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Research paper

A palynofacies study of past fluvio-deltaic and shelf environments, the Oligocene-Miocene succession, North Sea Basin: A reference data set for similar Cenozoic systems

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A R T I C L E I N F O

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A B S T R A C T

Correct interpretations of depositional environments are fundamental for evaluating the geological history of a sedimentary basin. Palynofacies analyses are a valuable supplement to sedimentological and seismic studies. In order to develop a palynofacies reference dataset for fluvio-deltaic and shelfal successions, a study of the assemblages of sedimentary organic particles from seven different well-defined depositional environments within the uppermost Oligocene – lower Miocene succession onshore Denmark (eastern North Sea Basin) has been performed. The study deals with the following environments; floodplain, lagoon, washover-fan flat, prodelta, shoreface, offshore transition and shelf.

The sedimentary organic particles were grouped into four major categories; 1) Structured wood particles, 2) Amorphous organic matter (AOM, in the present study mainly consisting of partly degraded vitrinite), 3) Cuticle and membranes and 4) Palynomorphs. The palynomorphs were grouped into eight subcategories; 1) Microspores, 2) Non-saccate pollen, 3) Bisaccate pollen, 4) *Botryococcus*, 5) Other freshwater algae, 6) Fungal hyphae and –spores, 7) Acritarchs and 8) Organic-walled dinoflagellate cysts.

A combination of a univariate box plots and a multivariate Principal Component Analysis (PCA) of the palynofacies data clear revealed the quantitative characteristics and variations within each discrete environment as well as their principal similarities and differences. In spite of some natural overlaps, for example between the lagoon and offshore transition environments, the data revealed distinct characteristics, e.g. a strong dominance of wood particles in the shoreface environment, a strong dominance of bisaccate pollen in the washover-fan flat environment and a near absence of dinocysts in the floodplain environment. An overall increase in relative abundances of dinocysts and a decrease in abundances of non-saccate pollen in the proximal-distal trend were also outlined.

This study outlines a palynofacies reference dataset that can be used as a tool for interpreting depositional environments in equivalent settings, preferentially combined with other information such as seismic data, well logs, and/or lithology.

1. Introduction

During the last 15 years the uppermost Oligocene to Miocene succession onshore Denmark has been studied intensively, with main the purpose to develop a 3-dimensional model for the fluvio-deltaic sand layers within the succession, as they are important groundwater reservoirs (aquifers). A huge dataset from more than 50 boreholes, 25 outcrops and a number of seismic profiles has been generated and the geological development in the area is therefore very well known (Fig. 2) and well documented through a series of papers, e.g. Rasmussen (2004a; 2004b; 2014), Rasmussen and Dybkjær (2005), Rasmussen et al. (2006, 2010), Hansen and Rasmussen (2008) and Dybkjær and Piasecki (2010).

The assemblage of sedimentary organic particles (the palynofacies) in a sediment sample reflects the depositional environment in which the sediment was deposited. Different depositional environments will have

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a different composition of organic particles, e.g. lagoonal clay will have a higher content of terrestrial palynomorphs (spores and pollen) and of freshwater algae than for example clay deposited in an offshore setting. In contrast, offshore clay will contain higher relative abundances of marine algae, e.g. dinoflagellate cysts (dinocysts) – see also the comprehensive evaluations of this matter by Traverse (1994) and Tyson (1995) and references therein.

Palynofacies studies are therefore a good tool for interpreting the depositional history of a study area, providing information about; i) The type of sedimentary setting (i.e. either marine, brackish or freshwater) (Traverse, 1994; Tyson, 1995). ii) Deepening or shallowing upwards trends for a succession. Increase in e.g. non-saccate pollen, microspores and/or freshwater algae and fungal hyphae and spores in a succession otherwise interpreted to be fully marine, may be a good indication of a prograding coastline, either due to a eustatic sea-level fall or to increased sedimentation rates. In contrast, an increase in abundance of dinocysts and of bisaccate pollen is a good indicator of deepening/flooding events (Tyson, 1995; De Vernal, 2009). iii) Positions and types of stratigraphic surfaces such as sequence boundaries, flooding surfaces and other surfaces important for subdividing into system tracts and thus strengthening the predictive tool of sequence stratigraphy (Tyson, 1995). Sequence boundaries may be identified as a break in the natural succession of environments, indicating an unconformity (Catuneanu et al., 2011). Flooding surfaces may, in the distal parts of a fluvio-deltaic system, be recognized as levels with increased abundances of dinocysts. In more proximal portions, a flooding surface may be indicated by a sudden influx of dinocysts into an otherwise fluvial succession (Tyson, 1995). iv) Positions and types of system tracts, e.g. forced regression and transgressive system tracts. The former should be identified by a dominance of floodplain environments and the latter by the dominance of lagoonal and estuarine environments (Rasmussen, 2009a). Good reservoirs are commonly associated with forced regression; clean and thick sand deposits have for instance been found on the delta platform of the Billund Formation (Rasmussen and Bruun-Petersen, 2010). Well-developed basin-floor fans are also commonly associated with forced regression (Hunt and Tucker, 1992). Tidal bars and barrier complexes are the typical reservoirs found in transgressive system tracts (Catuneanu et al., 2011).

In order to interpret the palynofacies data from a specific sediment sample, or a series of samples, it is helpful to have a robust and synoptic reference dataset from a comparable and coeval succession; same time-interval, similar climate (humid, warm-temperate), similar tectonic regime – ideally from the same basin. The purpose of the present study was to develop a robust reference dataset of palynofacies that documents the characteristic assemblages of organic particles within seven sedimentologically well-constrained shallow-marine depositional paleo-environments. The palynofacies data are obtained from sediment samples collected from the uppermost Oligocene – lower Miocene succession onshore Denmark (eastern North Sea Basin). The succession covers seven environments; Floodplain, lagoon, washover-fan flat, prodelta, shoreface, offshore transition and shelf (Fig. 1). The distribution of palynofacies is presented in univariate box plots. The data are also analysed using multivariate data analysis, Principal Component Analysis (PCA), targeting the palynological data in the conventional format using relative frequencies based on the total number of counts, see further below. The PCA approach reveals simultaneous discriminating trends and correlations between all characterizing variables used in the study, both discriminating features *between* the depositional environments as well as the dominant *within*-environment specifics. As part of the PCA a small number of distinct *outliers* were identified, which were carefully documented and investigated. Comprehensive arguments are presented for why these were removed from analysis of the coherent core of the data corpus. The reference dataset presented here will provide an important supplementary help for interpretation depositional environments from coeval successions.

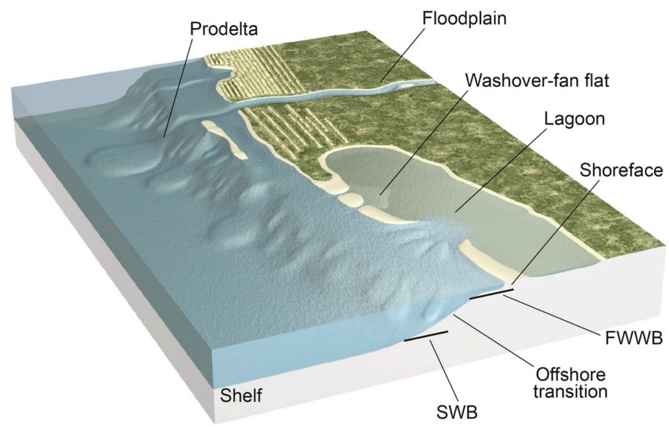

Fig. 1. Schematic figure showing the seven depositional environments. FWWB: Fair weather wave-base, SWB: Storm wave-base.

1.1. Previous studies

Studies of the distribution of sedimentary organic particles in recent environments have formed the base for interpreting palynofacies data obtained from older deposits. In the classical study from the Orinoco delta, Muller (1959) studied the distribution of sedimentary organic particles in different parts of the delta, especially the dispersal of pollen grains. His results illustrated the gradual settling of pollen in the marine environment during transport away from the source area (the local swamp areas and the river mouths). Muller (1959) concluded that "palynology, in conjunction with sedimentological studies, can make a valuable contribution to paleogeographic interpretation". Mudie (1982) studied the spore- and pollen distribution in recent marine sediments off eastern Canada. She concluded that the overall pollen and spore concentrations decreased offshore as a function of distance from vegetation sources (and northwards as a function of lower vegetation density north of the summer Arctic Frontal Zone). In addition, she registered a selective offshore transport of bisaccate pollen, which she interpreted as reflecting wind transport combined with the floating abilities of bisaccate pollen ("Neves effect") (Traverse, 1994).

One of the studies dealing with the palynofacies analysis in a geological record was published by Roncaglia and Kuijpers (2006). They studied palynofacies assemblages from the last 1500 years in sediments from Greenland, in the Faroe Islands fjords and from North Atlantic deep-water sites. They concluded that the distribution of particulate organic matter at high latitudes is controlled by the distance from the shore and water depth.

One example of a combined palynofacies and palynological study from the Cenozoic in the North Atlantic region comprise the study of Eldrett and Harding (2009) in which they reconstructed the subsidence history of the Eocene–Oligocene transition on the Outer Vøring Plateau (the Norwegian - Greenland Sea).

Palynofacies studies and studies of pollen assemblages of the late Eocene to Miocene succession at the New Jersey margin, were used to interpret changes in vegetation, climate and relative sea-level (e.g. McCarthy et al., 2013; Kotthoff et al., 2014; Prader et al., 2017).

In a series of three recent publications McArthur et al. (2016a, 2016b, 2017) presented a palynofacies classification scheme aiming to assist the interpretation of submarine fan environments. Their study is based on samples from the well-studied outcrops of the Miocene Marnoso-Arenacea Formation, Appenines, northern Italy.

Previous (traditional) palynofacies studies from the upper Oligocene – Miocene in the North Sea Basin are confined to Dybkjær (2004); Rasmussen and Dybkjær (2005), Rasmussen et al. (2006) and Śliwińska et al. (2014). These studies all present palynofacies analysis closely corresponding to the one presented here, aiming to supply data useful

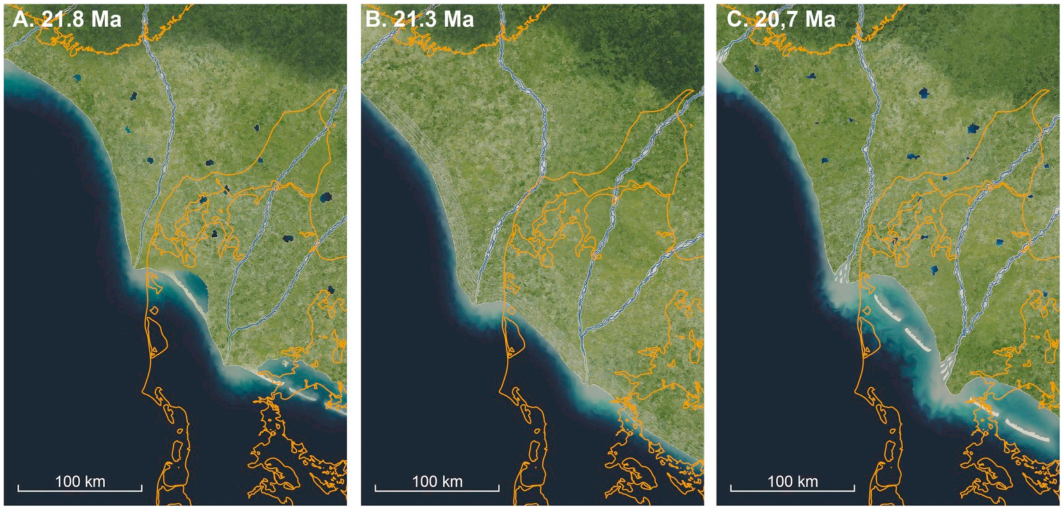

Fig. 2. A-C.- Detailed paleogeographic maps for the study area in the uppermost Oligocene – lower Miocene, Jylland, showing rivers, deltas, estauries, barrier islands, etc. Modified from Rasmussen et al. (2010).

for the interpretation of the depositional environments. Larsson et al. (2010) studied the spore- and pollen assemblages in the uppermost Oligocene – lowermost Miocene successions in the Dykær and Hindsgavl outcrops in the eastern part of Jylland, and included the relative abundances of *Botryococcus* and the marine versus terrestrial palynomorph-ratio in addition. An increase in the relative abundance of bisaccate pollen was interpreted to indicate an increase in relative sea-level (the "Neves-effect") rather than a change towards a colder climate. In a study from the southern part of the North Sea Basin Donders et al. (2009) applied the relative amount of terrestrial palynomorphs for indicating variations in terrestrial run-off. Furthermore, they used variations in the dinocyst assemblages for interpreting variations in sea surface temperatures and variations in the pollen records for interpreting variations in terrestrial temperatures.

2. Geological setting

The eastern North Sea Basin area was formed as a result of Mesozoic rifting and subsequent thermal sagging (Ziegler, 1990). In the late Mesozoic and Tertiary inversion tectonism dominated the development of the basin (Ziegler, 1990; Mogensen and Korstgård, 1993; Rasmussen, 2009b; 2013). One of these inversion pulses was in the Miocene. The overall compressional regime formed by the Alpine Orogeny and the opening of the North Atlantic, also resulted in uplift of the Fennoscandian Shield during the Neogene (Japsen et al., 2007; Gabrielsen et al., 2010). Due to uplift of the shield, sediments were shed into the basin from the north and northeast.

In the Late Oligocene a shelf setting dominated. The water depth was more than 200 m (e.g. Rasmussen et al., 2010). The basin was sediment starved which resulted in the formation of glaucony rich sediments. Associated with inversion of the Norwegian-Danish Basin in the latest Oligocene, transient progradation of the shoreline occurred, but the shoreline only reached the easternmost part of the study area.

In the early Miocene the North Sea was a restricted basin, with only a narrow connection to the North Atlantic between the Shetland Islands and present day Norway. The lower Miocene succession comprise three periods of shoreline progradation (Fig. 2). The first two prograding systems, the Billund and Bastrup formations (Fig. 3), consist of wave-dominated deltas. The delta progradation occurred into water depth of up to 100 m. Due to the location in the westerly dominated wind-belt, spit and barrier systems with lagoons formed southeast of the main deltas (Rasmussen and Dybkjær, 2005; Rasmussen et al., 2010). In the initial phase, associated with inversion tectonism, braided fluvial river-systems dominated, but later in the early Miocene, the rivers were predominantly meandering river-systems (Rasmussen, 2009b; 2015; Rasmussen et al., 2010). The third prograding system, the Odderup Formation, was formed in shallow water and thus characterized by coastal plains with widespread lagoons and swamps. The three prograding systems are separated by marine mud referred to the Vejle Fjord, Klintinghoved and Arnum formations. This overall pattern of progradation and transgression was controlled strongly by eustatic sea-level changes and correlate with the so-called Mi glaciations (Miller et al., 1991; Rasmussen, 2004a). The climate was warm temperate to subtropical and humid, ca. 1500 mm annual precipitation (Larsson et al., 2011; Rasmussen et al., 2013). The coastal areas were dominated by Taxodium swamp forests also hosting other angiosperms such as *Alnus*, *Betula*, *Nyssa* and *Salix*. A mixed deciduous-evergreen forest hosting e.g. *Areacaceae*, *Carya*, *Engelhardia*, *Fagus*, *Ilex*, *Liquidambar*, *Podocarpus*, *Sabal* and *Ulmus* prevailed further inland, while gymnosperm conifer forests of *Abies*, *Cathaya*, *Larix*, *Picea*, *Pinus*, *Sequoia*, *Sciadopitys* and *Tsuga* grow in the more well-drained hinterland and in elevated areas (Larsson et al., 2010, 2011).

3. Depositional environments

The samples included in the palynofacies study come from one of the following seven well-documented depositional environments; floodplain, lagoon, washover-fan flat, prodelta, shoreface, offshore transition and shelf (Fig. 1). In the following, the criteria for identifying each of these environments/facies associations, based on sedimentology and seismic data, will be presented. Samples were preferentially taken from outcrops. Outcrops provide the most reliable identification of the depositional environments. However, the prodelta and shelf environments were not represented in outcrops and samples from these environments thus had to be collected from boreholes. See Fig. 4 for the location of outcrops and boreholes. In the boreholes, the seismic patterns combined with lithology formed the basis for identifying the depositional environments. A correlation of the studied outcrops and boreholes is presented in Fig. 5. This correlation shows how the interpretations of the outcrops and borehole successions have supported each other. No samples have been analysed from the "delta plain" and the "fluvial sand and gravel" environments. Samples from the former environment have never been sampled for palynology, while deposits from the latter environment does not contain any organic microparticles due to the very high energy level in this environment. Each of the sampled boreholes are located close to a seismic line and the depositional environment of the intersected successions has been interpreted based on a combination of the seismic data and the borehole

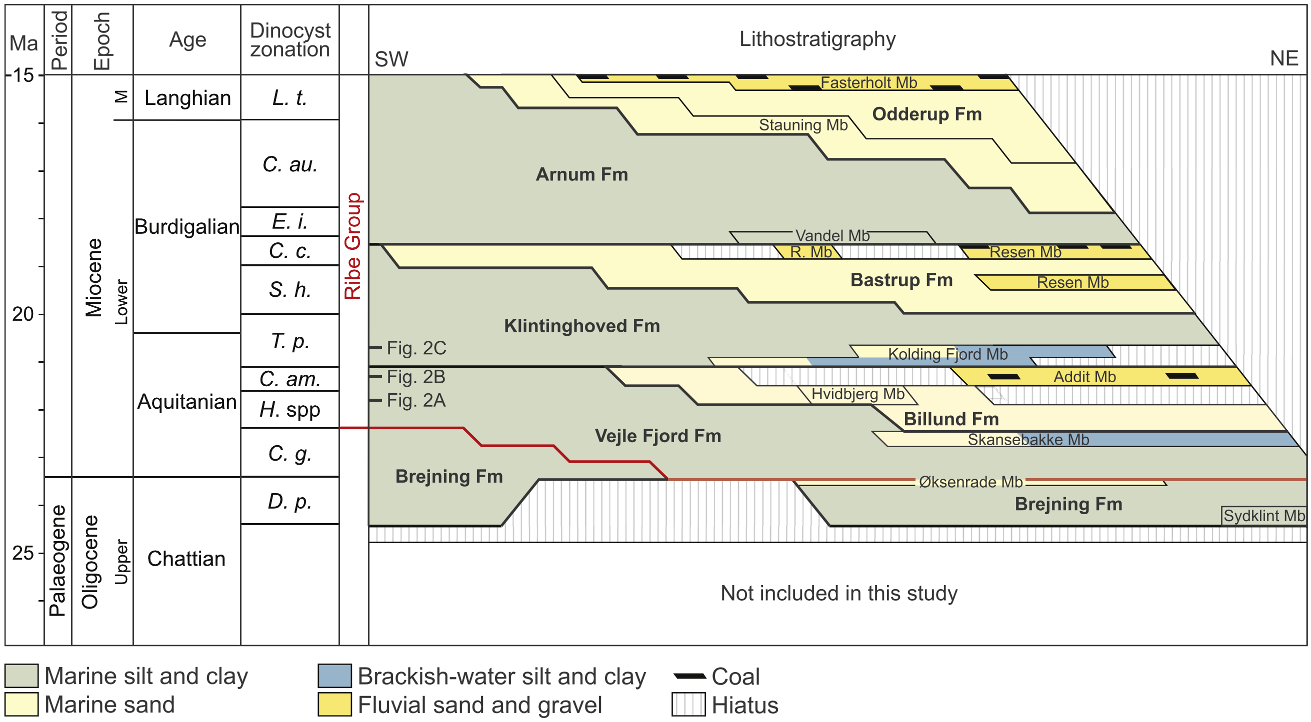

Fig. 3. Lithostratigraphic scheme, chronostratigraphy and dinocyst zonation. Modified from Rasmussen et al. (2010). The time intervals represented by the palaeogeographical maps shown in Fig. 2 are indicated. *D. p.*: *Deflandrea phosphoritica*; *C.g.*: *Chiropteridium galea*; *H.* spp: *Homotryblium* spp.; *C.am.*: *Caligodinium amiculum*; *T. p.*: *Thalassiphora pelagica*; *S.h.*: *Sumatradinium hamulatum*; *C. c.*: *Cordosphaeridium cantharellus*; *E. i.*: *Exochosphaeridium insigne*; *C. au.*: *Cousteaudinium aubryae*; *L.t.*: *Labyrinthodinium truncatum*.

log/lithology (Rasmussen and Dybkjær, 2005; Hansen and Rasmussen, 2008; Rasmussen, 2009a; 2014) (Fig. 6). The interpretations of the depositional environments in the outcrops are based on detailed sedimentological studies, including studies of lithology variations, sedimentary structures and tracefossils (Friis et al., 1998; Rasmussen and Dybkjær, 2005; Rasmussen, 2014) (Fig. 7a–h). The tracefossils terminology applied in our study is described in McIlroy (2004).

The abbreviations indicated in parentheses after each subheading below are those used for the depositional environment/facies association in question in the PCA analysis (Figs. 10–20; Appendices 1a,b). Each abbreviation is followed by a color denoting the polygon representing the specific depositional environment/facies association in the PCA-plots.

Flood-plain Facies Association (F; green); The flood-plain facies association is composed of dark brown mud alternating with sand layers up to 10 cm in thickness (Fig. 7a). The sand layers are homogenous to inverse graded and interpreted as crevasse splays (Rasmussen, 2014). Rootlets are found in the upper part of crevasse splays. Thin coal-layer and scattered macro-scale wood particles are common (Fig. 7b).

Lagoonal Facies Association (L; purple); The lagoonal facies association consists of dark brown mud with an organic content of 5–10% (Fig. 7c). The facies association is normally heavily bioturbated, but discrete wave-ripples and tidal rhytmites may be visible (Rasmussen and Dybkjær, 2005). Lignite occurs especially in the upper part of the facies. A lag of lignite may occur capping the facies.

Washover-fan flat Facies Association (W; orange); The washover-fan flat facies association (NCSS, 2005) is dominated by fine-grained, yellowish to white sand deposited as washover fans (Rasmussen and Dybkjær, 2005; Rasmussen et al., 2010, Fig. 7c). The succession formed gently dipping clinoforms. The trace fossil assemblage is characterized by *Macaronichnus* (Fig. 7d), but *Ophiomorpha* and *Diplocraterion* may occur.

Shoreface Facies Association (SF; yellow); The shoreface facies association (i.e. Dashtgard et al., 2012) is composed of white, fine-to medium-grained sand. Hummocky -, swaley cross-stratified sand and other tempestites, dominate the facies association (Fig. 7e). Thin, light brown mud beds occur in isolated troughs in the distal part of the facies or associated with fair-weather wave ripples (Rasmussen and Dybkjær, 2005; Rasmussen et al., 2010). The trace fossil assemblage is dominated by *Ophiomorpha* (Fig. 7f), but *Skolithos* and *Diplocraterion* has also been found.

Prodelta Facies Association (P; brown); This facies association, corresponding to delta platform slope facies, is limited to successions covered by seismic data and boreholes (Fig. 6). It consists of alternating dark brown mud and white, medium to cross-grained sand. Amalgamation of sand is common in the upper part of the delta platform succession and dominates the down drift portion of the delta platform (Rasmussen and Bruun-Petersen, 2010). Pebbles occur as lags at the base of discrete sand beds and clasts up to 4 cm are found scattered within the succession. On seismic data, the prodelta facies is characterized by clinoforms dipping 2–7° and migration azimuths of 135°–225°. The clinoform height is commonly between 50 and 100 m.

Offshore Transition Facies Association (O; dark blue); Offshore transition facies association consists of alternating brown to dark brown mud and wave-rippled sand. Hummocky cross-stratified sand layers (Fig. 7g) are common in the proximal part of the offshore mud. The trace fossil assemblage is characterized by *Scolicia, Schaubcylindrichnus* and *Chondrites* (Fig. 7h).

