interval, whereas *Taxodium* pollen amounts vary. Thus, the abundance of *Taxodium* pollen grains is to some degree linked to facies. An example of this is the marked decline in *Taxodium* in the beginning of the Gram Fm. There, only *Taxodium* decreases, not the other swamp-forest taxa. Hence, this is not a climatic signal. Instead, it probably occurs because of the subsidence of the North Sea Basin and a related rise in sea level (Rasmussen 2005). Consequently, the taxodiacean pollen grains are deposited in a more near-shore environment and taxa from different vegetations had the possibility to outnumber the otherwise predominant taxodiacean pollen. This interpretation is also supported by the increase in bisaccate pollen grains at the same level as the Taxodiaceae-Cuppressacea decrease, which is consistent with the previously mentioned Neve's effect.

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). These species-rich forests were inhabited by both deciduous and evergreen trees and shrubs; however, the deciduous elements prevailed and the evergreen elements are mostly smaller trees and shrubs (Kovar-Eder et al. 2001). This vegetation probably responds to Koch's (1989) hard-wood forests of the middle Miocene Søby-Falsterholt Flora. There is also a strong resemblance to the flora discerned by work conducted by Manum (1962) on material from Spitsbergen.

The conifer-forest group is an artificial group that was constructed herein as an analogy for a mid-altitude group including gymnosperms that thrive in well-drained areas, such as *Sciadopitys* and *Cathaya*. However, the genus *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. Nevertheless, I chose to include *Pinus* in this group as an aid to lump them to other bisaccates in this assemblage. In that way they have easily been excluded when seen to be disturbing and masking the results of other important taxa.

High-altitude forests consisting of cool-temperate gymnosperms are less common than the above-mentioned groups.

Surprisingly, in some samples their pollen reach 13% (Fig. 4), which is a fairly high amount when considering their temperature preference. However, they increase together with high amounts of freshwater taxa, which might imply that they are more represented in transgressional phases because they have the advantage of travelling longer distances than nonsaccate pollen grains. This is further evident as e.g., *Tsuga* and *Abies* occur in larger numbers together with other bisaccate taxa independent of eco-climatological preferences.

Freshwater taxa 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 in the marine depositional area. The only taxon representing a sea-coastal environment is *Ephedra*, and the low diversity within this group probably indicates that the coastal dunes were difficult to colonize since they consisted in migrating and unstable habitats.

The similarities between the palynological assemblages in this study and the ”Søby-Fasterholt flora” (Koch 1989), which were collected from the middle Miocene brown coal-bearing deposits in the central parts of Jutland are strikingly. As here, Koch (1989) concluded that the governing vegetation was the swamp-forest association bordered by a deciduous-evergreen mixed forest, which he referred to as a hard-wood forest. In the Søby-Fasterholt flora there are also indications of vegetation growing in upland areas, which Koch (1989) entitled the ”slope- or upland forest”. The latter probably corresponds to those designated ‘High-altitude forests’ herein. Other work conducted on the Sdr. Vium drill core (Larsson et al. 2006) reveals a similar composition of the paleoenvironment and vegetation. Thus it seems that, despite climate changes, the dominance of swamp forests prevailed throughout the Miocene.

5.3 Palaeoclimate

The palaeoclimatic trends have been discerned based on CA analysis revealing several climatic events during the deposition of the studied sediments of the Sdr. Vium drill core. The MAT varies between 15.5–20 ºC throughout the sampled section. This is consistent with that based on coeval palynological assemblages from Germany (Utesher et al. 2000). Four fluctuations (Fig. 4) are detected by the CA-method, which are also visible in the pollen assemblages that were constructed from the eco-climatologically preferred palaeotemperatures in the pollen assemblages.

The first event is recorded at a depth of 150–155 meters in the drill core (Fig. 4) where the MAT decreases from 20ºC to 15.5ºC. According to Rasmussen (2005), this interval represents an age of approximately 20 Ma, based on sequence stratigraphy in Denmark (Rasmussen 2003, 2005) and European stratigraphy (Berger et al. 2005). This event correlates with the Mi-1a event, 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). This event also coincides with an incursion of deltaic sediments called the Bastrup sand, which might indicate a sea level fall caused by increased glaciations on Antarctica.

The second cooling event recorded in the Sdr. Vium section occurs in the interval between 125–110 metres, corresponding to around 18.5 Ma. During this event the CMM and MAT drop only a few degrees, whereas there is a major dip from 26–22 ºC in the WMM. The floral response to this is a clearly marked increase in mesothermic and meso-microthermic taxa, and only a slight increase within the mega-mesothermic group. The change does not coincide with anything in the sedimentological record, which clearly indicates that it is climatically induced. Nonetheless, this particular event has not previously been detected in NW Europe, which might be due to the the lack of sediments of this age.

The third and most prolonged climatic trend, a warming trend, occurs in the sample interval 100–50 metres, which according to Rasmussen (2005) corresponds to an age of 17–14 Ma. The warming that can be discerned from the palynological record in this study perfectly matches the MCO that is detected all over the Northern Hemisphere (Utescher et al. 2000). Several previous palaeobotanical investigations have detected this warm interval (e.g. Thomson & Pflug 1953; von der Brelie 1967; Zagwijn & Hager 1987; Mai 1995; Ashraf & Mosbrugger 1995, 1996; Mosbrugger & Utescher 1997; Figueral et al. 1999; Utescher et al. 2000, 2007; Ivanov et al. 2007; Moreno et al. 2005; Mosbrugger et al. 2009). Even in Denmark this warming interval has previously been noted by e.g Ingwersen (1954); Koch et al. (1973); Christensen 1975, 1976; Friis 1975, 1978; and Koch 1989). As Koch (1989) also noted, there is a higher abundance of tricolporate pollen grains during this stratigraphic interval signifying the increase of *T. microhenrici, T. fusus* and *T. villensis*. In the marine realm, a corresponding signal to the MCO of the terrestrial record has been detected in oxygen isotopes from foraminifera (e.g. Miller et al. 1991; Zachos et al. 2001).

