A sporomorph ecogroup model for the Northwest European Jurassic – Lower Cretaceousi: concepts and framework

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Abstract

Based on recent vegetation distribution and an integration of macropalaeobotanical and palynological information, a palaeo-community model is explored that may permit detailed interpretations of quantitative sporomorph distribution patterns in the Jurassic and Early Cretaceous of NW-Europe in terms of changes in palaeoenvironment (sea-level, climate). The conceptual model is based on the recognition of Sporomorph Ecogroups (SEGs) that reflect broad co-existing plant communities, viz. upland, lowland, river, pioneer, coastal, and tidally-influenced SEGs. In successive palynological assemblages, shifts in the relative abundance of SEGs are thought to be indicators of sea-level changes. Climatic changes may be recognised through significant shifts within the quantitative composition of individual SEGs.

Keywords: palynology, palaeobotany, Late Jurassic, palaeo-ecology, palaeoclimate, sea-level

Introduction

Paralic Jurassic sediments in the North Sea form an important economic objective (Brown, 1990; Ziegler, 1990). In these sediments, palynomorphs are the most abundant (micro) fossil group. The marine component in the palynological associations (e.g. dinoflagellate cysts, acritarchs) from these paralic sediments is small or absent, while the terrestrial component (spores, pollen) is high. Consequently, spore/pollen (sporomorph) palynology is increasingly challenged to improve the interpretation of data sets that can be used for dating and characterisation of paralic depositional sequences. The recognition of these depositional sequences is an important aid in hydrocarbon geology. Conventional sporomorph stratigraphy does, however, not provide the required temporal resolution to recognise such sequences (Abbink, 1998). It may even be argued that the required resolution will never be reached due to the relatively slow evolution rate of landplants. Moreover, qualitative analysis does hardly provide information about past environmental changes. Only quantitative data may reflect the relationship between sporomorph assemblages and (spatial, temporal) environmental gradients (e.g. Brugman et al., 1994). Surprisingly few detailed quantitative palynological studies have been carried out on Jurassic paralic sediments (e.g. Whitaker et al., 1992; Hubbard & Boulter, 1997), whereas palaeoenvironmental interpretation of the identified changes in the composition of Jurassic sporomorph assemblages is still ambiguous.

A realistic interpretation of Jurassic sporomorph signals is largely dependent on the ability to distinguish palaeocommunities by using information on the ecology of the parent plants of quantitatively important spores and pollen. Based on recent vegetation distribution and an integration of environmentally significant macropalaeobotanical and palynological information, in this paper a palaeocommunity model
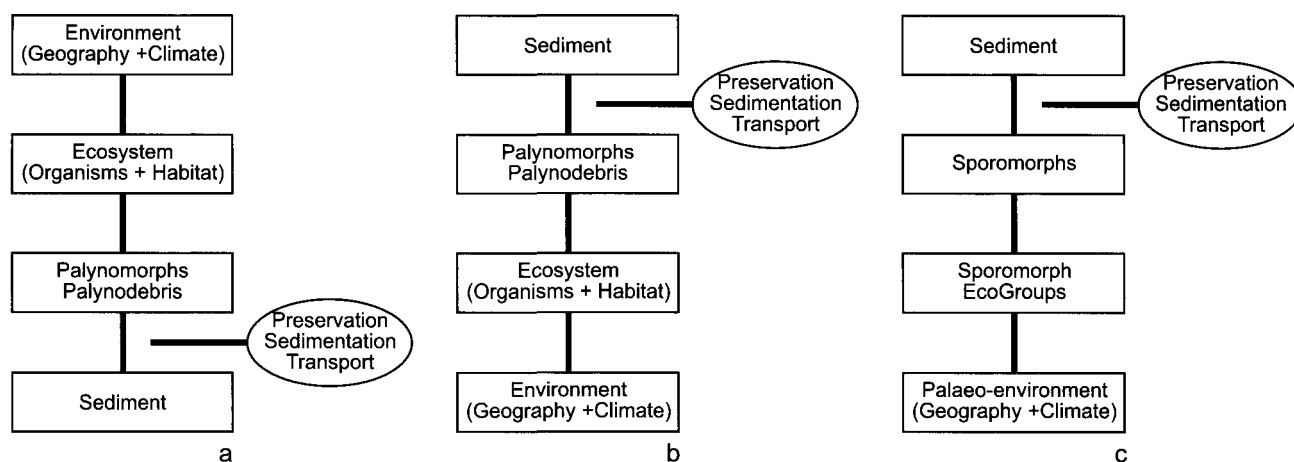
Fig. 1. Simplified diagram of he followed hypotheses for a) present-day situations b) quaternary palaeo-environmental reconstructons and c) the Sporomorph EcoGroup concept (modified after Janssen, 1980; Traverse, 1994; Tyson, 1995).