Shelf Facies Association (S; light blue); A shelf is defined by a depositional package with a low gradient surface (< 0.1°) and formed at water depths of more than 70 m (Fig. 1). The shelf facies association is represented only in successions covered by seismic data and boreholes (Fig. 6). It is composed of dark brown and dark grey mud. The pyrite content is between 1 and 10% (Rasmussen and Larsen, 1989; Rasmussen, 1995) and at certain levels glaucony is common. The organic content varies from 2 to 5%. Shells are present but mostly dissolved.

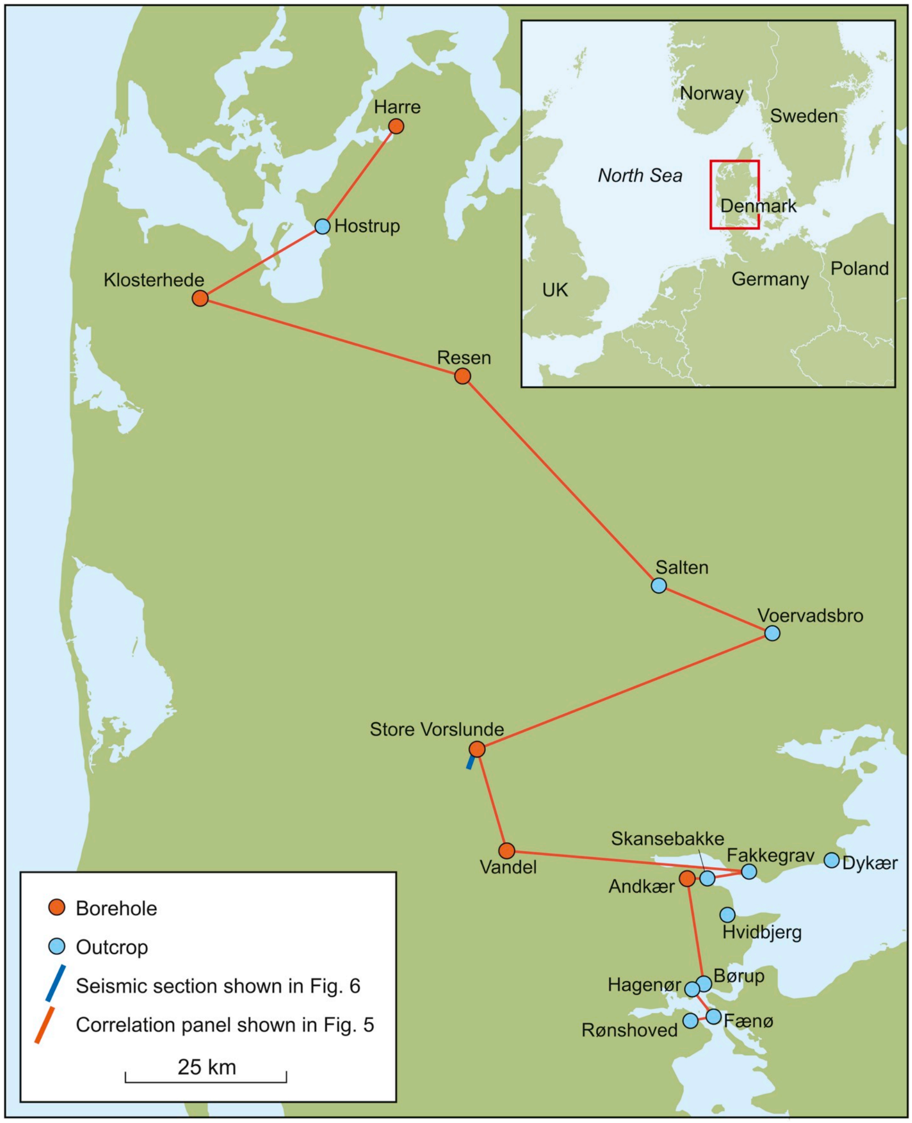

Fig. 4. Location of studied boreholes and outcrops and locations of correlation panel shown in Fig. 5 and of seismic line shown in Fig. 6.

4. Material and methods

Spreading, transport and deposition of organic particles is a complex story with many influencing factors. The origin of the organic particles (terrestrial vs. marine) and the transport mechanisms (e.g. wind, water) are important. The depositional energy-level has a strong sorting effect and post-depositional degradation has different impact on selected particles. For more detailed discussions of these effects, see e.g. Traverse (1994), Tyson (1995) and Appendices 2a,b.

During the latest Oligocene – early Miocene time, swamp forests, covering large parts of the coastline, delivered large amounts of wood particles, partly degraded vitrinite (here referred to as amorphous organic matter, AOM, see example in Fig. 8 D) and cuticle to the lagoonal and nearshore marine depositional settings. Terrestrial palynomorphs (spores and pollen) were deposited on land and in ponds and lakes, and some of them were transported to the sea by wind, streams and rivers. Some of the terrestrial palynomorphs were probably deposited directly into lagoons and in the sea from the swamp forest covered shorelines. Limnic/fluvial palynomorphs (freshwater algae, e.g. *Pediastrum*, *Mougeotia laetevirens*, *Pseudokomewuia* aff. *granulata* and the brackish-water tolerant freshwater algae *Botryococcus*) thrived in freshwater and brackish-water environments (floodplains, ponds, lakes, lagoons) and were transported into the sea via the large rivers and delta-systems (e.g. Friis, 1975, 1977, 1978; Koch, 1989; Larsson et al., 2006, 2010; Rasmussen et al., 2010). At the same time marine algae, especially dinoflagellates, thrived in the marine depositional environment (Rasmussen and Dybkjær, 2005; Dybkjær and Piasecki, 2010; Śliwińska et al., 2014). The variations through time, in the studied succession, in the relation between the terrestrial/fluvial and the marine palynomorphs probably reflect the global climatic variations in the latest Oligocene – early Miocene and the resulting variations in eustatic sea-level (e.g. Miller et al., 2005).

In the following collection of a series of samples representing the fluvio-deltaic and shelf environments in the uppermost Oligocene – lower Miocene succession in the western part of Denmark was carried out. The preparation and counting methods are outlined and the methods used for data analysis are presented.

4.1. Sampling

The present study is based on a total of 169 sediment samples, collected from 6 boreholes and 11 outcrops (Figs. 4 and 5). All analysed samples are listed in Appendices 1a,b.

Outcrop samples were collected during a total of 17 years of fieldwork campaigns in the period 1999–2016. The samples were selected randomly from each of the well-defined depositional environments in

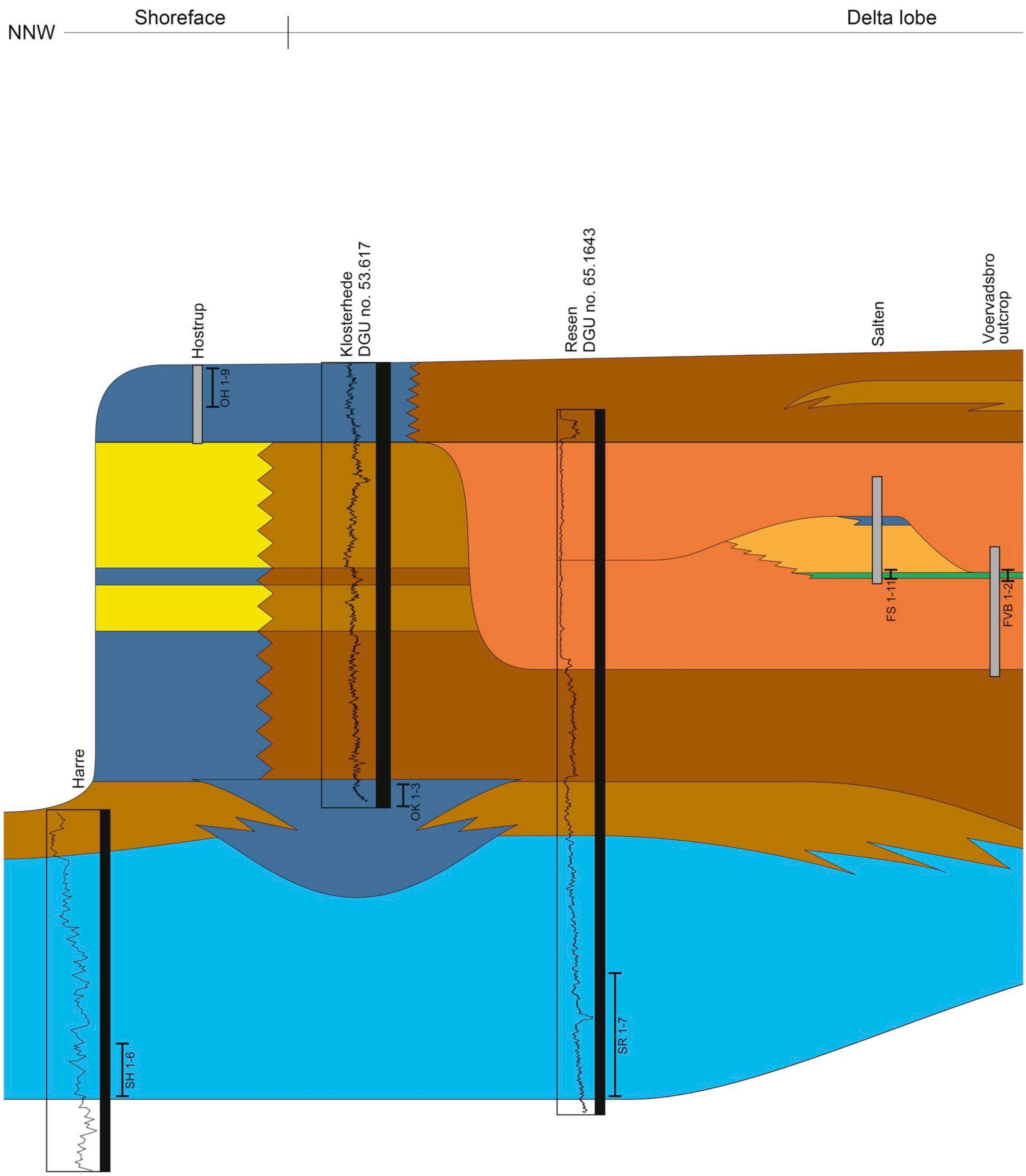

Fig. 5. Log-correlation panel showing sample locations in boreholes and outcrops (compare with "Samples" in Appendices 1a and 1b) and illustrating the depositional environments. In order to show a simplified geological model of a NNW-SSE striking correlation of the studied boreholes and outcrops, it was necessary to exclude the two outcrops Hvidbjerg and Dykær. All samples from the Hvidbjerg outcrop (samples SFH 1–11) represent shoreface deposits and were sampled within the Hvidbjerg Member, see further Rasmussen et al. (2010; their Figs. 31 and 33). The position of the two lagoonal samples from the Dykær outcrop (LD 1–2) are shown in Rasmussen and Dybkjær (2005; their Figs. 5–7). Inserted principal sketch shows the lateral distribution of the different facies defined in this study.

an attempt to represent the environment facies as objectively as possible. The palynological analyses of the borehole samples were performed in the same period.

The samples were collected from a succession deposited between 25 and 21 Ma, i.e. representing the uppermost Oligocene – lower Miocene. At any specific field location, the depositional environment varied through this timespan as the relative sea-level changed, partly due to tectonism and partly due to changes in the global climate (Zachos et al., 2001; Miller et al., 2005) (Figs. 2 and 3). Therefore, the sampled succession (as observed in sediment cores and outcrops) represent different, but generically related parts of the geological history of the study area (Fig. 5).

In order to gain enough palynomorphs to make a proper data analytical analysis, all samples were selected from clayey sediment. In e.g. the sand-dominated shoreface environment, palynomorphs are generally rather sparse due to sorting effects. Therefore, only the thin clay-laminae representing fair weather conditions were selected for the present study (Fig. 7f).

The aim of the present study is to provide a reference dataset which is useful for a wide group of palynologists, not necessarily experts in

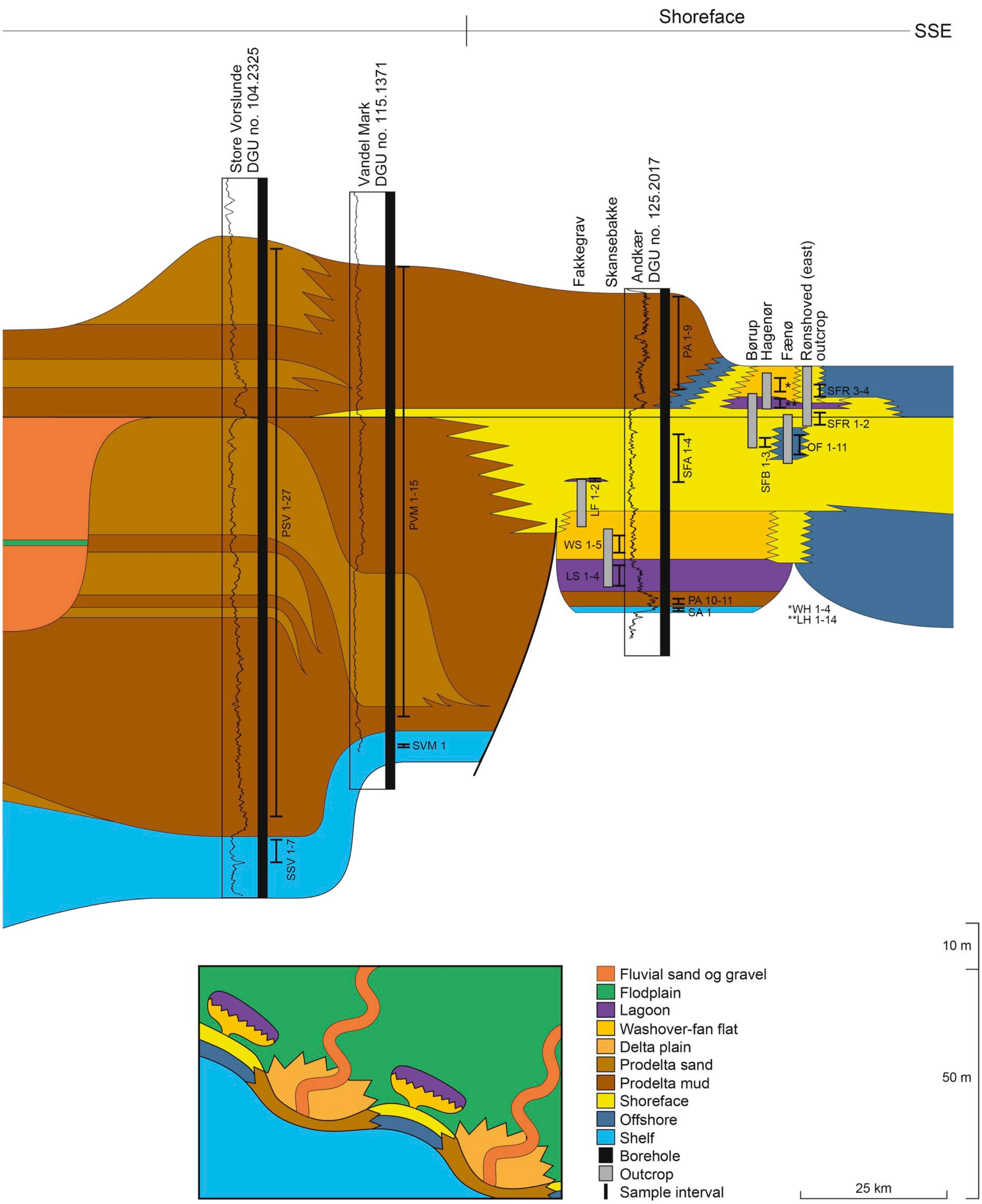

Fig. 5. (*continued*)

Miocene dinocysts – or multivariate data analysis for that matter - and simultaneously not too time-consuming. Therefore, the dinocysts were not separated into different taxa, although finer resolution variations in the dinocyst assemblages could perhaps have been useful in characterising the different depositional environments in even more detail than the present, see further the discussion. This would however require some degree of expertise in identification of the uppermost Oligocene to Miocene dinocysts. For the present purpose, grouping all dinocysts in one classification unit is considered sufficient.

This sampling approach makes the relative frequency of the sedimentary organic particles and palynological variables used in data analysis contingent upon the assumption that random samples from the clay-containing layers can be viewed as representative of the full variability of the influencing depositional environments.

4.2. Preparation of samples

In order to extract the organic particles for the palynofacies study, all sediment samples were processed in the Palynological Laboratorium at GEUS. The preparation included the following steps:

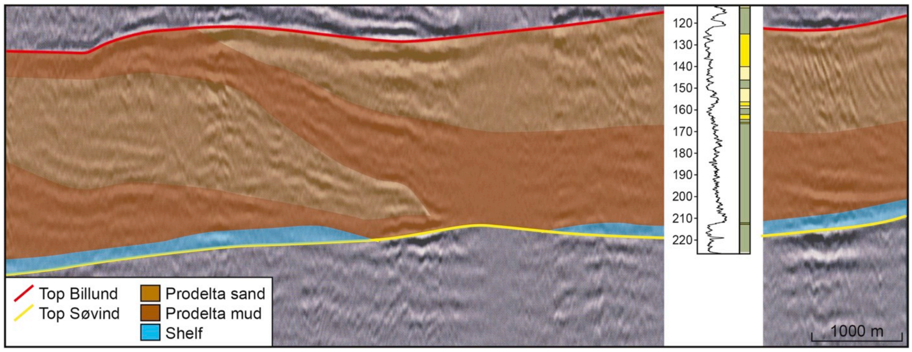

Fig. 6. Example of combined seismic data and borehole data (logs and lithology), the St. Vorslunde borehole, prodelta and shelf environments.

1) Drying the sediment sample and crushing it to all particles are < 2 mm. Approximately 20 gr. of the well-mixed, dried sediment sample were extracted and used for further treatment.
2) Dissolution of carbonates using HCl 3.5% to end of reaction followed by HCl 17.5% for 24 h. Followed by treatment with 70 °C warm, mild solution of citric acid.
3) Dissolution of silicates using cold HF (40%) for a minimum of 6 days, followed by treatment with 70 °C warm, mild solution of citric acid.
4) Brief oxidation with concentrated HNO_3 and KOH 5%.
5) Heavy liquid separation with ZnBr (2.3 g/ml).
6) Filtering on 11 µm nylon mesh.
7) The acid-resistant organic particles larger than 11 µm are mounted in glycerine gel on glass slides and studied using a normal light microscope.

4.3. Counting

In each sample a minimum of 200 sedimentary organic particles were identified and referred to one of the four major categories; 1) Structured wood particles, 2) non-structured, partly degraded vitrinite (AOM) (see below), 3) cuticle and 4) palynomorphs. Subsequently, a minimum of 300 palynomorphs were identified and referred to one of the following subcategories; Microspores, bisaccate pollen, non-saccate pollen, *Botryococcus*, other freshwater algae, fungae (-hyphae and -spores), acritarchs and dinocysts (marine algae).

Information on the origin, distribution and preservation for each of these categories is presented in Appendices 2a,b. Examples of palynofacies composition from the seven depositional environments are presented in Fig. 8.

In this way, a minimum of 500 sedimentary organic particles were identified and categorized in each sample, in accordance with the recommendation by Tyson (1995). In total more than 85.000 organic particles are included in the study. The resulting relative abundances are shown in Appendices 1a,b.

The counted particles comprise both whole particles, e.g. whole pollen grains, and fragments, e.g. of bisaccate pollen. Due to the preparation procedure, including sieving on 11 µm filters, all counted particles are larger than 11 µm. When a category or subcategory is shown to represent 1%, it may just indicate that the category/subcategory is present (= minimum 1 particle referable to that category/subcategory was recorded during counting).

Prasinophycean algae were recorded very rarely (below 0.5% of the total assemblage) and limited to the shelf environment, and were therefore not included in the summary statistics.

Palynofacies data from the Harre borehole, from 58.25m to 48.25 m, were previously published in Śliwińska et al. (2014). Palynofacies data from the Dykær profile, from lagoonal deposits, were previously published in Rasmussen and Dybkjær (2005) and these are the data used here. However, in these previous studies only 200 palynomorphs were counted in each sample. For the present study, counting was therefore resumed and continued until an additional 100 palynomorphs had been encountered to make the reference data set fully consistent.

4.4. Data analysis

Based on the complete reference data matrix, Appendices 1a,b, this study employs Principal Components Analysis (PCA) which transforms and visualizes matrices of observational/measured numerical data from a series of samples (N) characterized by a number of variables (P) into sets of projection sub-spaces used for visualization of 'hidden' data structures. In the present study N = 169 and P = 4 for the data set MVDA-I, P = 12 for data set MVDA-II and P = 8 for MVDA-III (see further below). PCA makes use of 'principal components' which are variance-maximized interrelationships between samples and variables respectively. The principal components are used as a new coordinate system. Full methodological description can be found in the extensive literature e.g. Esbensen and Swarbrick (2018), Esbensen and Geladi (2009), Martens and Næs (1992).

Operationally PCA constructs 'super-variables' which are linear combinations of the P original variables, used for displaying the data structure (i.e. "patterns") in the data. There can be derived any number of principal components (up to P) in order to model the dominant proportions of the total data variance, but often the first two (three …) principal components capture a dominant major fraction hereof, allowing a comprehensive overview of the full multivariate data structure in just one or two cross-plots (see below). In this fashion, what was originally a P-dimensional issue, becomes a projected, two or three-dimensional, version of the data structure, reducing the complexity of the original data to a manageable few new dimensions which are much easier to interpret. Thus PCA score-plots display groupings, clusters and trends between samples based on the degrees of compositional similarities and differences, as described by the variable correlations which are shown in accompanying loading-plots. PCA also quantifies the proportion (%) of total data set variance that can be modelled by each PC-component. Thus a score plot shows the major similarity, or dissimilarity, between groups of samples (for example groups of samples coming from specific depositional environments) that can be delineated individually and discriminated from other groups. PCA score plots comprise an easy-to-interpret, visualization tool with which to overview complex within- and between-sample as well as within- and between-group relationships even when expressed by a relatively high dimensionality (in the present work P reaches 12). In addition, complementary scores- and loading plots easily identify aberrant samples, *outliers* and/or variables displaying aberrant behavior not always constructive to analyze together with the gamut of all other samples; examples are presented and described below.