Based on the miospore assemblages from the Sdr. Vium samples, the WMM temperature stays more or less consistent at 27 ºC throughout the MCO. The Miocene Climatic Optimum is also the first detectable climatic change in this study indicating a warming phase. The MAT for the interval from late Burdigalian to late Langhian is 15–17 ºC and the CMM is rather unstable and varies between 9.5–12.5 ºC. However, earlier palaeobotanical and palynological studies conducted on Miocene sediments of Denmark have not included any method to estimate palaeotemperatures, hence these are the first numerical records from Denmark. Confusing in retrospect, Koch (1989) only identified one tropical, and few subtropical taxa in the Søby-Fasterholt flora, and thus referred it to a climate that was ”neither tropical, nor subtropical”, even though the assemblages are strikingly common to those found in this present study. Nevertheless, all studies in Europe, including this one (Fig. 4), identifying the MCO have detected floras with increase in mega-mesothermic elements and with a related decreased in the microthermic taxa. The most significant difference occurs in the Upper Arnum and Hodde formations, corresponding to the Langhian and Serravallian stages. There is a clear decrease in the meso-microthermic taxa and a clear increase in megamesothermic taxa. However, there is also an increase in mesothermic taxa, which might reflect a wider tolerance to a broader temperature interval.

The fourth and youngest of the climatic stages detected in this investigation commences at the end of the MCO at the sample levels 35–24 metres, which is the top of the Miocene succession present in the Sdr. Vium core. The change is interpreted as a cooling period initiating the Late Miocene cooling (LMC) with MAT decreasing from 19ºC to 16ºC during the deposition of the sedimentary sequence of Gram Fm. The age of this event according to Rasmussen (2005) is approximately 11 Ma ago. The cooling is also clearly visible in the CMM and WMM, which drop off from 13.5–10ºC and 27–24ºC, respectively. Abrupt cooling is indicated 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. However, all the palynological changes occur within a stratigraphical interval that differs in facies compared to older sediments. Therefore, this complicates the palynological interpretation.

The Gram Fm. was deposited in an open marine environment, and a major facies shift at the beginning of the unit coincides with the palynological evidence of climatic cooling. The lowermost part of the formation commences with a glauconite-rich layer and continues with the deposition of a fully marine clay (Rasmussen 2005). This would certainly affect the constitution of the palynological associations with an increase in bisaccate pollen grains and lesser occurrences of terrestrial pollen that could be expected. However, facies-related problems were already considered and addressed during the construction of the palaeoclimatological data sets (Fig. 4). Consequently, there was a marked cooling associated with the deposition of the Gram Fm. and the end of the Serravallian and beginning of the Tortonian in Denmark.

Further evidence of the LMC exists both in Europe and globally (Utescher et al. 2007). This LMC event ushered in, apart from decreasing temperatures, a higher degree of seasonality (Utescher et al. 2007). 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 Siberia (Nikitin 1988), for example, and Japan (Flower & Kennett 1994), where the beginning 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 earlier cooling has, therefore, been referred to as the middle Miocene Cooling, whereas in this study it is referred to the LMC.

6. Conclusions

Samples from the Sdr. Vium drill core from central Jutland have by the aid of palynology provided information regarding the palaeoenvironment and palaeoclimate of Denmark during an interval spanning the lower–upper Miocene, which corresponds to a time interval between 20–8 Ma. The studied succession was deposited in a marine depositional environment, as shown by the relatively high abundances of dinoflagellate cysts in all samples. Even so, there are rich and diverse pollen assemblages throughout the sampled interval. During the Miocene of present-day Denmark, the coastal areas were dominated by *Taxodium* swamp forest. Further inland, a mixed deciduous-evergreen forest prevailed and in areas with better drained soils, or on elevated areas, gymnospermous conifer-forests prevailed. Pollen representing the upland vegetation probably derived from the Fennoscandian peninsula and constitutes relatively abundant cool-temperate pollen taxa. The combination of using the Coexistence Approach (Mosbrugger & Utescher 1997) and splitting the taxa into eco-climatological groups has provided new information regarding the Miocene climate of Denmark and Northwestern Europe.

The mean annual temperature throughout the sampled interval ranged between 15.5–20 ºC and four climatic events are detected. The first (oldest) identified is a cooling in the beginning of the Burdigalian, approximately 20 Ma, which coincides with the Mi-1a oxygen isotope excursion of Miller et al. (1991). The second event is also a slight cooling period at 18.5 Ma, which has not previously been described from European palaeobotanical investigations. Beginning at approximately 17 Ma was the warmest period that occurred in Denmark, lasting for approximately 3 My, which is also recognized throughout the Northern Hemisphere as the middle Miocene Climatic Optimum (MCO). Following this, a marked climate cooling is evident and is related to the previously well-known, late Miocene Cooling (LMC).

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