is explored that may facilitate the interpretation of quantitative sporomorph distribution patterns in the Jurassic and Early Cretaceous of NW Europe in terms of changes in palaeoenvironment. The resulting conceptual 'Sporomorph Ecogroup Model' will applied to and tested against data from a marginal marine, uppermost Callovian - Middle Oxfordian succession in exploration well F17-4 of the Nederlandse Aardolie Maatschappij B.V. (NAM), offshore The Netherlands (Abbink *et al.*, in press).

A sporomorph ecogroup model

Despite effects of preservation, transportation and sedimentation processes, assemblages of pollen and spores (sporomorphs) reflect the composition of terrestrial plant communities (e.g. Muller, 1959; Chaloner & Muir, 1968; Traverse, 1988; Tyson, 1995). In Quaternary palynology this relationship is successfully applied in the identification of local and regional environmental change. Quaternary studies strongly benefit from actualistic data and models of the relation between sporomorph signals and environmental gradients (e.g. Birks & Birks, 1980; Huntley, 1990). In the environmental interpretation of pre-Quaternary records, the ability to identify sporomorph categories in terms of environmentally significant plant categories becomes a major constraining factor. Going back in time, sporomorphs increasingly represent extinct plant taxa. However, in the Neogene and even in the Paleogene, identification of part of the sporomorph assemblages still enables direct floristic comparisons with extant plant communities. This correlation potential is a sound basis for the introduction of palaeocommunity models that may enable the environmental and climatic interpretation of sporomorph distribution patterns (Poumot, 1989;

Van der Zwan & Brugman, 1999; Van der Zwan, 2002).

In the Mesozoic, any application of palaeocommunity models is considerably hampered by uncertainties with respect to the botanical affinities of quantatively important sporomorphs and/or the ecological preference of the extinct parent plants. However, based on actualistic principles, one may assume the presence of distinctive habitat-bounded palaeocommunity types, each of which is characterised by taxa with broadly similar ecological preferences. These palaeocommunity types can serve as a palaeoecological framework for a conceptual Sporomorph Ecogroup model of co-existing sources of dispersed spores and pollen. The term Sporomorph Ecogroup (SEG) is introduced to denote the total of types of dispersed spores and pollen of land plants that reflects the composition of an individual source community. A schematic diagram of this concept is given in Fig. 1.

Definitions of the Jurassic – Early Cretaceous SEGs

In order to define SEGs for the Jurassic - Early Cretaceous and to model the response of SEGs to palaeoenvironmental change, the establishment of an ecological framework for the source communities is necessary. According to Grime (1979) two factors determine the type of plants defining a specific vegetation: stress and disturbance. The variation of the level of stress and disturbance results in three different plant strategies: a competitive strategy (low stress, low disturbance), a stress-tolerating strategy (high stress, low disturbance), and a ruderal strategy (low stress, high disturbance), whereas highly disturbed habitats with severe and continuous stress are not viable as plant habitats (Grime, 1979).