With PCA, each score plot is accompanied by a complementary loading plot; the latter is a visual rendition of the correlation

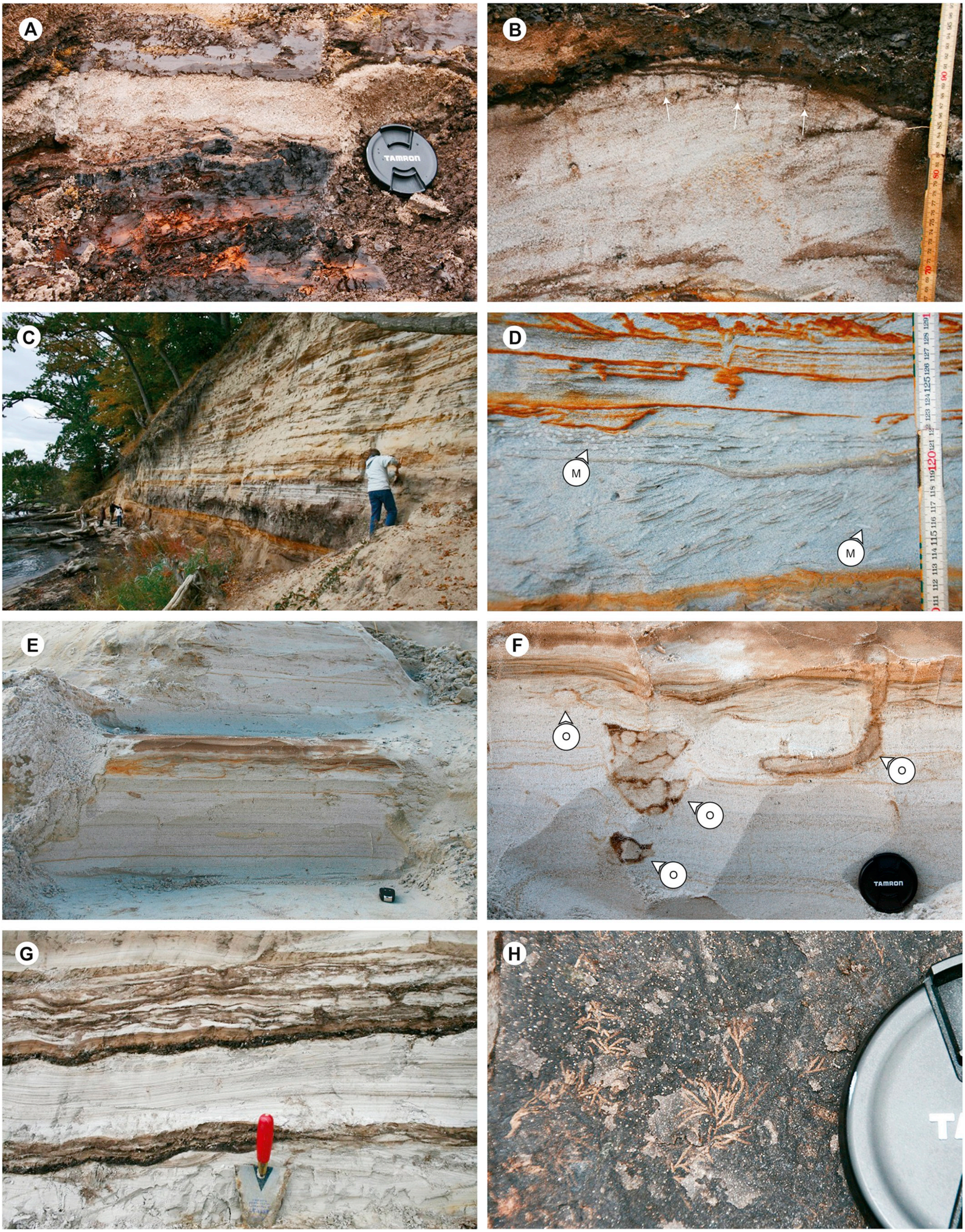

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Fig. 7. A-H.-Examples from outcrops showing sedimentary structures and trace fossils, based on which the depositional environments were interpreted. No photos of prodelta and shelf environments are shown, as they were only represented in boreholes and identified based on a combination of seismic data and borehole data (see Fig. 6). A) Floodplain, Salten profile, notice wood in orange. B) Floodplain, Salten profile, rootlets indicated by arrows. C) Lagoon deposits (dark layer in lower third part of the photo) overlain by washover-fan flat deposits. Hagenør profile. D) Washover-fan flat. *Macaronichnus* trace-fossils indicated (M), Hagenør profile. E) Shoreface, Hvidbjerg profile. F) Shoreface, Børup profile. Example of a storm sand layer capped by a ripple laminated sand. The samples for the palynofacies study were taken from the thin clay-layers. *Ophiomorpha* trace-fossils indicated (O). G) Offshore, Fænø profile, Hommocky Cross Stratification alternating with heterolithic deposits. H) Offshore, Hostrup profile. Example of *Chondrites* trace-fossils. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

relationships between all original P variables. The loading plot represents the same reduction in dimensionality from P to the small number of new dimensions (number of principal components) developed as for the score relationships. This model dimensionality is a function of the objective data structure of the original data matrix (X). Some data matrices can be of a particularly simple data structure requiring perhaps only two components, while other data may require additional components before a satisfactory proportion of the total data variance has been included in the PC-model (3,4,5 … components). The effective data structure is a reflection of the complexity of the geological/palynofacies context and the specific problem investigated. Model dimensionality is not a function of the number of original variables, P, in fact each principal component is a linear combination of all original P variables.

By a careful inspection of pairs of complementary scores and loadings plots it is possible to formulate descriptions of the visualized data patterns, often opening up for more direct scientific interpretation and hypothesis generation. Such patterns usually manifest themselves as prominent *between* - vs. *within* - group discriminability. E.g. individual sample clusters (data groups) with appreciable (separable) in-between distances – either as elongated groups spanning large compositional ranges while still retaining a defining data group coherence – or as *outlying samples* (singular, or more) often signifying particularly interesting, or particularly irrelevant, samples. Data groups may show little, or substantial overlaps, all as a reflection of the depositional environments and their constituent assemblages.

The reason for samples being recognizable as outliers is crucial: these may (i) represent true unique events, e.g. occurrences of critical importance in the interpretation, (ii) be the result of either sampling or measurement errors, identification mishaps, laboratory handling; or (iii) possibly, but always difficult to prove, singular “freak” events in nature. Inclusion of outliers of the latter categories in the data analytical interpretation may obscure distribution trends for the majority of samples. For this reason, outliers from the second category must be removed from the analysed data set. Then, the repeated PCA is better equipped to reveal the relevant data structure. Outliers representing “end-members” within a recognized sample group can be excluded from part of the data analysis, but should be included in the overall interpretations as they carry important information about the variability within the dataset. Therefore, the first step in any multivariate data analysis is to perform a careful outlier screening. For more details concerning the PCA method and identification of outliers see e.g. Esbensen and Swarbrick (2018); Martens and Næs (1992); Esbensen and Geladi (2009) and Esbensen et al. (2015).

5. Distribution of sedimentary organic particles - box plots

In Fig. 9 the results from the palynofacies analysis are presented as univariate box plots. The data are presented as relative abundances with a minimum and a maximum value, 25% and 75% values and a median value of each category/subcategory. These data are further shown in Appendices 1 a and b. Two plots are presented for the lagoonal environment due to the two outliers with extremely high relative percentages of AOM; one plot includes the outliers (end-members), while the other presents the data with these outliers excluded. Also for the floodplain environment two plots are presented, one includes the data from the two outlier samples (end-members) with extremely high relative abundances of microspores and one where data from these two outlier samples have been excluded.

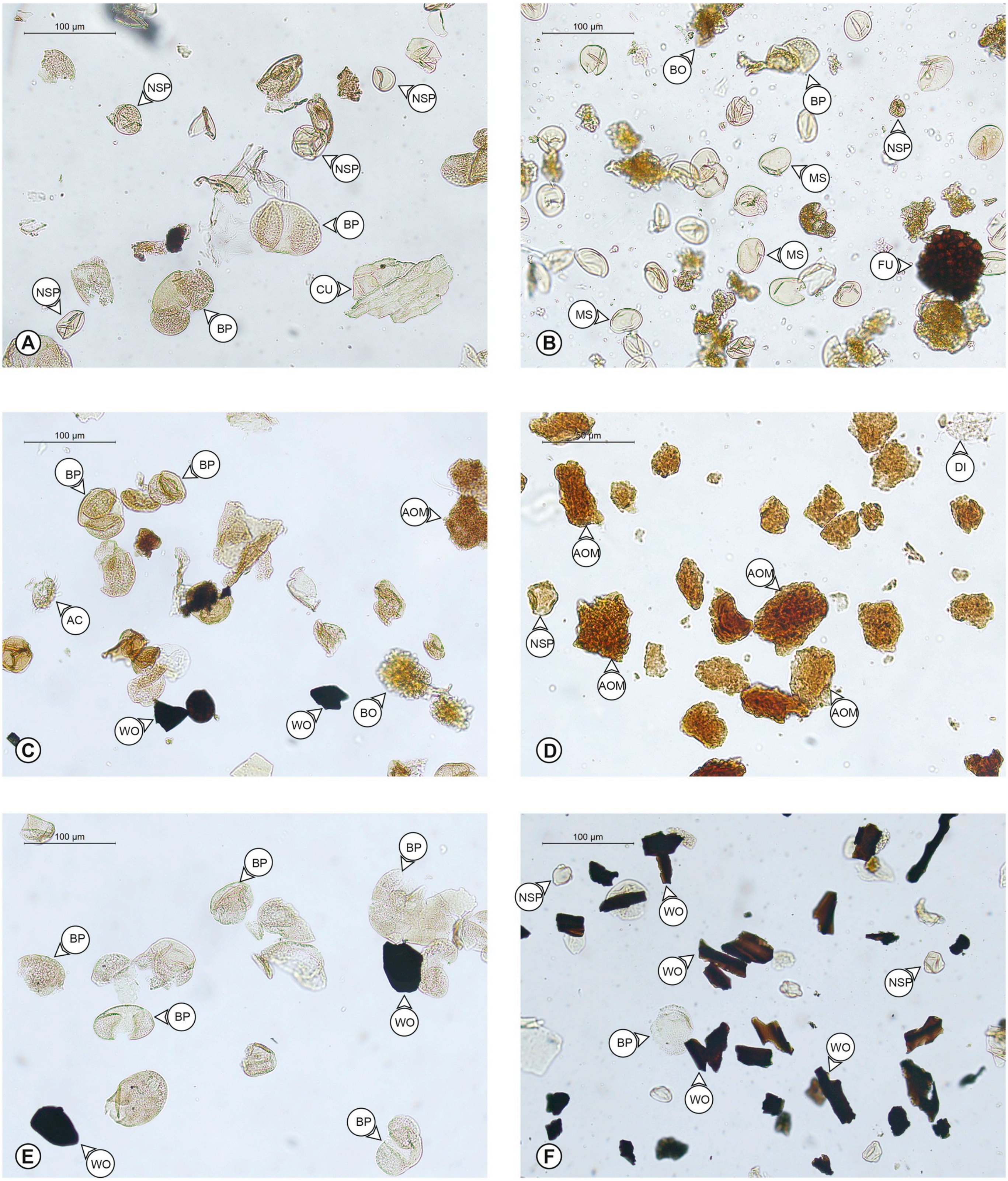
Looking at the relative abundances across the major categories, it is evident that in six out of the seven environments most samples are dominated by palynomorphs (median values between 50 and 87%), especially the floodplain, wash-over fan flat and the offshore transition environments which are characterized by medium values above 85% palynomorphs. Only the shore-face environment differs from this trend, with a medium abundance of palynomorphs of only 35% - most samples in this environment are dominated by wood particles (medium abundance of 57%). In none of the other six environments the medium percentages of wood particles exceed 16%. This dominance of wood particles probably reflects a higher wave energy, effectively sorting the organic particles and prohibiting the low-density palynomorphs from settling.

The highest relative abundances of AOM are found in the pro-delta and shelf environments (medium values of 31% and 23%, respectively), and in the lagoonal environment (including the two outlier samples with 86 and 94% AOM, respectively).

The relative abundances of cuticle are generally very low, with the highest maximum values of 12% found in a sample from the floodplain environment.

Among the subcategories (palynomorphs), bisaccate pollen dominates in most samples and show higher medium values than non-saccate pollen in all environments except for the lagoonal environment. The relatively high abundances of non-saccate pollen in the lagoonal samples possibly reflects the presence of Taxodium swamp vegetation (producing mostly non-saccate pollen) along the shoreline forming the landwards/inner part of the lagoon.

In the offshore transition environment the medium values are nearly equal (25% non-saccate and 32% bisaccate), while there is a clear difference in the shelf and pro-delta environments (17% non-saccate and 50% bisaccate in the shelf environment, and 20% and 56% in the prodelta environment). This difference may reflect the so-called “Neves-effect” – according to which the higher floating ability of the bisaccate pollen results in a gradually higher bisaccate/non-saccate ratio in a distal direction (Traverse, 1994; Tyson, 1995 and references therein, Armstrong and Brasier, 2005). The relatively high bisaccate/non-saccate ratio in the shoreface environment may reflect that these deposits are mainly storm-deposits and thus do not reflect a normal proximal-distal transport direction. The extremely high relative abundances of bisaccate pollen in the washover-fan flat environment may indicate (i) either the “Neves-effect” with preferentially bisaccate pollen being transported from the vegetation growing along the inner coastline of the lagoon before reaching the washover-fan flats, or (ii) it may reflect that the vegetation growing on the (sandy) barrier islands mainly was composed of bisaccate-producing plants, rather than Taxodium swamp vegetation producing mainly non-saccate pollen. The strong dominance of bisaccate pollen from the floodplain samples may be interpreted as reflecting sandy, nutrient poor soil, see further discussion. The two outlier samples showing extremely high abundances of microspores probably reflect the local flood-plain vegetation. Microspore-producing plants (e.g. ferns) often act as pioneer plants and thus microspores are common in unstable environments including e.g. flood-plain areas.



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The relative abundances of dinocysts show a clear pattern with an increase in medium abundances in a proximal-distal trend. The samples from the floodplain environment show very low abundances of dinocysts (medium of 0.5% and a maximum of 1%), the washover-fan flat samples show a medium of 1% and maximum abundances of 2%, the shoreface samples show a medium of 4%, the samples from lagoonal deposits show a medium of 10%, the prodelta samples show a medium of 15%, the samples from offshore transition environments show a medium of 16% and, finally, show the shelf samples a medium of 26% dinocysts.

Fig. 8. A-J.- Palynofacies from the seven depositional environments. A) Floodplain, Salten profile, overview, 40 cm over sandlayer, sl. 5, N38. Non-saccate pollen (NSP), bisaccate pollen (BP) and cuticle (CU) indicated. B) Floodplain, Salten profile, sample dominated by monolete spores, 60 cm over sandlayer, sl. 5, J31. *Botryococcus* (BO), non-saccate pollen (NSP), bisaccate pollen (BP), microspores (MS) and fungal spores (FU) indicated. C) Lagoon, Hagenør profile, overview, Lab nr. 21535,sl.4, E30. Amorphous organic matter (AOM), bisaccate pollen (BP), acritarchs (AC), wood (WO) and *Botryococcus* (BO) indicated. D) Lagoon, Dykær profile, close-up of sample dominated by AOM (=partly degraded vitrinite), Lab. Nr. 17877, 14.70 m, sl.4, W40-4. Amorphous organic matter (AOM), dinocysts (DI) and non-saccate pollen (NSP) indicated. E) Washover-fan flat, Hagenør profile. 4.0 m over base profile, sl. 5, L30-3. Bisaccate pollen (BP) and wood (WO) indicated. F) Shoreface, Hvidbjerg profile, lab nr. 26953, sl. 4, O35-2. Wood (WO), non-saccate pollen (NSP) and bisaccate pollen (BP) indicated. G) Prodelta. St. Vorslunde, 108 m, sl. 5, K35. Freshwater algae (FA), non-saccate pollen (NSP), wood (WO) and bisaccate pollen (BP) indicated. H) Offshore. Fænø, 5.01 m, sl.4, L37-2. Dinocysts (DI), bisaccate pollen (BP), non-saccate pollen (NSP) and wood (WO) indicated. I) Shelf, Klosterhede, overview, 267–268 m, sl.3, J34-3. Dinocysts (DI), acritarchs (AC) and wood (WO) indicated. J) Shelf, Harre, close-up, transition from structured wood to amorphous organic matter (AOM) (from 1 to 3) 48,25 m, sl. 4, N54-1. Dinocysts (DI), non-saccate pollen (NSP) and bisaccate pollen (BP) indicated.

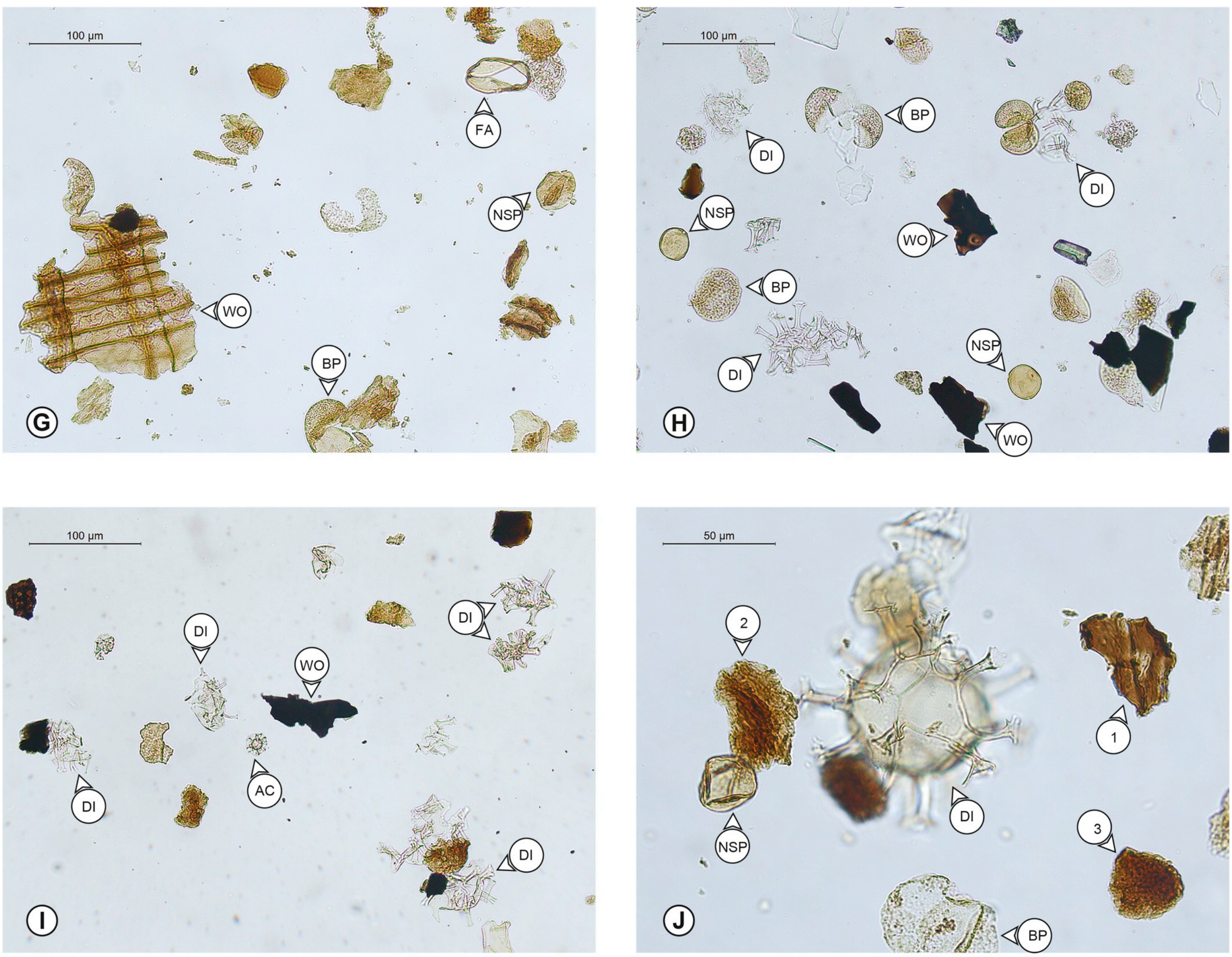

Fig. 8. (*continued*)

Botryococcus show the highest medium values and the highest maximum values in the offshore transition and the floodplain environments (8% medium value in offshore transition and 3% in the floodplain; maximum relative abundance of 35% in the offshore transition, 40% in the floodplain plot incl. outliers and 30% excl. outliers, respectively).

The medium value for freshwater algae does not exceed 1% in any environment. The highest relative abundances (17%) are found in samples from the floodplain environment in the plot incl. outliers, while samples with 10% freshwater algae were found in the lagoonal environment.

Fungal hyphae and spores follows the same trend, with a medium value not exceeding 1%, and the maximum relative abundances (12%) in the floodplain environment (the plot incl. outliers) and maximum values of 10% in the lagoonal environment.

Acritarchs occur sporadically and the medium value does not exceed 1% in any environment. The highest relative abundances were found in samples from the offshore transition (7%) and the lagoon (5%).

Two outlier samples with more than 88% microspores were found in the floodplain environment. Except for those, and a few samples from the shoreface environment with 9% microspores, the maximum abundance does not exceed 3%.

6. Principal component analysis of the palynofacies

The raw data, i.e. absolute numbers/values of the four main categories of organic particles and the eight palynomorph subcategories within the 169 sediment samples is presented in Appendices 1a, b. The data are treated statistically using Principle Component Analysis (PCA) (Figs. 10–20), based on a series of increasingly inclusive data sets in order to 'zoom in' and allow appreciation of the full complex relationships. On each of these figures the facies associations are delineated with convex polygons, allowing for detailed discrimination as commented upon for each plot. No PCA needed more than 4 components; data structures delineated by e.g. PC3 and PC4 represent objective relationships that are revealed after the more dominant PC1 and PC2 have been modelled.

The first step in the present Multivariate Data Analysis (MVDA-I) consists of a PCA based on the four major categories (P = 4): Wood (WO), Amorphous organic matter (AOM), cuticle and membranes (CU) and palynomorphs (PM) (Fig. 10). The four categories are reported in relative abundances summing to 100%.

In the second step (MVDA-II), the palynomorph (PM) category is subdivided into its eight subcategories, these adding up to 100%; microspores (MS), non-saccate pollen (NSP), bisaccate pollen (BP), *Botryococcus* (BO), freshwater algae (FA), fungal hyphae and –spores (FU), acritarchs (AC) and dinocysts (DI). In this step there are thus 12 variables (P = 12); the first four major categories and the eight palynomorph subcategories (Figs. 11–14). The purpose of subdividing the palynomorph category was to delineate the internal relationships between all depositional facies with maximum clarity. Summing up both of these categories to 100%, allow the major organic particles categories and the palynomorph subcategories both to be expressed as relative abundances. For the ensuing data analysis, the X matrix is therefore auto-scaled to allow for simultaneous interpretation (Esbensen and Swarbrick, 2018; Esbensen and Geladi, 2009).

The final PCA is carried out on the eight palynomorph subcategories alone (MVDA-III); (P = 8). The aim was to elucidate still more subtle relationships within this overall category (Figs. 15–20).

6.1. MVDA-I: four main categories

On the score cross plot PC1 vs. PC2 (Fig. 10) the two components collectively model 99% of the total data variance. In this analysis the shoreface (SF, yellow)- and washover-fan flat (W, orange)-facies are completely overlapping, and both are characterized by extreme compositional ranges due to highly varying relative abundances of wood (WO) (Fig. 10b). The lagoonal (L, purple)-facies is of even more variable composition, dominated by highly varying relative abundances of amorphous organic matter (AOM) (Fig. 10b). Two samples (marked orange on Fig. 10a) are characterized by extremely high AOM abundances. The prodelta (P, brown)- and shelf (S, light blue)-facies (stippled polygons) are extensively overlapping each other within the lagoonal-facies.

The loading plot PC1 vs. PC2 (Fig. 10b) shows that effectively only three major categories (amorphous organic matter (AOM), wood (WO) and palynomorphs (PM) are responsible for the overall facies disposition shown in Fig. 10a). While palynomorphs are present in all facies associations in average abundances (red ellipsoid), wood and amorphous organic matter vary extensively in the lagoonal- and shoreface-facies (as well as the prodelta- and shelf-facies), extending their compositional ranges to the left quadrants of the plot. Cuticle (CU) abundances are very low in the reference data set, and do not contribute to the disposition shown in Fig. 10a.

In this lead-in data-analysis, it is apparently only samples with higher than average abundances that discriminate between facies. Three of these four major categories discriminate the washover-fan flat (W)- and shoreface (SF)-facies from the lagoonal (L)-, prodelta (P)- and shelf (S)-facies, due to the "influencing variables" wood (WO) and amorphous organic matter (AOM), as evidenced by Fig. 10b. At low and intermediate abundance for these categories, all facies overlap and occupy the same location (red transparent ellipse in Fig. 10a.). Palynomorphs (PM) pools the facies along the PC1, but does not differentiate them. For this reason, the palynomorph (PM) category is subdivided into eight relevant subcategories below, anticipating more sensitive discriminations.

6.2. MVDA-II: main categories + Palynomorph subcategories

The score plot PC1 vs. PC2 (Fig. 11a) reveals the relationship between the flood-plain (F, green)- and lagoonal (L, purple)-facies in relation to all other facies associations. The palynofacies assemblage from the flood-plain (F)- facies is highly variable and isolated from marine influence, which distinguishes it from remaining facies. The flood-plain (F) facies is especially well discriminated from the lagoonal (L)- facies along PC2. The flood-plain (F)-facies display high palynomorph (PM) and microspore (MS) abundances, while the lagoonal (L)-facies is characterized by high abundances of amorphous organic matter (AOM) and dinocysts (DI), cfr. Appendices 1a, b.

The three rightmost samples (end-members: red color on Fig. 11a) of the flood-plain (F)-facies along PC1 are characterized by exceptionally high proportions of cuticle (CU), *Botryococcus* (BO), fungal hyphae and spores (FU) and freshwater algae (FA) (black ellipse) (Fig. 11b). The lagoonal (L)- facies is partially characterized by the same variables (BO, FU and FA), also extending this group in the PC1 direction. The two prominent L-outliers (orange color on Fig. 11a) are dominated by AOM (Fig. 11b), explaining their marked deviating location in the plot. Except for these discriminating features, there is an extensive overlap between all other facies (center and left side of Fig. 11a).

Due to the highly variable character of the palynofacies assemblages of the flood-plain (F)-facies -driven by high abundances of microspores (MS) and elevated abundances of *Botryococcus* (BO), freshwater algae (FA) and fungal hyphae and spores (FU) - this easily discriminated environment is removed from the following analysis of MVDA-II (Figs. 12–14). Removing the F-facies improved discrimination between the remaining six facies (see below).

The score plot of PC1 vs. PC3 reveals some discrimination of five of the six remaining facies. In this analysis the shelf (S, light blue)-facies is not clearly distinguished from the other five environments.

The lagoonal (L, purple)- and prodelta (P, brown)-facies occupy opposite positions along the PC1 component (with a minor overlap at low PC1-scores, Fig. 12a). This can be explained by the marked negative correlation between freshwater algae (FA), fungal hyphae and spores (FU), *Botryococcus* (BO) and non-saccate pollen (NSP) vs. bisaccate pollen (BP) (Fig. 12b). The shoreface (SF, yellow)- and washover-fan flat (W, orange)-facies are discriminated with respect to the prodelta (P, brown)-, lagoonal (L, purple)- and offshore transition (O, dark blue)-facies in the negative PC3 direction, notably because of very high bisaccate pollen (BP) abundances with simultaneous low dinocyst (DI) abundances. There is some overlap between the offshore transition (O, dark blue)- and the lagoonal (L, purple)-facies. However, the offshore transition (O, dark blue)-facies is extended in the PC3 direction due to high (er) dinocyst (DI) abundances., while The prodelta (P, brown)-facies manifests itself as a kind of "mixed bag", which is understandable because of its depositional position in a fully marine environment but with a high influx of material from both terrestrial and fluvial sources.

The score plot of PC3 vs. PC4 reveals that the shoreface (SF, yellow)- and the offshore transition (O, dark blue)- facies separate almost completely along the PC3 axis (Fig. 13a). Thus the PC3 vs. PC4 cross plot reveals a proximal-distal trend manifested along and modelled by the PC3 axis. Marine palynomorphs (dinocysts, DI) (rightmost) correlate negatively with fluvial and terrestrially derived palynomorphs (non-saccate pollen, NSP, microspores, MS, and bisaccate pollen, BP)

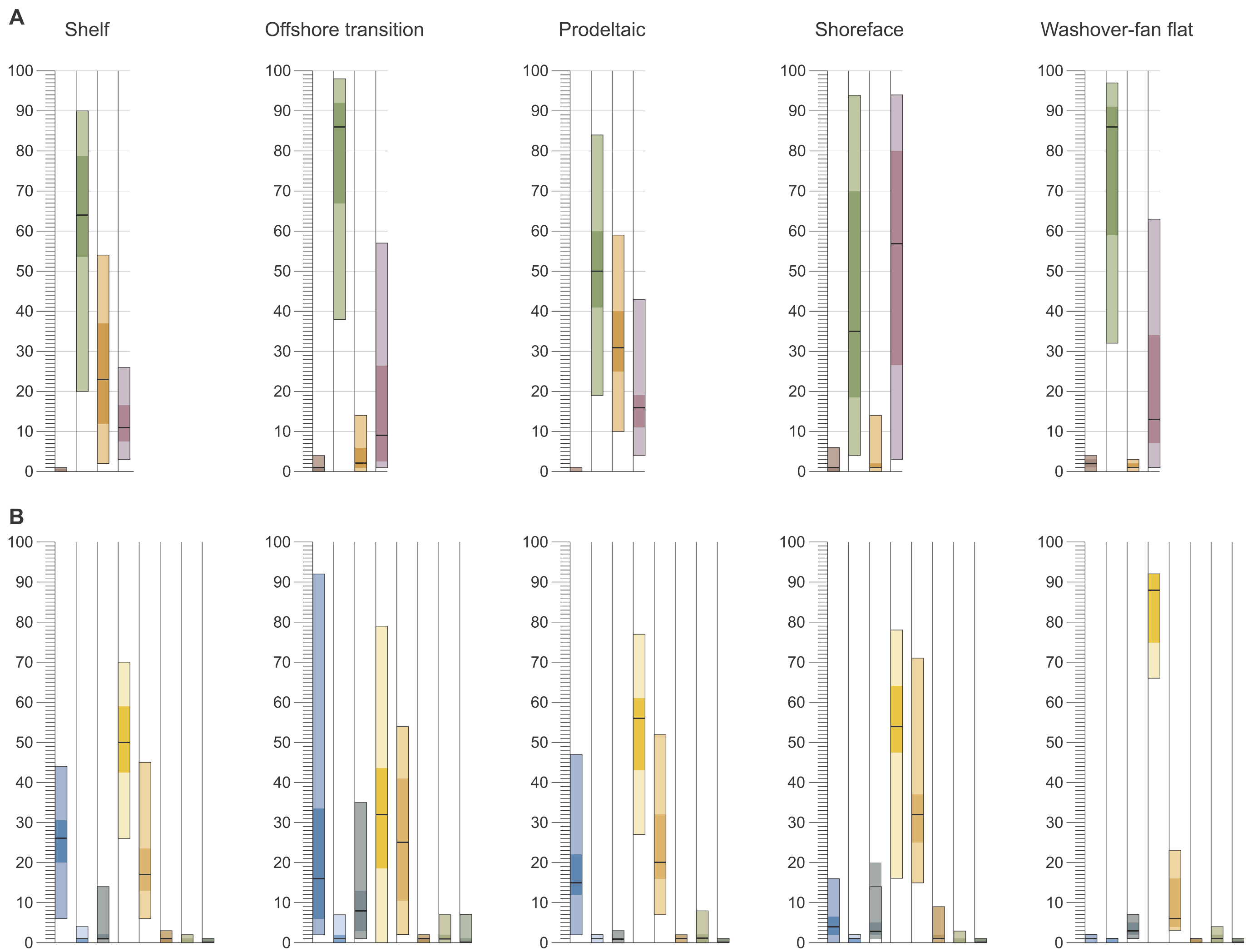

Fig. 9. Box Plot. A) The four main categories. B) The eight palynomorph-subcategories. Note that the data from the lagoonal facies and the floodplain facies are shown inclusive outliers and exclusive outliers, respectively. The data are presented as relative abundances with a minimum and a maximum value, 25% and 75% values and a median value of each category/subcategory.

and particles (cuticle, CU and wood, W) (leftmost). *Botryococcus* (BO) and acritarchs (AC), which are located in the central part of the PC3 axis with relative small loadings, are probably representing nearshore marine depositional regimes. Amorphous organic matter (AOM) appear to be correlated with acritarchs (AC), but this is only a reflection of the two end-members of the lagoonal (L)-facies that were identified above (Fig. 10a). The shelf (S, light blue)-facies that falls within the offshore transition (O, dark blue)-facies is discussed further below.

When PC2 is plotted versus PC3 (Fig. 14a), the washover-fan flat (W, orange)-facies is entirely overlapping the shoreface (SF, yellow)-facies but only for high palynomorph/wood (PM/WO)- ratios. The very large compositional extension of the shoreface (SF)-facies is due to the marked palynomorph (PM) *vs.* wood (WO) anti-correlation. The shoreface (SF)-facies has markedly higher relative abundances of wood particles in one end of the facies association (rightmost), while the opposite end is indistinguishable from the washover-fan flat (W)-facies. Both facies plot along the negative part of PC3, possibly due to low relative abundances of dinocysts (DI) and high relative abundances of bisaccate pollen (BP) and notably higher relative abundances of cuticle (CU) than in most other environments.

6.3. MVDA-III: Palynomorph subcategories

In this final step of data analysis data matrix from all seven facies are included. By correlating PC1 vs. PC2 (Fig. 15) we observe two outliers in the flood-plain (F)-facies. These samples (marked by green) are high in freshwater algae (FA) and fungal hyphae and spores (FU). After removing these two datapoints, a repeated PCA results in the pattern shown in Fig. 16.

The facies succession from floodplain (F, green), via shoreface (SF, yellow) to shelf (S, light blue)/offshore transition (O, dark blue) (Fig. 16 a) delineate a grading relationship from right to left, as indicated by the black arrow. Geologically this is interpreted to represent a proximal-distal spectrum of depositional environments, each with their distinctive palynomorphic characteristics. The apparent "reverse" location of the offshore transition (O)- in relation to the shelf (S)-facies (Fig. 16a) is most probably caused by extreme high dinocyst abundances in some of the offshore transition (O)-facies samples. We observe relatively high abundances of dinocysts (DI) in the shelf samples with the highest median of dinocysts (DI) among all seven environments, but very variable abundances of dinocysts (DI) in the offshore transition (O)-facies (Fig. 9; Appendix 1b). The offshore transition (O)-facies stretches along the PC2 axis with dinocysts (DI) as the end member to the far left and non-saccate pollen (NSP) to the far right. This may suggest that the offshore transition (O)-facies is influenced by pulses of dinocyst blooms ("red-tide" situations) (e.g. Millie et al., 1997; Hall et al., 2012) and/or pulses in the influx of non-saccate pollen, see further discussion below. Some of the most influential variables

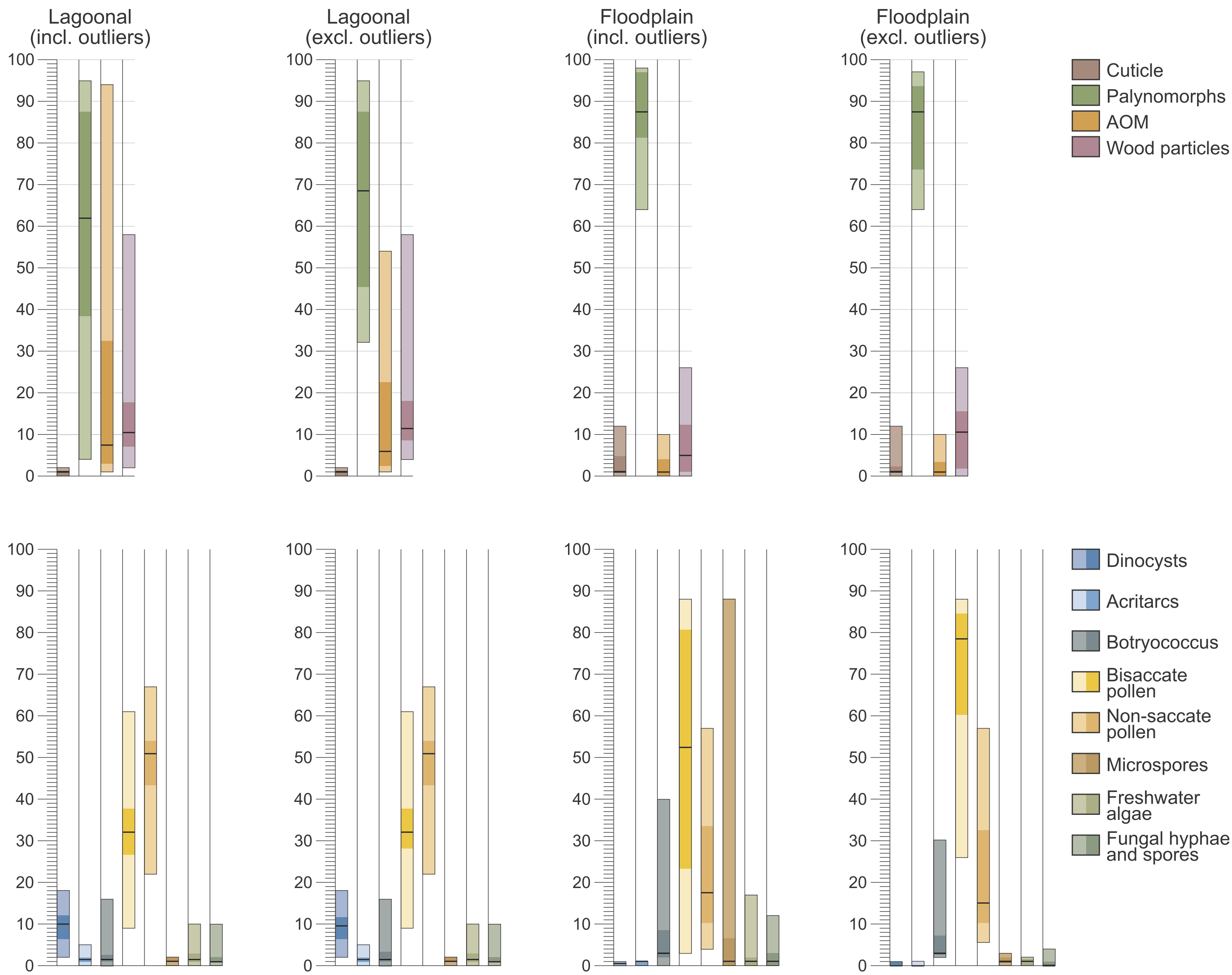

Fig. 9. (*continued*)

revealed by the multivariate approach, will also be amenable to univariate data analysis and interpretation, e.g. by box-plot characterization.

As expected, there is a marked overlapping along this gradation. The lagoonal (L, purple)- and the shoreface (SF, yellow)- facies associations are intermediate along this trend, in fact overlapping with the most distal part of the flood-plain (F)-facies and the most proximal parts of the offshore transition (O, dark blue) - and the shelf (S, light blue)-facies.

From the disposition shown in Fig. 16a, the lagoonal (L, purple)-facies is closest to the flood-plain (F, green)- and shoreface (SF, yellow)-facies, probably reflecting that the organic particles found here mainly originates from fluvial and shoreface sources – with occasional contributions from shelf (S, light blue) and offshore transition (O, dark blue) marine influences (storm activity and/or high tide).

For the further analysis, the other two end-members (outliers) of the flood-plain (F)-facies (characterized by high microspores, MS; marked by red in Fig. 15a) are also removed. The resulting PCA (Fig. 17) show two new floodplain (F, green)-facies outliers (marked by red) also characterized by high microspores (MS), but at a lower level.

All these six, successively identified outliers were removed from the flood-plain (F)-facies in the next iteration of the data analysis (Figs. 18–20).

The score plot of PC1 vs. PC2 (Fig. 18) shows that in spite of substantial overlapping of nearly all facies, the lagoonal (L, purple)- and the washover-fan flat (W, orange)- facies are completely discriminated from each other along the PC1 axis. PC1 may be interpreted as a “buoyancy component”. Other possible interpretations are outlined in the Discussion (Washover-fan flat Facies Association). The offshore transition (O, dark blue)-facies and the shoreface (SF, yellow)-facies discriminates, albeit not completely, along the PC2 axis. PC2 is interpreted as a land-sea discriminating component reflecting terrestrial (microspores, MS and non-saccate pollen, NSP) vs. marine (dinocysts, DI) origins.

The score plot of PC1 vs. PC3 (Fig. 19) discriminates the washover-fan flat (W, orange)-facies completely from the shoreface (SF, yellow)-facies. This discrimination appears to be controlled by very high abundances of bisaccate pollen (BP) in the washover-fan flat (W)-facies vs. microspores (MS), dinocysts (DI) and non-saccate pollen (NSP) in the shoreface (SF)-facies. The extensive overlap between prodelta (P, brown)- and shelf (S, light blue)-facies indicates high similarity between these two environments, which is to be expected.

The three compositionally most varying facies in the score plot of PC2 vs. PC3 (Fig. 20) are offshore transition (O, dark blue)-, lagoonal (L, purple)- and shoreface (SF, yellow)-facies. The plot (Fig. 20) discriminate between these three facies associations much more effectively than the PC1 vs. PC2 plot (Fig. 18), because the dominating PC1 facies extensions have been projected away. Bisaccate pollen (BP) is not correlated with freshwater algae (FA) and fungal hyphae and spores (FU) as it may seem from Fig. 20b; the association seen in this plot is

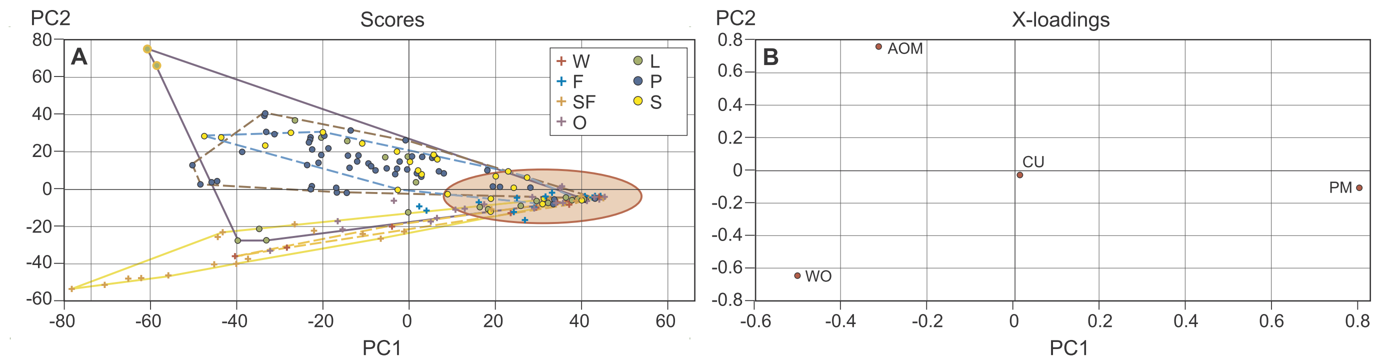

Fig. 10. A) MVDA-I score plot (PC1 vs. PC2). All facies except (O) and (F) are delineated as convex polygons. O and F are not delineated in this plot, but are treated below. Note the two end-members of the (L)-facies (orange). W: Washover-fan flat, F: Flood-plain, SF: Shoreface, O: Offshore transition, L: Lagoonal, P: Prodelta, S: Shelf. B) MVDA-I loading plot. The disposition of depositional facies in Fig. 10A is overwhelmingly due to variations in the three main variables (categories) wood (WO), amorphous organic matter (AOM) and palynomorphs (PM), while the fourth category, cuticle (CU) does not seem to have any influence. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

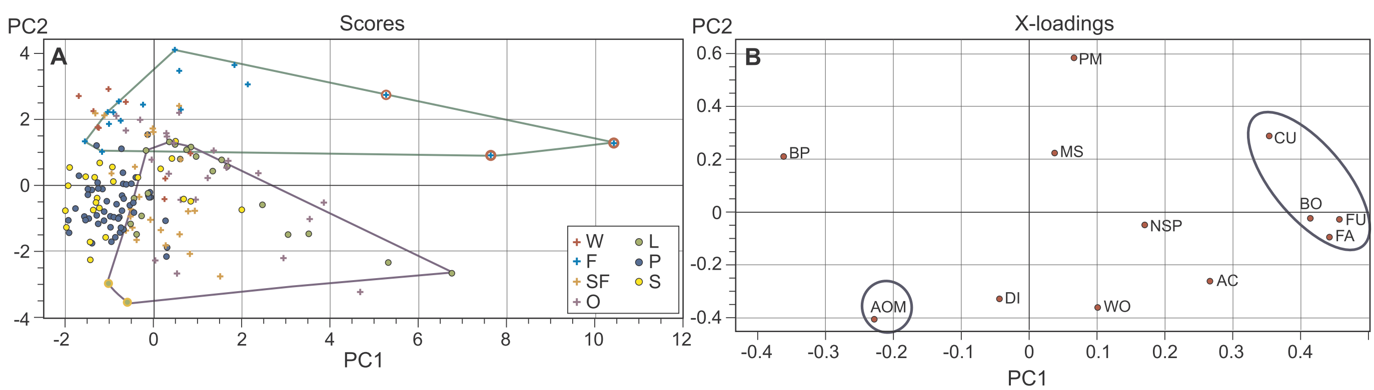

Fig. 11. A) MVDA-II score plot (PC1 vs. PC2), based on 12 variables. This PCA plot is collectively accounting for 44% of the total data variance. Note two end-members of the L-facies (marked orange) and three end-members of the F-facies (marked red). W: Washover-fan flat, F: Flood-plain, SF: Shoreface, O: Offshore transition, L: Lagoonal, P: Prodelta, S: Shelf. B) MVDA-II loading plot (PC1 vs. PC2). The black ellipse highlights the most influencing variables controlling the distribution of the three end-members of the F-facies (red). The stippled ellipse highlights the AOM, which is driving the two end-members of the L-facies (orange). Wood (WO), amorphous organic matter (AOM), palynomorphs (PM), cuticle (CU), bisaccate pollen (BP), non-saccate pollen (NSP), microspores (MS), dinocysts (DI), acritarchs (AC), *Botryococcus* (BO), freshwater algae (FA), fungal hyphae and spores (FU). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

only a reflection of bisaccate pollen (BP) having a very high loading on PC1 (Figs. 18 and 19).

The PC2 vs. PC3 plot (Fig. 20) reveals a distinct three-fold variable grouping (ellipses). There is a large overlap between facies associations in the center of this plot, prodelta (P, brown), shelf (S, light blue), flood-plain (F, green), washover-fan flat (W, orange), – only more distinctive samples from the offshore transition (O, dark blue), lagoonal (L, purple) and the shoreface (SF, yellow) facies show extensions away from this average cluster, "driven by" higher relative abundances of dinocysts (DI), freshwater algae and fungal hyphae and spores (FA, FU) and non-

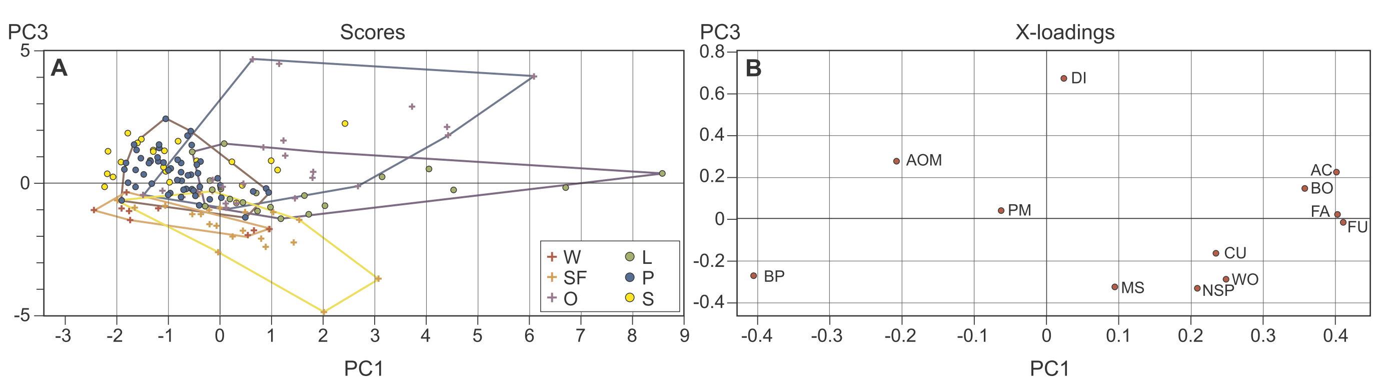

Fig. 12. A) MVDA-II score plot (PC1 vs. PC3) is collectively accounting for 39% of the total data variance. After removal of the F-facies, discrimination between the L-, O-, P-, SF- and W-facies is more distinct, but the data points of the S-facies do not show a clear pattern in this plot. W: Washover-fan flat, SF: Shoreface, O: Offshore transition, L: Lagoonal, P: Prodelta, S: Shelf. B) Corresponding loading plot for PC1 vs. PC3 (Fig. 12A). Wood (WO), amorphous organic matter (AOM), palynomorphs (PM), cuticle (CU), bisaccate pollen (BP), non-saccate pollen (NSP), microspores (MS), dinocysts (DI), acritarchs (AC), *Botryococcus* (BO), freshwater algae (FA), fungal hyphae and spores (FU).