If we translate these strategies into a conceptual SEG model for the Jurassic - Early Cretaceous landscape of NW Europe, we contemplate one SEG reflecting the vegetation present in the main lowland area, where there is an optimum of nutrients and fresh water (low stress and low disturbance). The lowland plants will follow a competitive strategy and, consequently, the ecological boundaries of the plants reflected by this SEG are determined by less-than-optimum conditions surrounding this lowland area. The plants within the communities reflected by other SEGs will follow a stress-tolerating or ruderal strategy. Seaward, ecological stress is introduced by the influence of salt water (in a tidally-influenced area) and salt spray (in a coastal area), landwards the lack of freshwater and the possible deficiency of nutrients (in the upland area) may introduce ecological stress. Along rivers, periodical submersion and erosion of riverbanks will cause plants to follow a more ruderal strategy. A ruderal strategy will also be employed by first colonisers or pioneer plants. As for plants in the lowland area, the plants *within* the other ecologically defined areas will also show a competitive strategy, as they are optimised for the ecology of that particular habitat. Following this concept for the Late Jurassic - Early Cretaceous of NW Europe the following six

SEGs are taken into consideration (Fig. 2):

(A) Upland SEG, reflecting upland communities: vegetation on higher terrain well above groundwater level that is never submerged by water,

(B) Lowland SEG, reflecting lowland communities; vegetation on plains and/or in fresh water swamps; the plains may (periodically) be submerged by fresh water, resulting in the possible presence of 'wetter' (marsh) and 'drier' taxa in this group; there is no influence of (sea) salt, except, perhaps, under extreme circumstances,

(C) River SEG, reflecting riverbank communities; vegetation on river banks which are (periodically) submerged and subject to erosion,

(D) Pioneer SEG, reflecting pioneer communities: vegetation at instable and recently developed ecospace (e.g. vegetation growing at places that had been submerged by the sea for a longer period),

(E) Coastal SEG, reflecting coastal communities: vegetation growing immediately along the coast, never submerged by the sea but under a constant influence of salt spray, and

(F) Tidally-influenced SEG, reflecting tidally influenced communities: vegetation that is daily influenced by tidal changes (regularly submerged at high tide).
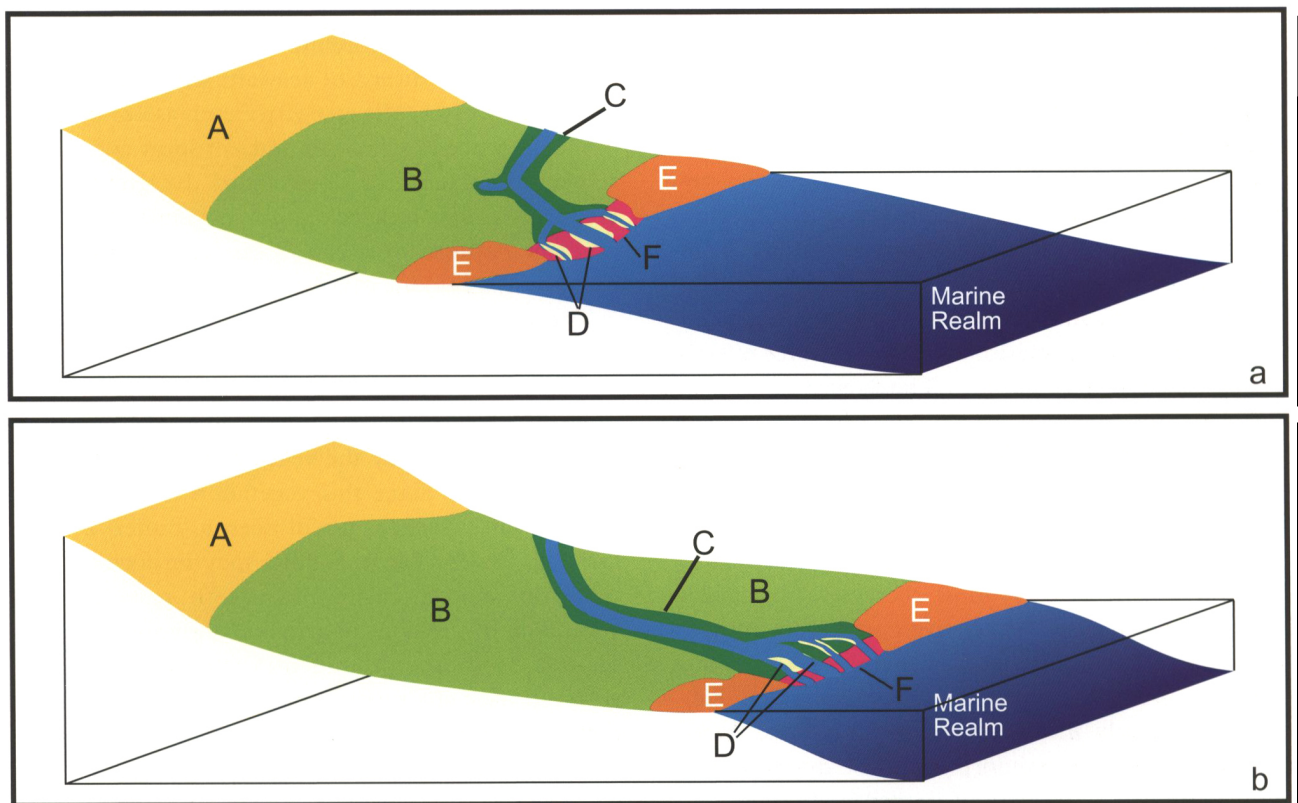