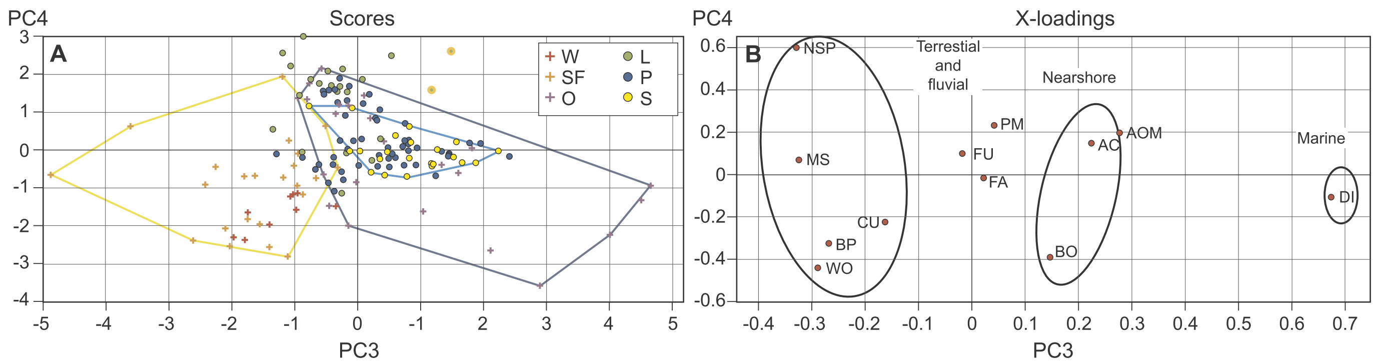

Fig. 13. A) MVDA-II score plot (PC3 vs. PC4). While collectively accounting for only 27% of the total data set variance, this plot gives a nearly complete separation of the SF-facies and the O-facies. Note how the S-facies is fully embedded in the O-facies. W: Washover-fan flat, SF: Shoreface, O: Offshore transition, L: Lagoonal, P: Prodelta, S: Shelf. B). Corresponding loading plot to the PC3-PC4 score plot in Fig. 13A. A clear grouping of categories can be observed: the distinctly marine DI influence (rightmost) contrast markedly with fluvial and terrestrially derived particle types (NSP, MS, CU, BP, WO) (leftmost). (BO, AC) also contribute to the positive PC3 but with significantly lower loadings than DI. Wood (WO), amorphous organic matter (AOM), palynomorphs (PM), cuticle (CU), bisaccate pollen (BP), non-saccate pollen (NSP), microspores (MS), dinocysts (DI), acritarchs (AC), *Botryococcus* (BO), freshwater algae (FA), fungal hyphae and spores (FU).

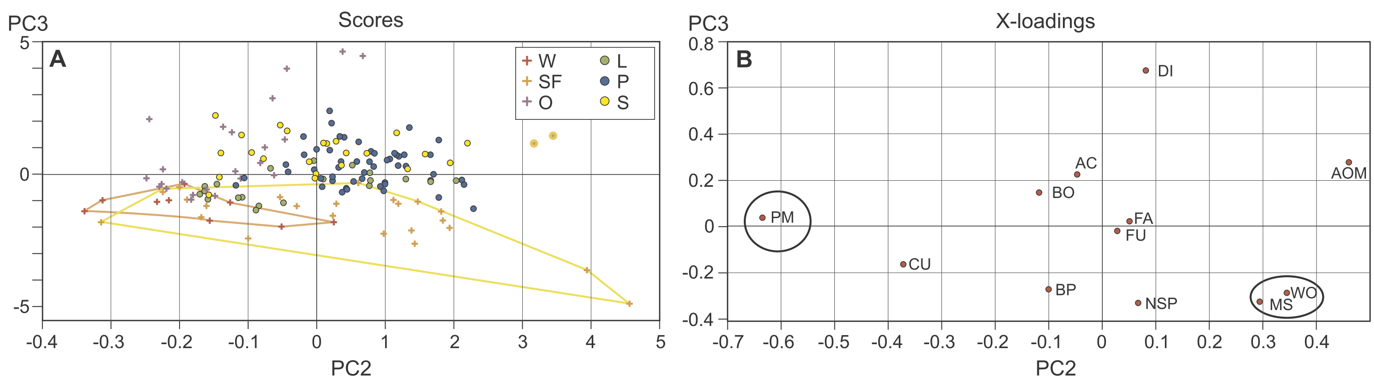

Fig. 14. A) MVDA-II score plot (PC2 vs. PC3), collectively accounting for 31% of the total data set variance. W: Washover-fan flat, SF: Shoreface, O: Offshore transition, L: Lagoonal, P: Prodelta, S: Shelf. B) Corresponding loading plot to Fig. 14A, showing a negative correlation between PM and W. The variable MS has an extreme bimodal distribution; only the two rightmost SF samples in Fig. 14A have very high MS abundances. Wood (WO), amorphous organic matter (AOM), palynomorphs (PM), cuticle (CU), bisaccate pollen (BP), non-saccate pollen (NSP), microspores (MS), dinocysts (DI), acritarchs (AC), *Botryococcus* (BO), freshwater algae (FA), fungal hyphae and spores (FU).

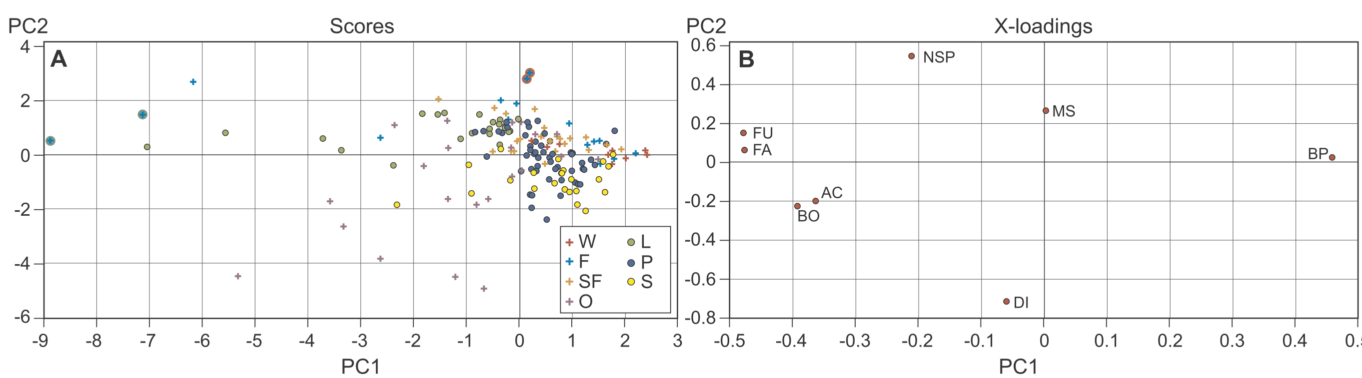

Fig. 15. A) MVDA-III score plot (PC1 vs. PC2), collectively accounting for 52% of the total data set variance. Overview of the seven facies, as characterized by the eight individual palynomorph subcategories only. Two marginal F-samples (outliers), high in FA and FU, are marked green, while two other marginal F samples (marked red) display the highest PC2 scores reflecting a high proportion of MS (cfr. Fig. 15B). W: Washover-fan flat, F: Flood-plain, SF: Shoreface, O: Offshore transition, L: Lagoonal, P: Prodelta, S: Shelf. B) Corresponding loading to Fig. 15A explaining the marginal behavior of the four marked samples in Fig. 15A. Bisaccate pollen (BP), non-saccate pollen (NSP), microspores (MS), dinocysts (DI), acritarchs (AC), *Botryococcus* (BO), freshwater algae (FA), fungal hyphae and spores (FU). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

saccate pollen (NSP), respectively. The PC2 vs. PC3 plot (Fig. 20) shows evidence that even the compositionally most varying facies associations are overlapping in the center of the plot when their relative abundances are at average levels.

6.4. P/D index

The relative amount of terrestrial palynomorphs have often been used as an indicator of the relative distance to the coast (e.g. McCarthy

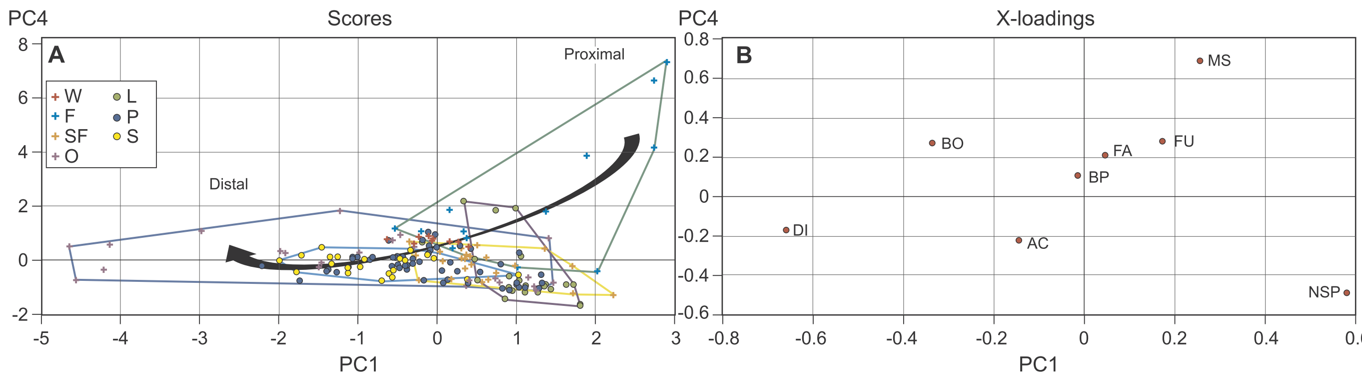

Fig. 16. A) MVDA-III score plot (PC1 vs. PC4), with two marginal F-samples excluded, collectively accounting for 32% of the total data set variance. This visualization shows a gradation from the F-facies (green) → SF-facies (yellow) → S- and O-facies (light blue and dark blue, respectively) (black arrow) described as a proximal-distal palynomorph spatial framework in the text. W: Washover-fan flat, F: Flood-plain, SF: Shoreface, O: Offshore transition, L: Lagoonal, P: Prodelta, S: Shelf. B) Corresponding loading plot to Fig. 16A. Bisaccate pollen (BP), non-saccate pollen (NSP), microspores (MS), dinocysts (DI), acritarchs (AC), *Botryococcus* (BO), freshwater algae (FA), fungal hyphae and spores (FU). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

et al., 2003; Donders et al., 2009). In order to test this approach we calculated the P/D index (P/(D + P)*100), see Appendix 1b. The terrestrial palynomorphs (P) include the non-saccate pollen (NSP), the microspores (MS), the freshwater algae (FA) and the fungal hyphae and –spores (FU). The marine palynomorphs (D) only comprise the dinocysts (DI). The bisaccate pollen have been excluded due to the "Neves effect" which can result in a disturbed proximal-distal trend. *Botryococcus* and acritarchs have also been excluded as our study shows that these two sub-categories thrive best in brackish water environments in the study area (see chapter 7.2). Therefore, they would probably not be useful in order to gain a clear terrestrial/marine index.

7. Discussion

7.1. Palynofacies characteristics of the seven facies associations

7.1.1. Flood-plain facies association (F) (green)

7.1.1.1. Characteristics. This facies is characterized by high variability of terrestrially and fluvially derived organic particles, while marine derived particles (dinocysts, DI) are almost absent (not above 1%, Fig. 9; Appendix 1b). The samples show very highly variable relative abundances of e.g. cuticles (CU) (0–12%), microspores (MS) (0–88%), *Botryococcus* (BO) (0–40%), freshwater algae (FA) (0–17%) and fungal hyphae and spores (FU) (0–12%).

In contrast to other environments microspores (MS) may be very abundant, i.e. seven out of 17 samples yielded between 3% and 88% of microspores (MS) (Appendix 1b). In all other environments (except for two samples from the shoreface (SF)-facies with 9% and 5%, respectively) the relative abundance of microspores (MS) is at or below 3%.

Some samples are characterized by elevated values of freshwater algae (FA) and fungal hyphae and spores (FU). However, this is also seen in samples from the lagoonal (L)-facies. The floodplain (F)-facies can be discriminated from the lagoonal (L)-facies by the higher amounts of amorphous organic matter (AOM) and the lower bisaccate/non-saccate pollen ratio in the latter (Figs. 9 and 10).

In addition, the floodplain (F)-facies is characterized by slightly elevated values of cuticle (CU) in some samples (up to 12%) (Appendix 1a).

The P/D-index has an average value of 97.1 for the floodplain environment (Appendix 1b), indicating a strong dominance of terrestrial palynomorphs.

7.1.1.2. Interpretation. As expected, the floodplain (F)-facies discriminates from the other facies as being the most proximal (Fig. 15a). This facies is characterized by maximum abundances of terrestrially and fluvially derived organic particles such as fungal hyphae and spores (FU), freshwater algae (FA), microspores (MS) and cuticle (CU) (Figs. 8A, 9 and 11A,B). These particles origin from the floodplain environment itself and are often not transported very far from the source. The very high abundances of microspores (MS) in some samples indicate that spore-producing plants, e.g. ferns, were an important part of the vegetation on the floodplain.

The high variability in the palynofacies associations probably reflects that a floodplain is a very dynamic setting with frequent avulsion of the channel systems and variable discharge of water, resulting in some periods with flooding of the floodplain areas. The samples further possibly represents different parts of this setting; some may represent river-channel deposits, others minor ponds (e.g. oxbow lakes) etc. During storms, eventually combined with high tide, marine water may reach far into the fluvial system, transporting e.g. dinocysts into the floodplain setting.

7.1.1.3. Comments. Due to its high variability, either all of the floodplain (F)-facies (Figs. 12–14) or only six floodplain (F)-outlier samples (Figs. 18 and 19) were removed from some of the analysis, improving the discrimination of the other facies.

7.1.2. Lagoonal facies association (L) (purple)

7.1.2.1. Characteristics. Like the floodplain (F)-facies, the palynofacies association of the lagoonal (L)-facies is markedly variable. Similarly to the flood-plain (F)-facies, freshwater algae (FA) and fungal hyphae and spores (FU) are common (up to 10%) (Figs. 9, 12, 16 and 18), but high amounts of amorphous organic matter (AOM) (up to 94%), common dinocysts (DI) (2–18%) and rare microspores (MS) (0–2%) discriminates the lagoonal (L)-facies from the flood-plain (F)-facies (Figs. 9 and 10).

In contrast to all other environments the relative abundances of amorphous organic matter (AOM) are extremely variable (2–94%), especially due to very high abundances (86% and 94%) in two end-member samples (Figs. 9 and 10; Appendix 1b), while non-saccate pollen (NSP) generally show high relative abundances (22–67%) (Figs. 9 and 18; Appendix 1b).

The higher relative abundances of freshwater algae (FA), fungal hyphae and spores (FU) and non-saccate pollen (NSP) differentiate the lagoonal (L)-facies from the prodelta (P)-facies (Fig. 12) and the washover-fan flat (W)-facies (Fig. 18). The last two facies further carry high loads of bisaccate pollen (BP); in the prodelta (P)-facies it varies between 27% and 76% and in the washover-fan flat (W)-facies bisaccate pollen (BP) varies from 66% to 92%, while the abundances of bisaccate pollen (BP) in the lagoonal (L)-facies yields maximum 47%

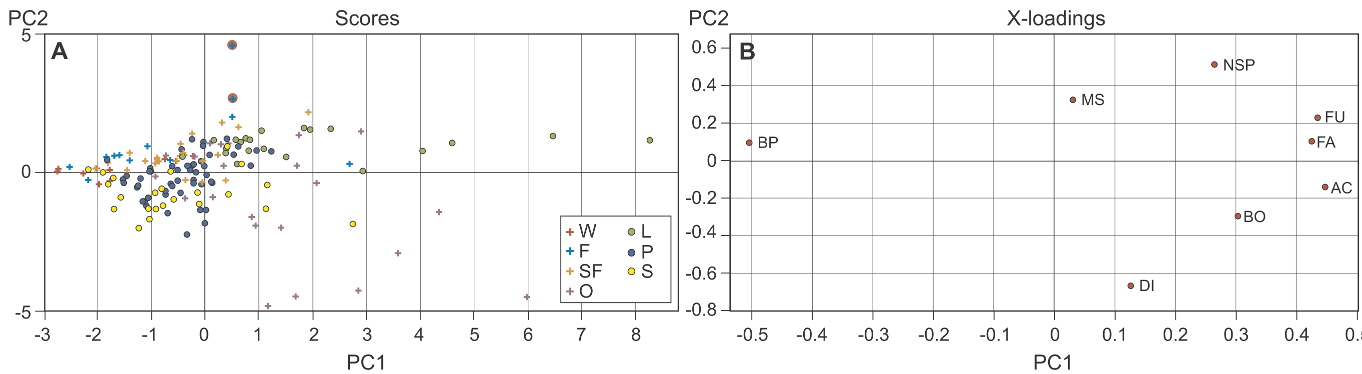

Fig. 17. A) MVDA-III score plot (PC1 vs. PC2), collectively accounting for 53% of the total data set variance. PCA with the previously found four F-facies samples excluded. Two more outlying F-samples (marked red) are identified here, along the positive PC2. W: Washover-fan flat, F: Flood-plain, SF: Shoreface, O: Offshore transition, L: Lagoonal, P: Prodelta, S: Shelf. B) Corresponding loading plot to Fig. 17A. Bisaccate pollen (BP), non-saccate pollen (NSP), microspores (MS), dinocysts (DI), acritarchs (AC), *Botryococcus* (BO), freshwater algae (FA), fungal hyphae and spores (FU). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

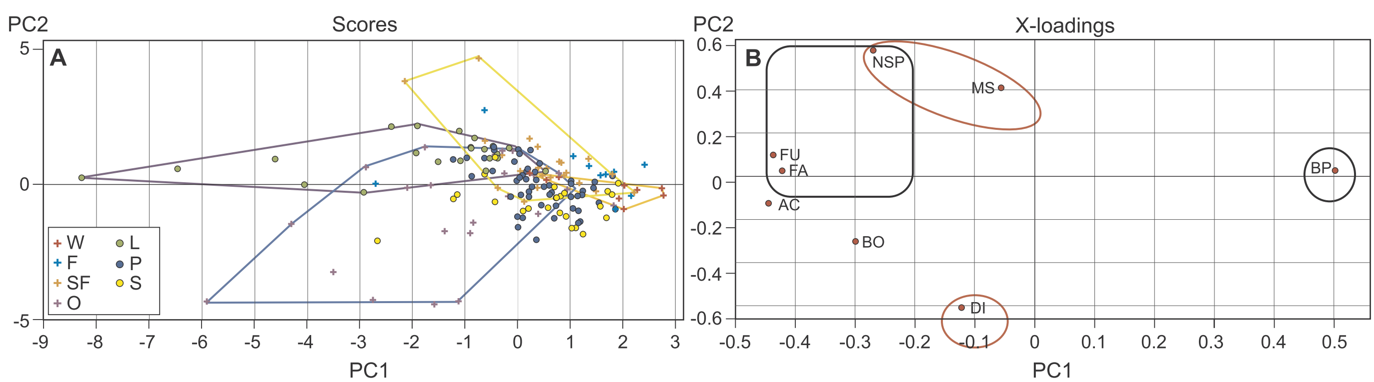

Fig. 18. A) MVDA-III score plot (PC 1 vs. -PC2), collectively accounting for 54% of the total data set variance. PCA with six extreme F-facies samples excluded. This visualization illustrates well the relationships between the L-, O-, SF- and W-facies. In spite of substantial overlapping, the L and W facies are completely discriminated from each other; see Fig. 18B for the determining category characteristics. W: Washover-fan flat, F: Flood-plain, SF: Shoreface, O: Offshore transition, L: Lagoonal, P: Prodelta, S: Shelf. B) Corresponding loading plot to Fig. 18A. Bisaccate pollen (BP), non-saccate pollen (NSP), microspores (MS), dinocysts (DI), acritarchs (AC), *Botryococcus* (BO), freshwater algae (FA), fungal hyphae and spores (FU).

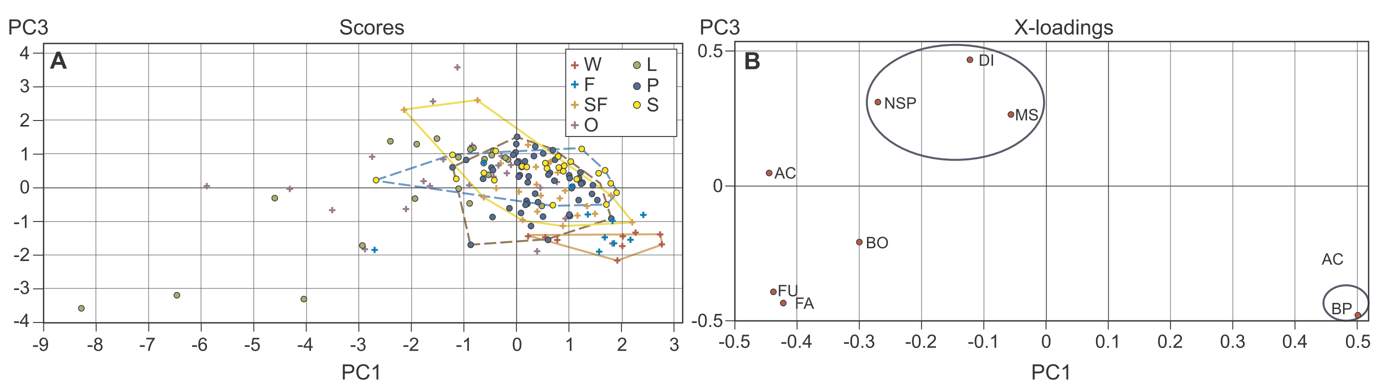

Fig. 19. A) MVDA-III score plo0074 of (PC1 vs. PC3) collectively accounting for 48% of total data variance. In this plot the SF-facies discriminates completely from the W-facies, while P and S are extensively overlapping. W: Washover-fan flat, F: Flood-plain, SF: Shoreface, O: Offshore transition, L: Lagoonal, P: Prodelta, S: Shelf. B) Corresponding loading plot to Fig. 19A.

(except for 1 sample at 61%) (Fig. 10; Appendix 1b). Additionally, the lagoonal (L)-facies discriminates from the prodelta (P)-facies by higher abundances of *Botryococcus* (BO) (0–16%) (Fig. 9).

The P/D-index has an average value of 84.3 (Appendix 1b), indicating a strong dominance of terrestrial palynomorphs – however, slightly lower than in the floodplain environment.

7.1.2.2. Interpretation. Lagoonal (L)-facies plot in between the proximal (floodplain, F-) and distal (offshore transition, O-and shelf, S-) facies (Fig. 16). It overlaps with the most distal part of the floodplain (F)-facies and with the most proximal parts of the offshore transition (O)- and shelf (S)-facies. This position may reflect the mixed terrestrially/fluvially and marine influence on the lagoonal (L)-facies.

The high abundances of non-saccate pollen probably reflect that the lagoonal areas were surrounded by swamp forests (Larsson et al., 2010, 2011). The very high abundances of AOM (degraded wood-particles) in some samples probably reflect the short distance from the source (decaying trunks from the swamp forest surrounding the lagoon),

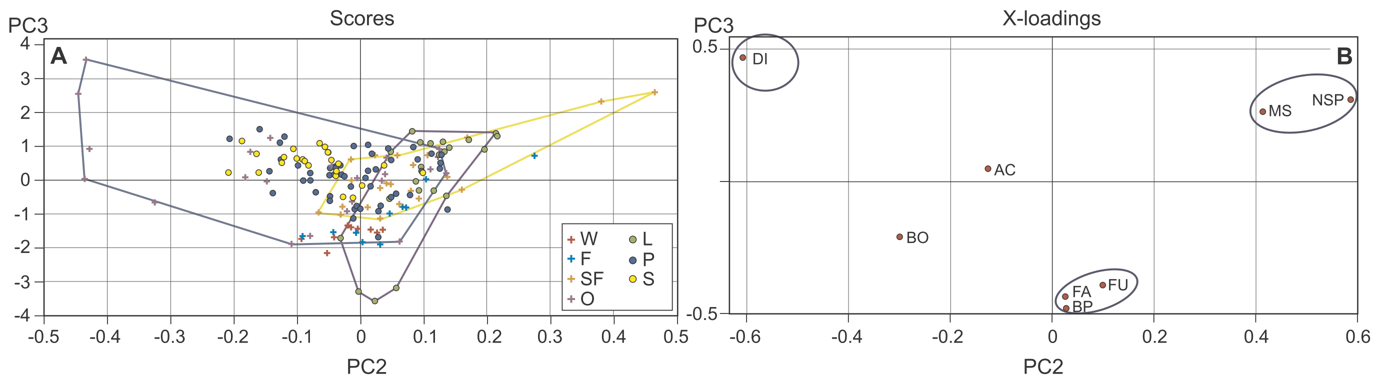

Fig. 20. A) MVDA-III score plot (PC2 vs. PC3), collectively accounting for 34% of total data variance. The three compositionally most varying facies are O, L, SF. W: Washover-fan flat, F: Flood-plain, SF: Shoreface, O: Offshore transition, L: Lagoonal, P: Prodelta, S: Shelf. B) Corresponding loading plot to Fig. 20A. This figure shows that DI is the main varying category in O; NSP plays a similar role for SF. The lagoonal facies (L) is more complex, also involving BP, FA and FU. The variable MS has an extreme bimodal distribution; only the two rightmost SF samples have high MS abundances. Bisaccate pollen (BP), non-saccate pollen (NSP), microspores (MS), dinocysts (DI), acritarchs (AC), *Botryococcus* (BO), freshwater algae (FA), fungal hyphae and spores (FU).

combined with the more quiet environment allowing bacterial degradation. This contrasts the high-energy shoreface (SF)-facies with high abundances of wood and almost no AOM (Figs. 9 and 10; Appendix 1a).

The low relative abundance of microspores (MS) in the lagoonal (L)-facies have also been observed in previous studies – compare Rasmussen and Dybkjær (2005) and Larsson et al. (2010). It can be speculated that either (i) the microspore-producing plants, e.g. ferns, were not that common in the swamp forests - perhaps not enough light could penetrate the canopy to allow ferns to thrive in the understory? However, ferns are common constituents of modern swamp forests; (ii) the clay-rich samples from the L-facies represent locations some distance away from the shoreline. As microspores are generally produced by plants (e.g. ferns) forming part of the undergrowth, they are not transported far away from their mother plants. Therefore, they may not have reached the middle to outer parts of the lagoonal setting. In contrast, spreading of pollen from trees forming the upper canopy are more effectively transported and spread by wind and water. As the deepest parts of lagoons have the highest preservation potential, the samples representing lagoonal depositional environments in the present study may in fact only be representative for the deeper parts of a lagoon. Alternatively (iii) the amount of bisaccate and non-saccate pollen produced by the trees in the swamp forest simply were so large that they diluted the input of microspores.

The inner parts of the lagoon were probably a fresh-to brackish-water environment, as suggested by the presence of freshwater algae (FA) and *Botryococcus* (BO). However, some of the freshwater algae (FA) and *Botryococcus* (BO) could also have been transported into the lagoon by rivers and streams.

The higher abundances of dinocysts in this environment compared with the floodplain reflect some connection to the marine environment. Some low-saline tolerant dinocyst taxa probably thrived within the lagoon, while others were transported into the lagoon from the normal marine settings by tidal currents.

7.1.3. *Washover-fan flat facies association (W) (orange)*

7.1.3.1. Characteristics. The assemblage is most similar to the floodplain (F)-facies. However, in contrast to the floodplain (F)-facies, in which the relative abundances of bisaccate pollen (BP) varies between 3% and 88%, all of the samples from the washover-fan flat (W)-facies are characterized by constantly very high abundances of bisaccate pollen (66–92%) (Figs. 9 and 17; Appendix 1b). The washover-fan flat (W)-facies, in contrast to all other five facies, shows a near absence of dinocysts (DI) (maximum 2%) (Fig. 9; Appendix 1b).

The washover-fan flat (W)-facies to a high degree overlap the shoreface (SF)-facies (Figs. 10, 12, 14 and 18), however this is only true for samples with high palynomorph/wood (PM/WO) ratios (Fig. 13). The relative abundance of wood is highly varying in the washover-fan flat (W)-facies (Figs. 9 and 10).

The washover-fan flat (W)-facies (like the shoreface, SF,-facies) differentiate from all other environments by high bisaccate pollen (BP) abundances (Fig. 12). When analyzing only palynomorphs (MVDA-III), the washover-fan flat (W)-facies discriminates completely from the shoreface (SF)-facies by distinctly high relative abundances of bisaccate pollen (BP) (66–92%) and low values of dinocysts (DI), non-saccate pollen (NSP) and microspores (MS) (Figs. 9 and 19).

The washover-fan flat (W)- and lagoonal (L)-facies discriminates completely from each other along the PC1 axis in Fig. 18 where the bisaccate pollen (BP) is negatively correlated with the freshwater algae (FA), fungal hyphae and spores (FU) and non-saccate pollen (NSP). Cuticle (CU) is slightly more common than in the lagoonal (L), prodelta (P)-, offshore transition (O)- and shelf (S)-facies (Fig. 9; Appendix 1b).

The P/D-index has an average value of 88.9 (Appendix 1b), indicating a strong dominance of terrestrial palynomorphs also for this environment.

7.1.3.2. Interpretation. The generally low abundances of wood (WO) compared with parts of the shoreface (SF)-facies probably reflect that the washover-fan flat (W)-facies represents a protected depositional environment on the backside of the barrier islands, while the shoreface (SF)-facies is prone to waves (high energy) (see further the part concerning the shoreface (SF)-facies).

The high relative abundances of bisaccate pollen (BP) in the washover-fan flat (W)-facies can be explained by either – or a combination of the following hypothesis;

1) The “Neves-effect” with bisaccate pollen floating further away from the vegetated coastline along the innerside of the lagoon.
2) The washover-fan flat facies are located on the landward side of barrier islands (Fig. 1). The barrier islands typically consist of sand and on such soils, which periodically may dry out and which are poor in nutrients, conifers (producing bisaccate pollen) thrive better than most non-saccate- and microspore-producing plants.

7.1.4. *Shoreface facies association (SF) (yellow)*

7.1.4.1. Characteristics. The shoreface facies association is characterized by varying, but generally much higher relative abundances of wood (WO) than in any other environment (Figs. 9 and 10). The abundance of wood varies between 3% and 94% (Fig. 9), but in 17 of the 23 samples the abundance is above 40% (Appendix 1a). Furthermore the shoreface (SF)-facies is characterized by generally high non-saccate pollen (NSP) (15–71%) and bisaccate pollen (BP) (16–78%)

abundances and rather low dinocyst (DI) abundances (0–16%) (Figs. 9, 12, 13 and 18).

A nearly complete differentiation between the shoreface (SF)- and offshore transition (O)-facies (Fig. 13) is due to high abundances of wood (WO), non-saccate pollen (NSP) and bisaccate pollen (BP) and to a minor degree microspores (MS), controlling the shoreface (SF)-facies in contrast to the high abundances of dinocysts (DI) controlling the offshore transition (O)-facies.

The shoreface (SF)-facies is seen to be located between the proximal and distal facies (Fig. 16). The location on the plot seems to be controlled mainly by high amounts of non-saccate pollen (NSP) and low amounts of dinocysts (DI).

The shoreface (SF)-facies and the washover-fan flat (W)-facies are completely discriminated (Fig. 19) by the anti-correlation of higher abundances of non-saccate pollen (NSP), dinocysts (DI) and microspores (MS) in the shoreface (SF)-facies versus higher relative abundances of bisaccate pollen (BP) in the washover-fan flat (W)-facies.

An average P/D-index value of 87 (Appendix 1b) indicates that the shoreface environment is characterized by a dominance of terrestrial palynomorphs, in the same order as the washover-fan flat and lagoonal environments.

7.1.4.2. Interpretation. The very high relative abundances of wood (WO) in most of the samples from the shoreface (SF)-facies likely reflect the high energy in this environment (above the fair-weather wave-base). Palynomorphs (PM) have a buoyancy comparable with clay and silt particles, and are, like clay and silt, only deposited in quiet periods (fair weather conditions). In contrast, wood particles are generally the only organic particles found in sandy deposits.

The overlap of the shoreface (SF)-facies and the washover-fan flat (W)-facies in the leftmost side on Fig. 14 may be interpreted as representing samples deposited in a low-energy environment, while the extreme right part of the shoreface (SF)-facies is reflecting the high-energy environment.

The high relative abundances of non-saccate pollen (NSP) among the palynomorphs probably reflect the presence of a Taxodium swamp forest growing along the coastline (Koch, 1989; Larsson et al., 2006, 2010; 2011) which produced very high amounts of pollen. The few samples with relative abundances of microspores (MS) slightly higher than normal (5% and 9%, respectively) seem to have influenced the PCA of this facies. The spore producing plants possibly formed the understorey of the swamp-forests, see further the discussion in the lagoonal (L)-facies.

The complete discrimination between the shoreface (SF)-facies and the washover-fan flat (W)-facies (Fig. 19) may reflect the nutrient-poor, sandy soils on the barrier-islands in contrast to the better soils along the coast (see discussion for the washover-fan flat facies in the previous section). The palynomorphs delivered to the washover-fan flat -facies possibly mainly came from the sandy barrier-islands on which only conifers (producing bisaccate pollen) could grow, while nutrient-rich, continuously wet peaty soils along the coastline formed the basis for a rich and diverse Taxodium swamp forest, delivering huge amounts of both non-saccate and bisaccate pollen to the shoreface environment.

The rather low relatively abundances of dinocysts (DI) (compared with the offshore facies) are probably the result of dilution due to the high influx of non-saccate pollen (NSP) and bisaccate pollen (BP). Dilution may also explain the surprisingly lower relative abundances of *Botryococcus* (BO) in the shoreface (SF)- facies compared with the offshore transition (O)- facies (Fig. 9; Appendix 1b).

7.1.4.3. Comments. As mentioned above, the samples from the shoreface (SF)-facies were taken so that they consisted of both the dominating sandy deposits, but also minor clay-layers in order to assure the presence of enough palynomorphs for the statistical analysis.

7.1.5. Prodelta Facies Association (P) (Brown)

7.1.5.1. Characteristics. The prodelta (P)-facies is characterized by well-mixed homogene assemblages of organic particles with no categories or subcategories becoming distinctly abundant (Fig. 9). The prodelta (P)-facies overlaps extensively with the shelf (S)-facies (Figs. 10, 12, 16 and 19).

When compared with the washover-fan flat (W)- and shoreface (SF)-facies, the prodelta (P)-facies show lower abundances of wood (WO) and constantly high abundances of amorphous organic matter (AOM) (Fig. 10). It shows extremely low abundances of microspores (MS), fungal hyphae and spores (FU), *Botryococcus* (BO) and acritarchs (AC) (max 2%), while freshwater algae (FA) show slightly increased abundances in some samples, up to 8% (Fig. 9; Appendix 1b).

In contrast to the lagoonal (L)- and shoreface (SF)-facies, the relative abundances of bisaccate pollen (BP) are generally higher (27–76%) than the abundances of non-saccate pollen (NSP) (7–52%) (Fig. 9). The prodelta (P)-facies also shows higher abundances of dinocysts (DI). However, the relative abundances of dinocysts are highly variable, from 2 to 47% (Fig. 9).

Compared with the offshore transition (O)-facies, the prodelta (P)-facies generally has lower abundances of dinocysts (DI) and *Botryococcus* (BO) and higher abundances of bisaccate pollen (BP) (Figs. 9, 17 and 18).

The average P/D-index value of 60.8 (Appendix 1b) show a less strong dominance of terrestrial palynomorphs, compared with the shoreface, washover-fan flat, lagoonal and floodplain environments.

7.1.5.2. Interpretation. The prodelta (P)-facies is characterized by generally well-mixed assemblages of organic particles. This probably reflects a high degree of re-deposition of the sediments, homogenizing the varying influx of fluvially and terrestrially derived particles via rivers and deltas, into the marine environment. The variations seen in the relative abundances of dinocysts (DI) may reflect delta-lobal shifts, resulting in variations in the influx of fluvial- and terrestrially derived particles, diluting the dinocyst-assemblages. The high amounts of partly degraded wood (AOM) are probably transported into the prodelta (P)-facies from floodplain areas via rivers.

The constantly high relative abundances of bisaccate pollen (BP) related to non-saccate pollen (NSP), which contrast what is seen in the lagoonal (L)- and shoreface (SF)-facies, probably reflect the "Neves-effect".

The extensively overlap with the shelf (S)-facies, probably reflects that both environments are well-mixed, being located in fully marine settings but also receiving large amounts of fluvial and terrestrially derived organic particles. Furthermore, coast-parallel currents probably eroded the pro-delta deposits and transported these sediments along the coast and deposited them on the shelf. Much of the shelf deposits thus probably originate from pro-delta settings.

7.1.5.3. Comments. For these reasons the compositional 'spread' of a facies in the score plot may be extensive, or may be strongly coherent – and may in fact sometimes appear uncorrelated to the number of samples included. Thus, despite a high total sample number, distinct discriminability between the shelf (S)- and the prodelta (P)-facies remains elusive.

7.1.6. Offshore Transition Facies Association (O) (dark blue)

7.1.6.1. Characteristics. The offshore transition (O)-facies discriminates from all other facies except the shelf (S)-facies, by showing very high relative abundances of dinocysts (DI), even extremely high abundances (83% and 92%) in a few samples (Figs. 9, 12 and 13). However, the abundances of dinocysts (DI) are very variable, ranging from 2% to 92%, and below 20% in most samples (Appendix 1b).

The relative abundances of non-saccate pollen (NSP) and bisaccate pollen (BP) are approximately equal (Fig. 9).

The abundances of microspores (MS) are extremely low (max 2%), while freshwater algae (FA), fungal hyphae and spores (FU) and acritarchs (AC) show slightly increased abundances in some samples, up to 7%.

The abundances of *Botryococcus* (BO) are remarkably high, up to 35% and above 10% in approximately half of the analysed samples.

Figs. 12, 13 and 16 show nearly completely discriminations of the offshore transition (O)- and the shoreface (SF)-facies, mainly driven by a negative correlation of dinocysts (DI) and Botryococcus (BO) versus wood (WO), non-saccate pollen (NSP), microspores (MS) and cuticle (CU).

The P/D-index has an average value of 60.0 (Appendix 1b), indicating an influx of terrestrial palynomorphs in the same order as for the prodelta environment.

7.1.6.2. Interpretation. The generally high relative abundances of dinocysts (DI) probably reflect optimal salinity and nutrient supply in which dinoflagellates thrive.

The clear discrimination between the offshore transition (O)- and the shoreface (SF)-facies may further reflect that the offshore transition (O)-facies is less influenced by fluvial- and terrestrially derived particles (non-saccate pollen, NSP, microspores, MS, wood, WO, cuticle, CU) due to the more distal location. The lower relative abundances of wood (WO) probably also reflects the increased water-depths of the offshore transition (O)-facies (below fair-weather wave-base), allowing palynomorphs to settle.

The high relative abundances of *Botryococcus* (BO) probably reflect that these freshwater algae are tolerant to brackish water and probably thrived in the shallow marine areas.

7.1.7. Shelf facies association (S) (light blue)

7.1.7.1. Characteristics. The shelf (S)-facies is characterized by well-mixed assemblages of organic particles (Figs. 9, 10 and 18) with no categories or subcategories becoming distinctly abundant. This feature was characteristic also for the prodelta (P)-facies. As was seen in the prodelta (P)-facies, the relative abundances of bisaccate pollen (BP) are constantly high and distinctly higher than non-saccate pollen (NSP) (Fig. 9). The shelf (S)-facies, like the offshore transition (O)-facies, is further characterized by high relative abundances of dinocysts (DI) and low abundances of freshwater algae (FA), fungal hyphae and spores (FU), and microspores (MS) (max 2% of the two former and max 3% of the latter). The relative abundance of *Botryococcus* (BO) is not as high as in the offshore transition (O)-facies, but reaches up to 14%. In Fig. 16 the shelf (S)-facies plots within the rightmost part of the offshore transition (O)-facies polygon.

The shelf facies are characterized by the lowest average value of the P/D index in the study area. The index has an average value of 45.5 (Appendix 1b), indicating a clearly lower influx of terrestrial palynomorphs than that of the other six studied environments.

7.1.7.2. Interpretation. The overlap pattern of the offshore transition (O)- and the shelf (S)-facies polygons (Fig. 16) probably reflects the more constantly high abundances of dinocysts (DI) in the shelf (S)-facies in contrast to the offshore transition (O)-facies where the dinocyst (DI) abundances vary extensively, with a few samples with extremely high dinocyst (DI) abundances pulling the offshore transition (O)-facies polygon towards the left, see also Appendix 1b. The apparent reverse locations of the offshore transition (O)- and shelf (S)-facies polygons, as seen in Figs. 13 and 16, with parts of the offshore transition (O)-facies polygon reaching further "distally" than the shelf (S)-facies polygon, is an artifact due to these extremely high dinocyst (DI) abundances.

The constantly high relative abundances of bisaccate pollen (BP) related to non-saccate pollen (NSP), as also seen in the prodelta (P)-facies but contrasting the lagoonal (L)- and shoreface (SF)-facies, probably reflect the "Neves-effect" (Fig. 9).

As seen in e.g. Figs. 10 and 19, there is an extensive overlap between the prodelta (P)- and shelf (S)-facies. It must be assumed that the prodelta environment received more fluvially and terrestrially derived organic particles (from the rivers forming the deltas). The overlap may indicate that currents associated with submarine gyres redistributed the prodeltaic deposits along the shelf (Hansen et al., 2004; Hansen and Rasmussen, 2008).

7.2. Distribution patterns of selected particles

a) Traditionally, in studies of marine depositional environments, high amounts of amorphous organic matter have been interpreted as an indicator of anoxic/dysoxic bottom waters and the origin of this organic matter have often been found to be mainly marine algae (e.g. Tyson, 1995; Pacton et al., 2011). However, in the present study, dealing with a fluvio-deltaic setting, the degraded organic matter found in the samples comprises degraded vitrinite, probably coming from the Taxodium swamp areas along the coast. Transitional stages from structured wood-particles and to totally structureless particles are shown in Fig. 8J (photos). It is difficult to know to which degree abundance of this degraded vitrinite can be used to indicate oxygen deficiency in the bottom waters, or rather indicate proximity to the swamp areas
b) In the PCA-plots (Figs. 10–20), freshwater algae (FA) and fungal hyphae and spores (FU) consistently plot closely together. This coupling probably reflects the mutual origin (fluvial environments and from the swamp forests) and riverine transport mode. *Botryococcus* (BO) and acritarchs (AC) also seem to be coupled, plotting in between the freshwater/fungal hyphae and spores (FA/FU) and the dinocysts (DI). Acritarchs (AC) originate from/live in shallow marine environments, which is in good agreement with its location in Fig. 20, indicating a relationship with dinocysts (DI). Freshwater algae (FA) and *Botryococcus* (BO) most often plot with some distance (e.g. Figs. 16, 17, 18, 20). The results thus show the importance of not including *Botryococcus* (BO) in the freshwater algae (FA)-subcategory. The positioning of *Botryococcus* (BO) on Fig. 20 probably reflects that this algae thrive in brackish water as well as freshwater and therefore can be found in both shallow marine and fluvial environments.
   The distance between the freshwater algae (FA) and *Botryococcus* (BO) in the plots, and the coupling between *Botryococcus* (BO) and acritarchs (AC) probably reflect that the euryhaline algae *Botryococcus* in the present study is more related to brackish water than freshwater environments. If *Botryococcus* only thrived in freshwater settings, it would be expected to be distributed together with the other freshwater algae (*Pediastrum* and *Pseudokomewuia*) rather than with the shallow marine acritarchs. The semi-enclosed situation for the North Sea Basin during the early Miocene in combination with a humid climate (ca. 1500 mm annual precipitation, Larsson et al., 2011; Rasmussen et al., 2013) may have resulted in a general lowered salinity – corresponding to the situation for the Baltic Sea today. It can be speculated if such an overall lowered salinity may have resulted in the possibility for *Botryococcus* to expand the area where it thrived from floodplain, lagoonal and deltaic settings to include shallow marine (low-salinity) settings.
c) Extremely high abundances of microspores (MS) (17–88%) are in the present study only found in samples from the floodplain (F) environment and are therefore a very good indicator for this environment. Relatively high abundances of freshwater algae (FA)

(12–17%) and fungal hyphae and spores (FU) (11–12%) are also characteristic for the floodplain (F) facies, although a few samples from the lagoonal (L) facies also reaches 10%. The samples from the lagoonal facies differ however, in their distinctly higher abundances of dinocysts (DI). Extremely high abundances of AOM (degraded vitrinite) have only been recorded from the lagoonal (L) depositional environment and are thus a very good indicator for this environment, when observed.

d) The dominance of bisaccate pollen (BP) in most of the floodplain (F) samples (and of microspores (MS) in a few samples) rather than non-saccate pollen (NSP), may be interpreted as reflecting a floodplain mainly consisting of sandy deposits with frequent avulsions of channels, not offering good, stable conditions for development of a rich and variable vegetation. This may suggest a relatively high relief of the floodplain, which is also supported by the fact that the gravel front reached the delta outlet (Rasmussen et al., 2010; Helland-Hansen et al., 2016).

e) The P/D-index show a clear trend in the distribution of palynomorphs with a decreasing ratio of terrestrial palynomorphs in a proximal-distal direction. The index show values ranges from close to 100 (97.1) in the floodplain environment to 45.5 in the shelf environment. The most variable ratios are observed in the offshore environment and to a lesser degree in the shelf and prodelta environments. The remaining environments are characterized by high and relatively stable ratios.

7.3. Evaluation of statistical methods

a) Univariate Box-plots are very efficient in outlining the general distribution of sedimentary organic particles for each depositional environment. Furthermore, they clearly show the overall trends across depositional environments, however, only as expressed by one parameter at the time.
In contrast, the multivariate PCA plots effectively present the characteristics and the variability of each depositional environment as expressed simultaneously by up to 12 palynofacies variables. The major PCA plots show both the degree of overlap and the resolvable distinctions between the seven environments. One issue that must be borne in mind during the multivariate data analysis interpretations is that depending on the degree, sometimes bimodal distributions may have a marked influence on the data disposition in certain score cross-plots, even when the relative abundances all are low (e.g. microspores (MS) in the shoreface (SF)-facies), see comments regarding outliers below. More constant high abundances does not bias much towards a specific PCA component direction (e.g. dinocysts (DI) in the shelf (S)-facies). It is the effective *combination* of both PCA-plots and Box-plots that reveal both general trends and outliers in the presented palynofacies data-set.

b) The recognized and deleted outlier samples (two samples from the lagoonal (L)- facies showing extremely high relative abundances of AOM, two samples from the floodplain (F)- facies showing relatively high abundances of freshwater algae (FA) and fungal hyphae and spores (FU), and four samples from the floodplain (F)- facies showing high abundances of microspores (MS), should not be forgotten although these samples (at some point) were removed from the dataset in the latter part of the statistical analyses. None of these samples were interpreted as representing erroneous identification of environments, faults in processing etc. They simply represent extreme end-members of the natural variations of the environment they come from. Bimodal distributions and end-member dispositions are always to be expected to the degree that the data sets are able, or not fully able, to represent complete depositional facies variabilities. It is to be expected that such lacunae will be filled-in when more samples are analysed in future studies.

8. Conclusions

A palynofacies reference dataset for seven different depositional environments from the upper Oligocene - lower Miocene of the North Sea Basin has been established. The dataset have been treated statistically using univariate Box Plots and multivariate Principal Component Analysis (PCA).

Three depositional environments can be fully differentiated using the palynofacies dataset:

- The floodplain environment is characterized by the near absence of dinocysts. Some samples from this environment are further characterized by relatively high abundances (compared with the other environments) of freshwater algae, fungal hyphae and spores and *Botryococcus* and (in other samples) very high relative abundances of microspores.
- The washover-fan flat environment is characterized by high relative abundances of bisaccate pollen.
- The shoreface environment is characterized by high relative abundances of wood particles.

The data from the other four environments reveal various degrees of overlaps, but also depicts clear overall trends. The proximal-distal trend expressed as increased relative abundances of dinocysts and decreased non-saccate pollen, are valuable and useful information, e.g. for differentiating lagoonal mud from shelfal mud. Lithologically these two environments are difficult to distinguish. The median for dinocysts in the lagoonal facies is 10% and never higher than 18%. The median for the shelf facies is 26%. In most samples from the lagoonal facies the relative abundance of non-saccate pollen are higher than the abundance of bisaccate pollen. In most samples from the shelf facies a clear dominance of bisaccate pollen in relation to non-saccate pollen is found.

The increase in relative abundances of bisaccate pollen from offshore transition to shelf, possibly reflecting the “Neves-effect”, can, possibly in combination with increase in dinocysts, be used to indicate a deepening/flooding trend.

The present reference dataset can be used for identifying the overall depositional setting, e.g. floodplain, lagoon, shoreface etc. at a specific time. Such reconstruction of the palaeogeography is important for the understanding of basin development.

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Appendices

Appendix 1a

Results of the counts of sedimentary organic particles, main categories. The numbers shown are relative abundances within the main categories. Palynofacies data, main categories, relative abundances (100% = total).

Palaeoenvironment: Shelf	Samples		Cuticle	Palynomorphs	AOM/degraded vitrinite	Wood-particles	Total %
St. Vorslunde	SSV1		0	61	25	14	100
	SSV2		0	63	23	14	100
	SSV3		0	60	29	11	100
	SSV4		1	23	52	24	100
	SSV5		0	32	46	22	100
	SSV6		0	50	40	10	100
	SSV7		0	20	54	26	100
Vandel Mark	SVM1		0	36	49	15	100
Andkær	SA1		0	81	11	8	100
Resen	SR1		1	59	18	22	100
	SR2		0	69	13	18	100
	SR3		1	77	8	14	100
	SR4		1	90	2	7	100
	SR5		1	87	4	8	100
	SR6		0	78	3	19	100
	SR7		1	87	2	10	100
Harre	SH1		0	64	29	7	100
	SH2		0	57	34	9	100
	SH3		0	64	30	6	100
	SH4		0	79	18	3	100
	SH5		0	83	14	3	100
	SH6		0	77	17	6	100
Number of samples:	22	MIN	0	20	2	3	
		25%	0	57.5	11.5	7.25	
		Median:	0	64	20.5	10.5	
		75%	0.75	78.75	33	17.25	
		MAX	1	90	54	26	

Palaeoenvironment: Offshore	Samples		Cuticle	Palynomorphs	AOM/degraded vitrinite	Wood-particles	Total %
Hostrup	OH1		0	90	8	2	100
	OH2		0	98	1	1	100
	OH3		2	89	7	2	100
	OH4		3	84	5	8	100
	OH5		3	72	5	20	100
	OH6		1	76	6	17	100
	OH7		1	94	2	3	100
	OH8		1	97	0	2	100
	OH9		1	97	1	1	100
Fænø	OF1		1	89	1	9	100
	OF2		1	89	3	7	100
	OF3		0	90	2	8	100
	OF4		1	71	6	22	100
	OF5		1	96	1	2	100
	OF6		1	95	0	4	100
	OF7		1	51	6	42	100
	OF8		4	66	2	28	100
	OF9		3	38	2	57	100
	OF10		1	65	1	33	100
	OF11		0	86	1	13	100
Klosterhede	OK1		1	68	4	27	100
	OK2		0	50	10	40	100
	OK3		1	59	14	26	100
Number of samples:	23	MIN	0	38	0	1	
		25%	1	67	1	2.5	
		Median:	1	86	2	9	
		75%	1	92	6	26.5	
		MAX	4	98	14	57	

Palaeoenvironment: Prodeltaic	Samples		Cuticle	Palynomorphs	AOM/degraded vitrinite	Wood-particles	Total %
St. Vorslunde	PSV1		1	19	43	37	100
	PSV2		1	78	12	9	100
	PSV3		0	43	26	31	100
	PSV4		1	52	31	16	100
	PSV5		0	43	25	32	100
	PSV6		0	40	46	14	100
	PSV7		0	47	46	7	100
	PSV8		0	65	28	7	100
	PSV9		0	53	30	17	100
	PSV10		0	84	10	6	100
	PSV11		0	60	26	14	100
	PSV12		0	50	35	15	100
	PSV13		0	49	31	20	100
	PSV14		0	41	35	24	100
	PSV15		0	40	44	16	100
	PSV16		0	62	25	13	100
	PSV17		0	62	30	8	100
	PSV18		0	65	29	6	100
	PSV19		0	59	27	14	100
	PSV20		0	41	41	18	100
	PSV21		0	43	35	22	100
	PSV22		0	58	30	12	100
	PSV23		0	43	45	12	100
	PSV24		0	58	27	15	100
	PSV25		0	48	36	16	100
	PSV26		0	67	22	11	100
	PSV27		0	62	24	14	100
Vandel Mark	PVM1		0	22	35	43	100
	PVM2		0	24	35	41	100
	PVM3		1	31	51	17	100
	PVM4		0	28	45	27	100
	PVM5		0	50	21	29	100
	PVM6		0	50	33	17	100
	PVM7		0	40	45	15	100
	PVM8		0	41	41	18	100
	PVM9		0	30	59	11	100
	PVM10		0	43	38	19	100
	PVM11		0	56	28	16	100
	PVM12		0	33	50	17	100
	PVM13		0	30	58	12	100
	PVM14		0	48	24	29	101
	PVM15		0	44	40	16	100
Andkær	PA1		0	65	28	7	100
	PA2		0	58	38	4	100
	PA3		0	66	23	11	100
	PA4		0	60	31	9	100
	PA5		0	54	28	18	100
	PA6		0	58	25	17	100
	PA7		0	63	22	15	100
	PA8		0	48	22	30	100
	PA9		0	25	35	40	100
	PA10		0	75	20	5	100
	PA11		0	77	13	10	100
Number of samples:	53	MIN	0	19	10	4	
		25%	0	41	25	11	
		Median:	0	50	31	16	
		75%	0	60	40	19	
		MAX	1	84	59	43	

Palaeoenvironment: Shoreface	Samples	Cuticle	Palynomorphs	AOM/degraded vitrinite	Wood-particles	Total %
Andkær	SFA1	0	46	8	46	100
	SFA2	1	28	12	59	100
	SFA3	0	42	12	46	100
	SFA4	0	29	14	57	100
Børup	SFB1	0	14	2	84	100
	SFB2	0	63	1	36	100
	SFB3	0	10	1	89	100
	SFB4	1	29	1	69	100

Hvidbjerg	SFH1		3	77	3	17	100
	SFH2		6	86	2	6	100
	SFH3		4	54	2	40	100
	SFH4		0	14	2	84	100
	SFH5		0	4	2	94	100
	SFH6		0	59	0	41	100
	SFH7		0	10	1	89	100
	SFH8		1	33	0	66	100
	SFH9		1	16	1	82	100
	SFH10		1	35	1	63	100
	SFH11		1	21	0	78	100
Rønshoved	SFR1		1	93	1	5	100
	SFR2		1	91	1	7	100
	SFR3		1	94	2	3	100
	SFR4		1	90	1	8	100
Number of samples:	23	MIN	0	4	0	3	
		25%	0	18.5	1	26.5	
		Median:	1	35	1	57	
		75%	1	70	2	80	
		MAX	6	94	14	94	

Palaeoenvironment: Washover fan flat	Samples		Cuticle	Palynomorphs	AOM/degraded vitrinite	Wood-particles	Total %
Hagenør	WH1		3	91	0	6	100
	WH2		4	59	3	34	100
	WH3		2	32	3	63	100
	WH4		3	41	2	54	100
Skansebakke	WS1		4	88	1	7	100
	WS2		0	86	1	13	100
	WS3		1	97	1	1	100
	WS4		1	92	0	7	100
	WS5		0	82	1	17	100
Number of samples:	9	MIN	0	32	0	1	
		25%	1	59	1	7	
		Median:	2	86	1	13	
		75%	3	91	2	34	
		MAX	4	97	3	63	

Palaeoenvironment: Lagoonal	Samples		Cuticle	Palynomorphs	AOM/degraded vitrinite	Wood-particles	Total %
			CU	PM	AOM	WO	
Dykær, data from Rasmussen and Dybkjær (2005)	LD1		0	4	94	2	100
	LD2		0	7	86	7	100
Hagenør	LH1		1	77	4	18	100
	LH2		2	62	8	28	100
	LH3		2	75	5	18	100
	LH4		2	35	12	51	100
	LH5		0	86	4	10	100
	LH6		1	88	2	9	100
	LH7		1	32	9	58	100
	LH8		1	62	20	17	100
	LH9		2	37	7	54	100
	LH10		1	59	31	9	100
	LH11		0	55	33	12	100
	LH12		0	42	45	13	100
	LH13		0	47	42	11	100
	LH14		0	36	54	10	100
Fakkegrav	LF1		1	83	3	13	100
	LF2		1	91	3	5	100
Skansebakke	LS1		2	89	2	7	100
	LS2		1	94	1	4	100
	LS3		1	93	1	5	100
	LS4		0	95	1	4	100
Number of samples:	22	MIN	0	4	1	2	
		25%	0	38.25	3	7	
		Median:	1	62	7.5	10.5	
		75%	1	87.5	32.5	17.75	
		MAX	2	95	94	58	

Palaeoenvironment: Lagoonal Note: dataset is excl. outliers	Samples		Cuticle	Palynomorphs	AOM/degraded vitrinite	Wood-particles	Total %
			CU	PM	AOM	WO	
Hagenør	LH1		1	77	4	18	100
	LH2		2	62	8	28	100
	LH3		2	75	5	18	100
	LH4		2	35	12	51	100
	LH5		0	86	4	10	100
	LH6		1	88	2	9	100
	LH7		1	32	9	58	100
	LH8		1	62	20	17	100
	LH9		2	37	7	54	100
	LH10		1	59	31	9	100
	LH11		0	55	33	12	100
	LH12		0	42	45	13	100
	LH13		0	47	42	11	100
	LH14		0	36	54	10	100
Fakkegrav	LF1		1	83	3	13	100
	LF2		1	91	3	5	100
Skansebakke	LS1		2	89	2	7	100
	LS2		1	94	1	4	100
	LS3		1	93	1	5	100
	LS4		0	95	1	4	100
Number of samples:	20	MIN	0	32	1	4	
		25%	0	45.75	2.75	8.5	
		Median:	1	68.5	6	11.5	
		75%	1.25	88.25	22.75	18	
		MAX	2	95	54	58	

Palaeoenvironment: Fluvial/floodplain	Samples		Cuticle	Palynomorphs	AOM/degraded vitrinite	Wood-particles	Total %
Voervadsbro	FVB1		1	86	1	12	100
	FVB2		1	94	1	4	100
Salten	FS1		1	64	10	25	100
	FS2		1	82	1	16	100
	FS3		0	66	8	26	100
	FS4		12	71	4	13	100
	FS5		3	97	0	1	101
	FS6		8	92	0	0	100
	FS7		2	97	1	0	100
	FS8		4	86	4	6	100
	FS9		9	79	4	8	100
	FS10		1	89	1	9	100
	FS11		1	97	0	2	100
	FS12		7	86	4	3	100
	FS13		1	98	0	1	100
	FS14		1	97	1	1	100
Number of samples:	16	MIN	0	64	0	0	
		25%	1	81.25	0.75	1	
		Median:	1	87.5	1	5	
		75%	4.75	97	4	12.25	
		MAX	12	98	10	26	

Palaeoenvironment: Fluvial/floodplain	Samples		Cuticle	Palynomorphs	AOM/degraded vitrinite	Wood-particles	Total %
Note: dataset is excl. outliers							
Voervadsbro	FVB1		1	86	1	12	100
	FVB2		1	94	1	4	100
Salten	FS1		1	64	10	25	100
	FS2		1	82	1	16	100
	FS3		0	66	8	26	100
	FS7		2	97	1	0	100
	FS11		1	97	0	2	100
	FS12		7	86	4	3	100
	FS13		1	98	0	1	100
	FS14		1	97	1	1	100
Number of samples:	10	MIN	0	64	0	0	
		25%	1	83	1	1.25	
		Median:	1	90	1	3.5	
		75%	1	97	3.25	15	
		MAX	7	98	10	26	

Appendix 1b

Results of the counts of sedimentary organic particles, subcategories (palynomorphs). The numbers shown are relative abundances within the subcategories (the palynomorphs). Palynofacies data, subcategories, relative abundances (100% = total).

Palaeoenvironment: Shelf	Samples		Dinocysts	Acritarchs	Botryococcus	Bisaccate pollen	Non-saccate pollen	Microspores	Freshwater algae	Fungal hyphae and -spores	Total %	P/D index
			DI	AC	BO	BP	NSP	MS	FA	FU		
St. Vorslunde	SSV1		30	1	2	54	12	1	0	0	100	**30.2**
	SSV2		13	1	1	64	18	1	1	1	100	**61.8**
	SSV3		31	1	1	50	16	1	0	0	100	**35.4**
	SSV4		24	1	0	59	13	2	1	0	100	**40.0**
	SSV5		26	0	1	59	13	1	0	0	100	**35.0**
	SSV6		21	1	2	53	22	1	0	0	100	**52.3**
	SSV7		28	1	1	51	17	1	1	0	100	**40.4**
Vandel Mark	SVM1		14	0	1	70	13	1	1	0	100	**51.7**
Andkær	SA1		24	1	1	50	23	1	0	0	100	**50.0**
Resen	SR1		21	1	10	31	33	1	2	1	100	**63.8**
	SR2		33	1	11	30	19	3	2	1	100	**43.1**
	SR3		29	4	14	26	24	0	2	1	100	**48.2**
	SR4		6	1	4	41	45	1	1	1	100	**88.9**
	SR5		14	2	1	43	37	1	1	1	100	**74.1**
	SR6		26	1	2	42	28	0	1	0	100	**52.7**
	SR7		29	2	1	39	27	1	0	1	100	**50.0**
Harre	SH1		12	0	0	69	18	1	0	0	100	**61.3**
	SH2		19	0	0	65	15	1	0	0	100	**45.7**
	SH3		32	0	0	60	7	1	0	0	100	**20.0**
	SH4		44	0	1	48	6	1	0	0	100	**13.7**
	SH5		34	0	1	53	11	0	0	1	100	**26.1**
	SH6		42	0	0	50	6	1	0	1	100	**16.0**
											Avg-ratio	**45.5**
Number of samples:	22	MIN	6	0	0	26	6	0	0	0		
		25%	19.5	0	1	42.25	13	1	0	0		
		Median:	26	1	1	50.5	17.5	1	0	0		
		75%	30.75	1	2	59	23.75	1	1	1		
		MAX	44	4	14	70	45	3	2	1		

Palaeoenvironment: Offshore	Samples	Dinocysts	Acritarchs	Botryococcus	Saccate pollen	Non-saccate pollen	Microspores	Freshwater algae	Fungal hyphae and -spores	Total %	**P/D index**
Hostrup	OH1	12	2	2	43	39	1	1	0	100	**77.4**
	OH2	6	1	1	53	39	0	0	0	100	**86.7**
	OH3	5	1	2	40	50	1	1	0	100	**91.2**
	OH4	16	2	4	30	44	0	3	1	100	**75.0**
	OH5	36	4	10	13	28	1	6	2	100	**50.7**
	OH6	11	1	5	32	42	0	2	7	100	**82.3**
	OH7	6	2	2	31	54	1	2	2	100	**90.8**
	OH8	7	1	2	35	53	1	1	0	100	**88.7**
	OH9	6	1	3	49	40	0	1	0	100	**87.2**
Fænø	OF1	4	0	8	79	8	0	1	0	100	**69.2**
	OF2	6	1	3	40	47	1	1	1	100	**89.3**
	OF3	19	1	12	31	28	2	7	0	100	**66.1**
	OF4	19	1	12	44	21	2	1	0	100	**55.8**

	OF5		2	0	24	64	7	1	2	0	100	**83.3**
	OF6		4	1	8	69	16	1	1	0	100	**81.8**
	OF7		43	7	35	5	4	1	4	1	100	**18.9**
	OF8		31	3	32	17	13	0	2	2	100	**35.4**
	OF9		53	2	30	4	9	0	2	0	100	**17.2**
	OF10		28	2	14	41	12	1	2	0	100	**34.9**
	OF11		30	1	22	20	25	1	1	0	100	**47.4**
Klosterhede	OK1		41	1	6	26	23	1	1	1	100	**38.8**
	OK2		83	1	8	1	5	0	1	1	100	**7.8**
	OK3		92	1	3	0	2	1	1	0	100	**4.2**
											Avg-ratio	**60.0**
Number of samples:	23	MIN	2	0	1	0	2	0	0	0		
		25%	6	1	3	18.5	10.5	0	1	0		
		Median:	16	1	8	32	25	1	1	0		
		75%	33.5	2	13	43.5	41	1	2	1		
		MAX	92	7	35	79	54	2	7	7		
Palaeoenvironment: Prodeltaic	Samples		Dinocysts	Acritarchs	Botryococcus	Saccate pollen	Non-saccate pollen	Microspores	Freshwater algae	Fungal hyphae and -spores	Total %	**P/D index**
St. Vorslunde	PSV1		12	1	2	59	16	2	8	0	100	**68.4**
	PSV2		9	1	1	70	16	1	2	0	100	**67.9**
	PSV3		10	1	0	58	26	1	4	0	100	**75.6**
	PSV4		12	0	1	68	13	1	4	1	100	**61.3**
	PSV5		12	0	1	65	18	1	3	0	100	**64.7**
	PSV6		12	1	1	65	16	1	3	1	100	**63.6**
	PSV7		15	2	2	63	15	1	1	1	100	**54.5**
	PSV8		25	1	1	57	14	1	0	1	100	**39.0**
	PSV9		5	0	1	76	16	1	0	1	100	**78.3**
	PSV10		11	1	1	69	17	1	0	0	100	**62.1**
	PSV11		18	1	1	43	35	1	1	0	100	**67.3**
	PSV12		17	1	0	47	32	1	1	1	100	**67.3**
	PSV13		21	1	0	53	23	1	1	0	100	**54.3**
	PSV14		24	1	1	47	24	1	1	1	100	**52.9**
	PSV15		21	1	1	51	23	1	1	1	100	**55.3**
	PSV16		30	0	1	54	13	1	1	0	100	**33.3**
	PSV17		27	1	1	58	13	0	0	0	100	**32.5**
	PSV18		47	1	1	42	7	1	1	0	100	**16.1**
	PSV19		35	1	1	47	15	1	0	0	100	**31.4**
	PSV20		39	1	1	37	20	1	0	1	100	**36.1**
	PSV21		21	1	1	53	22	1	1	0	100	**53.3**
	PSV22		22	0	1	58	17	1	1	0	100	**46.3**
	PSV23		21	1	1	45	31	1	0	0	100	**60.4**
	PSV24		12	1	1	59	26	1	0	0	100	**69.2**
	PSV25		24	1	1	50	23	1	0	0	100	**50.0**
	PSV26		23	1	1	63	10	1	1	0	100	**34.3**
	PSV27		40	2	1	40	16	1	0	0	100	**29.8**

Vandel Mark	PVM1		2	1	1	56	33	2	4	1	100	**95.2**
	PVM2		4	1	1	59	32	1	1	1	100	**89.7**
	PVM3		19	0	1	58	20	1	1	0	100	**53.7**
	PVM4		4	2	0	61	30	1	2	0	100	**89.2**
	PVM5		12	1	1	65	17	1	2	1	100	**63.6**
	PVM6		13	1	1	56	26	1	1	1	100	**69.0**
	PVM7		16	2	2	60	16	1	2	1	100	**55.6**
	PVM8		19	1	2	58	19	1	0	0	100	**51.3**
	PVM9		25	1	1	56	14	1	1	1	100	**40.5**
	PVM10		14	1	0	69	16	0	0	0	100	**53.3**
	PVM11		30	2	2	50	14	1	1	0	100	**34.8**
	PVM12		13	1	1	70	13	2	0	0	100	**53.6**
	PVM13		17	1	1	63	17	1	0	0	100	**51.4**
	PVM14		10	1	3	60	21	2	2	1	100	**72.2**
	PVM15		23	1	1	65	9	0	1	0	100	**30.3**
Andkær	PA1		6	2	1	44	44	1	1	1	100	**88.7**
	PA2		6	1	0	41	50	1	1	0	100	**89.7**
	PA3		8	1	0	41	48	1	1	0	100	**86.2**
	PA4		8	0	0	43	46	1	1	1	100	**86.0**
	PA5		13	1	0	38	46	1	1	0	100	**78.7**
	PA6		7	1	1	38	50	1	1	1	100	**88.3**
	PA7		13	1	1	33	50	0	2	0	100	**80.0**
	PA8		14	1	1	28	52	1	3	0	100	**80.0**
	PA9		15	1	1	27	51	1	4	0	100	**78.9**
	PA10		14	1	2	43	39	1	0	0	100	**74.1**
	PA11		21	1	1	38	37	1	1	0	100	**65.0**
											Avg-ratio	**60.8**
Number of samples:	53	MIN	2	0	0	27	7	0	0	0		
		25%	12	1	1	43	16	1	0	0		
		Median:	15	1	1	56	20	1	1	0		
		75%	22	1	1	61	32	1	2	1		
		MAX	47	2	3	76	52	2	8	1		

Palaeoenvironment: Shoreface	Samples		Dinocysts	Acritarchs	Botryococcus	Saccate pollen	Non-saccate pollen	Microspores	Freshwater algae	Fungal hyphae and -spores	Total %	**P/D index**
Andkær	SFA1		16	2	1	53	27	1	0	0	100	**63.6**
	SFA2		15	1	1	49	33	1	0	0	100	**69.4**
	SFA3		9	2	1	47	38	2	0	1	100	**82.0**
	SFA4		11	1	1	48	38	1	0	0	100	**78.0**
Børup	SFB1		3	1	9	49	36	1	1	0	100	**92.7**
	SFB2		4	0	9	54	32	1	0	0	100	**89.2**
	SFB3		4	1	19	41	34	1	0	0	100	**89.7**
	SFB4		3	0	20	48	28	0	1	0	100	**90.6**
Hvidbjerg	SFH1		4	1	3	66	23	2	0	1	100	**86.7**
	SFH2		7	1	3	57	30	2	0	0	100	**82.1**
	SFH3		1	1	3	56	36	2	0	1	100	**97.5**
	SFH4		1	0	10	32	47	9	0	1	100	**98.3**
	SFH5		0	2	4	16	71	5	1	1	100	**100.0**
	SFH6		4	1	3	72	20	0	0	0	100	**83.3**
	SFH7		2	1	3	72	19	1	1	1	100	**91.7**
	SFH8		1	0	4	38	52	1	3	1	100	**98.3**
	SFH9		2	1	4	61	29	1	1	1	100	**94.1**

	SFH10		3	0	6	62	28	0	1	0	100	**90.6**
	SFH11		2	0	4	69	22	2	0	1	100	**92.6**
Rønshoved	SFR1		7	0	1	68	23	1	0	0	100	**77.4**
	SFR2		5	0	2	78	15	0	0	0	100	**75.0**
	SFR3		5	0	2	32	60	1	0	0	100	**92.4**
	SFR4		6	1	2	54	36	0	0	1	100	**86.0**
											Avg-ratio	**87.0**
Number of samples:	23	MIN	0	0	1	16	15	0	0	0		
		25%	2	0	2	47.5	25	1	0	0		
		Median:	4	1	3	54	32	1	0	0		
		75%	6.5	1	5	64	37	2	1	1		
		MAX	16	2	20	78	71	9	3	1		

Palaeoenvironment: Washover fan flat	Samples		Dinocysts	Acritarchs	Botryococcus	Saccate pollen	Non-saccate pollen	Microspores	Freshwater algae	Fungal hyphae and -spores	Total %	**P/D index**
Hagenør	WH1		0	1	1	92	4	0	2	0	100	**100.0**
	WH2		1	1	4	66	23	1	4	0	100	**96.6**
	WH3		2	1	5	71	17	1	2	1	100	**91.3**
	WH4		1	1	3	75	16	1	2	1	100	**95.2**
Skansebakke	WS1		0	0	2	92	6	0	0	0	100	**100.0**
	WS2		1	1	7	88	3	0	0	0	100	**75.0**
	WS3		2	0	2	92	3	1	0	0	100	**66.7**
	WS4		1	1	2	91	4	1	0	0	100	**83.3**
	WS5		1	0	5	83	9	1	1	0	100	**91.7**
											Avg-ratio	**88.9**
Number of samples:	9	MIN	0	0	1	66	3	0	0	0		
		25%	1	0	2	75	4	0	0	0		
		Median:	1	1	3	88	6	1	1	0		
		75%	1	1	5	92	16	1	2	0		
		MAX	2	1	7	92	23	1	4	1		

Palaeoenvironment: Lagoonal	Samples		Dinocysts	Acritarchs	Botryococcus	Saccate pollen	Non-saccate pollen	Microspores	Freshwater algae	Fungal hyphae and -spores	Total %	**P/D index**
Dykær, data from Rasmussen and Dybkjær (2005)	LD1		18	2	1	21	55	1	1	1	100	**76.3**
	LD2		18	1	2	33	43	1	1	1	100	**71.9**
Hagenør	LH1		6	1	2	61	27	1	1	1	100	**83.3**
	LH2		16	3	5	43	23	1	6	3	100	**67.3**
	LH3		7	1	1	47	37	2	3	2	100	**86.3**
	LH4		18	1	7	36	22	1	9	6	100	**67.9**
	LH5		7	1	1	29	57	2	2	1	100	**89.9**
	LH6		4	2	1	31	57	0	3	2	100	**93.9**
	LH7		12	2	15	9	44	1	10	7	100	**83.8**
	LH8		11	5	2	19	54	1	4	4	100	**85.1**
	LH9		11	5	16	9	40	1	8	10	100	**84.3**
	LH10		12	1	2	32	51	1	1	0	100	**81.5**
	LH11		10	0	1	32	54	1	2	0	100	**85.1**
	LH12		12	1	0	37	46	2	1	1	100	**80.6**

	LH13		7	1	1	35	54	0	1	1	100	**88.9**
	LH14		10	1	1	30	54	2	1	1	100	**85.3**
Fakkegrav	LF1		2	3	1	26	64	2	1	1	100	**97.1**
	LF2		5	3	1	19	67	2	2	1	100	**93.5**
Skansebakke	LS1		9	2	3	35	48	2	0	1	100	**85.0**
	LS2		10	1	2	32	53	1	1	0	100	**84.6**
	LS3		5	2	1	39	51	1	0	1	100	**91.4**
	LS4		5	2	4	41	44	1	2	1	100	**90.6**
											Avg-ratio	**84.3**
Number of samples:	22	MIN	2	0	0	9	22	0	0	0		
		25%	6.25	1	1	26.75	43.25	1	1	1		
		Median:	10	1.5	1.5	32	51	1	1.5	1		
		75%	12	2	2.75	36.75	54	2	3	2		
		MAX	18	5	16	61	67	2	10	10		

Palaeoenvironment: Lagoonal	Samples		Dinocysts	Acritarchs	Botryococcus	Saccate pollen	Non-saccate pollen	Microspores	Freshwater algae	Fungal hyphae and -spores	Total %	**P/D index**
Note: dataset is excl. outliers												
Hagenør	LH1		6	1	2	61	27	1	1	1	100	**83.3**
	LH2		16	3	5	43	23	1	6	3	100	**67.3**
	LH3		7	1	1	47	37	2	3	2	100	**86.3**
	LH4		18	1	7	36	22	1	9	6	100	**67.9**
	LH5		7	1	1	29	57	2	2	1	100	**89.9**
	LH6		4	2	1	31	57	0	3	2	100	**93.9**
	LH7		12	2	15	9	44	1	10	7	100	**83.8**
	LH8		11	5	2	19	54	1	4	4	100	**85.1**
	LH9		11	5	16	9	40	1	8	10	100	**84.3**
	LH10		12	1	2	32	51	1	1	0	100	**81.5**
	LH11		10	0	1	32	54	1	2	0	100	**85.1**
	LH12		12	1	0	37	46	2	1	1	100	**80.6**
	LH13		7	1	1	35	54	0	1	1	100	**88.9**
	LH14		10	1	1	30	54	2	1	1	100	**85.3**
Fakkegrav	LF1		2	3	1	26	64	2	1	1	100	**97.1**
	LF2		5	3	1	19	67	2	2	1	100	**93.5**
Skansebakke	LS1		9	2	3	35	48	2	0	1	100	**85.0**
	LS2		10	1	2	32	53	1	1	0	100	**84.6**
	LS3		5	2	1	39	51	1	0	1	100	**91.4**
	LS4		5	2	4	41	44	1	2	1	100	**90.6**
											Avg-ratio	**85.3**
Number of samples:	20	MIN	2	0	0	9	22	0	0	0		
		25%	5.75	1	1	28.25	43	1	1	1		
		Median:	9.5	1.5	1.5	32	51	1	2	1		
		75%	11.25	2.25	3.25	37.5	54	2	3.25	2.25		
		MAX	18	5	16	61	67	2	10	10		

Palaeoenvironment: Fluvial/floodplain	Samples		Dinocysts	Acritarchs	Botryococcus	Saccate pollen	Non-saccate pollen	Microspores	Freshwater algae	Fungal hyphae and -spores	Total %	**P/D index**
Voervadsbro	FVB1		0	0	10	85	4	1	0	0	100	**100.0**
	FVB2		1	1	8	85	5	0	0	0	100	**83.3**
Salten	FS1		1	0	4	88	4	3	0	0	100	**87.5**
	FS2		1	0	2	76	19	1	1	0	100	**95.5**
	FS3		1	0	2	80	14	1	1	1	100	**94.4**
	FS4		0	0	30	26	37	1	2	4	100	**100.0**
	FS5		0	0	5	55	39	1	0	0	100	**100.0**
	FS6		0	0	3	34	57	3	2	1	100	**100.0**
	FS7		1	0	1	5	33	60	0	0	100	**98.9**
	FS8		1	1	23	15	35	1	12	12	100	**98.4**
	FS9		1	1	40	8	21	1	17	11	100	**98.0**
	FS10		0	1	3	77	16	2	1	0	100	**100.0**
	FS11		1	1	2	50	25	17	1	3	100	**97.9**
	FS12		0	0	1	42	16	36	2	3	100	**100.0**
	FS13		0	0	0	3	8	88	0	1	100	**100.0**
	FS14		0	0	2	83	11	1	2	1	100	**100.0**
											Avg-ratio	**97.1**
Number of samples:	16	MIN	0	0	0	3	4	0	0	0		
		25%	0	0	2	23.25	10.25	1	0	0		
		Median:	0.5	0	3	52.5	17.5	1	1	1		
		75%	1	1	8.5	80.75	33.5	6.5	2	3		
		MAX	1	1	40	88	57	88	17	12		

Palaeoenvironment: Fluvial/floodplain	Samples		Dinocysts	Acritarchs	Botryococcus	Saccate pollen	Non-saccate pollen	Microspores	Freshwater algae	Fungal hyphae and -spores	Total %	**P/D index**
Note: dataset is excl. outliers												
Voervadsbro	FVB1		0	0	10	85	4	1	0	0	100	**100.0**
	FVB2		1	1	8	85	5	0	0	0	100	**83.3**
Salten	FS1		1	0	4	88	4	3	0	0	100	**87.5**
	FS2		1	0	2	76	19	1	1	0	100	**95.5**
	FS3		1	0	2	80	14	1	1	1	100	**94.4**
	FS7		1	0	1	5	33	60	0	0	100	**98.9**
	FS11		1	1	2	50	25	17	1	3	100	**97.9**
	FS12		0	0	1	42	16	36	2	3	100	**100.0**
	FS13		0	0	0	3	8	88	0	1	100	**100.0**
	FS14		0	0	2	83	11	1	2	1	100	**100.0**
											Avg-ratio	**95.8**
Number of samples:	10	MIN	0	0	0	3	4	0	0	0		
		25%	0	0	1.25	44	5.75	1	0	0		
		Median:	1	0	2	78	12.5	2	0.5	0.5		
		75%	1	0	3.5	84.5	18.25	31.25	1	1		
		MAX	1	1	10	88	33	88	2	3		

Appendix 2a

Major palynofacies categories counted in the present study ('variables' in the multivariate data analysis), their origin and comments on factors influencing the occurrence of the organic particles. The abbreviations used in the PCA loading plots are indicated in parentheses.

Wood particles (WO)

Description: Sharply edges wood particles or degraded wood particles with fluffy edges, but with recognizable internal structures. Varies from totally brown through mixed brown and black to totally black. Angular to rounded, some lath-shaped (see examples on Fig. 8f and g,h,j).

Origin and distribution: Terrestrial. During the Early Miocene swamp forests grew along large parts of the palaeo-coastline surrounding the North Sea Basin (Larsson et al., 2010, 2011). Therefore a major part of the recorded wood particles probably originate from trees that grew along the coast, some of them as mangrove, with submerged roots. When these trees died, the trunk ended up directly in the shallow water of the mangrove/swamp and slowly degraded. In a more traditional approach wood particles are seen as being mainly transported by streams and rivers from the inland vegetation (refs) to the sea. That also occurred during the Early Miocene in the Danish area, but have possible been a minor contribution to the total wood content.

Environmental significance: Wood-particles are generally more resistant to oxidation and decay than palynomorphs and are therefore generally concentrated in well-oxygenated, high-energy environments. In high-energy environments, there is also a sorting effect resulting in relatively higher abundances of wood in coarse grained deposits.

Non-structured, partly degraded vitrinite (AOM)

Description: This group comprises all forms from totally amorphous particles to strongly degraded vitrinite, with fluffy edges but without recognizable internal structures. The colors may range from lighter yellowish-grey to dark brown. See examples on Fig. 8 d, j.

Origin and distribution: The major part of particles referred to this category in the present study is of dark brown color and are probably of terrestrial origin, representing degraded vitrinite (see photos showing the entire spectrum of degradation from well-preserved structured wood to strongly degraded vitrinite, Fig. 8 j). The degraded vitrinite may have a similar origin and distribution pattern in our study area as the wood particles.

Very little (less than 1%) of the recorded amorphous organic matter consists of the yellowish-grey granular amorphous matter normally found in marine environments. These particles were mainly recorded from the shelf-environment. The origin of these particles is more difficult to determine, but they could be remnants from marine algae (e.g. *Tasmanites*, dinoflagellates) as well as freshwater algae or pollen/spores. They may have been deposited as pellets, or formed on or in the sea-bed by bacterial activity and/or by aquatic invertebrates.

Environmental significance: The particles presumed to represent degraded vitrinite have the same overall environmental significance as the wood particles. Traditionally high amounts of amorphous organic matter have been interpreted as an indicator of anoxic/dysoxic bottom waters (Tyson, 1995). However, it is not clear to which degree abundance of this degraded vitrinite can be used to indicate oxygen deficiency in the bottom waters, or rather indicate proximity to the swamp areas.

Cuticle and membranes (CU)

Description: Light, thin-walled (some transparent), small to large particles. Some (cuticle) show cellular structures, seldom stomata. Others (membranes) are unstructured, or show weak striation (see example on Fig. 8a).

Origin and distribution: Terrestrial, comprising leaf-cuticle and plant membranes. The majority of studies on the distribution of cuticle are from deltaic settings (See refs in Tyson p. 238). In the present study, the major source of terrestrially derived organic matter, including leaf cuticle and plant membranes, must be assumed to be the mangrove forest.

Environmental significance: Cuticle fragments are easily damaged by physical degradation and therefore cannot withstand longer periods of high-energy transportation. The size and shape of cuticles suggests that they are less resistant to degradation than wood (Fisher, 1980). In the modern sediments of the Orinoco Delta, studied by Muller (1959), the cuticle fragments were concentrated near the large delta estuaries and both size and abundance decreased rapidly offshore.

Palynomorphs (PM)

This group comprises microspores, non-saccate pollen, bisaccate pollen, fungal hyphae and –spores, *Botryococcus*, other freshwater algae, dinocysts and acritarchs.

Appendix 2b

Palynomorph subcategories counted in the present study ('variables' in the multivariate data analysis), their origin and comments on factors influencing the occurrence of the palynomorphs. The abbreviations used in the PCA loading plots are indicated in parentheses.

Microspores (MS)

Description: Spores are microscopic grains produced during the life cycle of plants. Spores from the Cenozoic and Mesozoic eras rarely exceed 50 µm in diameter. Their wall (like in pollen grains) is made of sporopollenin and is remarkably resistant to microbial, thermal or mechanical degradation. Morphologically, spores are divided into two types: trilete and monolete, see Fig. 8b.

Origin and distribution: Terrestrial. Spores are produced by ferns, scrubs, mosses and other 'lower' land plants. Spores are often deposited close to their parent plants. If transported, then primarily by water, mainly by streams and rivers and therefore deposited relatively close to river-mouths and coastal areas.

Environmental significance: High abundances of microspores indicate a terrestrial or nearshore marine environment (lake, floodplain, lagoon, estuary, delta) (Tyson, 1995). Because of the riverine transport and the low buoyancy of spores and pollen, they can be used for recognizing proximal-distal trends (Muller, 1959; Mudie, 1982).

Non-saccate pollen (NSP)

Description: Non-saccate pollen are microscopic grains produced during the lifecycle of ('higher') land plants. In contrast to saccate pollen they don't have saccae (airbags). The three important morphological features of non-saccate pollen are: (1) character (number, type, position, shape) of the aperture; (2) type and complexity of ornamentation; as well as (3) general shape/outline (e.g. round, oblate, prolate, lenticular), see examples in Fig. 8 a, f, h.

Origin and distribution: Terrestrial. Produced by higher land plants (e.g. Taxodiaceae-Cupresseae, Alnus, Betula, Salix). Some of the pollen found in the marine deposits originates from the hinterland vegetation (transported by wind and rivers) and some were deposited very close to their parent plants which grew along the coastline.

Environmental significance: Similar to microspores the relative abundance decrease offshore and therefore can be used for a proximal-distal trend recognition (Muller, 1959; Mudie, 1982).

Bisaccate pollen (BP)

Description: Saccate pollen are microscopic grains produced during the lifecycle of coniferous trees. Saccate pollen contains one, two or (rarely) three air-filled sacs (saccai, bladders) attached to the central body (colpus) (see Armstrong and Brasier, 2005). In the studied material, only pollen grains with two sacci (i.e. bisaccate) were found. See examples in Fig. 8 a,c,e.

Origin and distribution: Terrestrial. They can be distributed (mainly by water and wind) long distances from the parent plant. Their air-filled sacci, functioning as "swimming-belts", allow them to float on the sea-surface for some time before they sink to the bottom (the "Neves-effect") (Tyson, 1995 and references therein, Armstrong and Brasier, 2005).

Environmental significance: Not a good environmental indicator as they are widely distributed in both marine and terrestrial environments. Due to the higher buoyancy of the bisaccate pollen the bisaccate/non-saccate ratio increases in a proximal-distal trend (Tyson, 1995 and references therein).

Botryococcus spp. (BO)

Description: Colonial Botryococcaceaen algae with an orange-brown to lustrous yellow color. The colonies show a pseudo-radial appearance and a characteristic globular outline, resembling a cauliflower (Tyson, 1995) (Fig. 8c). Colonies of *Botryococcus braunii* are about 30 μm in diameter, but can grow to larger sizes up to 2000 μm in diameter (Tyson, 1995 and references therein).

Origin and distribution: Aquatic organisms, found in freshwater lacustrine, fluvial, lagoonal and deltaic areas (Tyson, 1995 and refs therein). They can be distributed by streams and rivers to nearshore marine depositional environments.

Environmental significance: *Botryococcus* are freshwater algae but also tolerant to brackish water conditions. *Botryococcus* spp. thrives in inland water-bodies (including lagoons) with salinities between 5 and 13‰ (Tyson, 1995 and references therein).

Other freshwater algae (FA)

Description: In the present study this group comprises *Pediastrum* spp., *Mougeotia laetevirans* and *Pseudokomewuia* aff. *granulata*.

Pediastrum is a genus of green algae, in the family Hydrodictyaceae. It is a colonial algae with a flat discoidal shape and a "cog wheel shaped" outline. The coenobia (colonies of *Pediastrum*) varies in diameter between 30 and 200 μm.

Mougeotia laetevirans (A. Braun) Wittrock 1877 is a species within the family of Zygnemataceaen algae. Zygospores form as conjugating tubes. In the palynological slides of the present study they appear as cylindrical tubes in combination with circular discs (Fig. 8g).

Pseudokomewuia aff. *granulata* He Chengquan 1980 is a minute fresh water dinocyst. It is an ovoidal to spindle-shaped cyst with an apical archaeopyle, a minute antapical horn and a characteristic granulate/baculate ornamentation. The length is between 42 and 65 μm (Batten, 1996).

Origin and distribution: All these algae are aquatic organisms, living in fresh water bodies, like ponds, lakes and rivers. They may be relocated into near-coastal areas by fluvial transport.

Environmental significance: These algae do not tolerate brackish or saline waters. High abundances indicate either a fluvial depositional environment or a near-coastal setting, close to a larger river mouth.

Fungal hyphae and –spores (FU)

Description: The fungal hyphae are thin, branching tubular structures 1–30 μm wide. They may be internally divided by septae. The fungal spores are typically rounded to elongate grains, small (10–20 μm in diameter; 20–30 μm in length) with a smooth surface. Some of the spores show a "bottleneck-shaped" opening. Both hyphae and -spores have a characteristic dark brownish color (Fig. 8b). In the present study, in contrast to the approach by Tyson (1995, p. 162), both hyphae and spores are considered as palynomorphs.

Origin and distribution: The fungi included in the present study are terrestrial organisms thriving mainly in humid environments as peats and bogs. Comparable to other terrestrial palynomorphs with low buoyancy they are most abundant near their place of origin and tend to sink in still water. However, they can be transported by streams and rivers to near-coastal areas (Ingold, 1971; Rees, 1980, Tyson, 1995 and references therein).

Environmental significance: Fungal hyphae and spores generally do not occur in high abundances in Danish Miocene successions, and rarely exceed a few percentages of the total palynomorph counts. The presence of fungal tissues indicates either a fluvial depositional environment or a near-coastal setting, close to a river mouth (Elsik, 1976). Fungal spores were found to be most abundant in delta top facies compared to prodelta and outer shelf deposits (Muller, 1959, Tyson, 1995 and references therein). Lagoonal facies are generally characterized by a higher fungal spore content than adjacent marine shelf facies (Oboh, 1992).

Acritarchs (AC)

Description: Acritarchs are hollow, organic-walled cysts. Their size (5–240 μm), shape (e.g. round, fusiform), ornamentation (from smooth to a variety of spinose, granulate or reticulate) and other morphological features (e.g. presence, length and termination of processes) are highly variable and important for defining species or genera. Acritarchs differ from dinocysts in the absence of reflected tabulation and pre-formed excystment openings of definitive form, see example in Fig. 8c.

Origin and distribution: Eukaryotic unicells of unknown biological affinity (Armstrong and Brasier, 2005). However, they are considered to be resting cysts of (marine) phytoplanktonic algae (Strother, 1996).

Environmental significance: Acritarchs have mostly been found in marine deposits and probably indicate proximity to the shoreline as they often occur together with known terrestrially derived palynomorphs, (Tyson, 1995).

Organic-walled dinoflagellate cysts (dinocysts) (DI)

Description: The most important defining features for dinocysts are their tabulation pattern and the type of archaeopyle. On top of that, secondary characteristics like their size (20–150 μm), shape, ornamentation and other morphological features (e.g. presence, positioning, length and termination form of processes), are highly variable and important for defining species or genera, see further Fensome et al. (1996). See examples in Fig. 8h and i,j.

Origin and distribution: Dinoflagellates are organic-walled, eukaryotic unicells, both auto- and heterotrophic. Some of them produce a resting cyst (dinocyst) as part of their lifecycle, which are preserved in the geological record. The absolute majority of dinoflagellates are marine algae and their cysts are thus indicators for marine settings. Dinocysts can be found in an array of marine environments, ranging from inner neritic to oceanic settings. Occasionally dinocysts are found far up in river systems, probably as a result of transport by high tides and storm-waves.

Environmental significance: Dinocysts are most abundant and diverse in outer neritic settings. Some dinoflagellates are tolerant to lower salinities and thrive in back-barrier environments, while others, at the contrary, prefer oceanic settings (Brinkhuis, 1994). Blooms of specific autotrophic dinoflagellate taxa occur in high nutrient environments Armstrong and Brasier (2005). However, the environmental preferences of extinct dinoflagellates are not fully understood, sometimes even contradicting (see discussion about the genus *Homotryblium* spp. in Śliwińska et al., 2014). Therefore, in the present study, dinocysts are treated as a uniform group indicating an overall marine depositional environment.

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