Fig. 2. Schematic representation of the spatial distribution of the SEG. The upper figure (a) depicts the situation during a sea-level high, the lower figure (b) during a sea-level low. A = Upland, B = Lowland, C = River, D = Pioneer, E = Coastal and F = Tidally-influenced SEG.

Effects of transportation on SEG characteristics

The fundamental point of consideration in the environmental interpretations of SEG signals is the relationship between the relative abundance of sporomorphs in the sediment and the abundance of their parent plants in plant communities. Apart from differences in sporomorph production, this relationship is subject to the effects of transportation, preservation and sedimentation processes (e.g. Heusser, 1979; Traverse, 1988, 1994; Tyson, 1995). Yet, it is understood that within terrestrial to marginal marine settings the changes within the sporomorph assemblages dominantly reflect changes in the palaeovegetation rather than differences in transportation, preservation or sedimentation (see discussions in e.g. Muller, 1959; Chaloner & Muir, 1968; Traverse, 1988; Heusser, 1979; Van der Kaars, 1991; Tyson, 1995). Moreover, empirical studies show the relative abundances of sporomorphs to be correlative with distribution of plant communities (e.g. Chaloner & Muir, 1968; Suc, 1984; Poumot, 1989; Van der Kaars, 1991; Brush & Brush, 1994; Chmura, 1994).

Although the studies on recent pollen distribution as well as empirical data on fossil sporomorph distribution imply that changes within the sporomorph assemblages can well be interpreted in terms of palaeoenvironmental changes, there are a few, well described effects of transportation that can not be neglected when interpreting the composition of Jurassic – Early Cretaceous SEGs. Since the configuration of the Jurassic – Early Cretaceous landscape of northwestern Europe was largely determined by a low-relief, fluvio-deltaic environmental regime (Ziegler, 1990), sporomorph transportation must have been dominated by water dispersal (Traverse, 1988). In such a setting the most common and widely accepted effect of transportation is the so-called "Neves effect" of Chaloner & Muir (1968). The Neves effect describes a trend in which the abundances of the broad characters of sporomorph assemblages in depositional environments are generally inversely proportional to the distance of the source communities (see discussions in e.g. Chaloner & Muir, 1968; Traverse, 1988; Tyson, 1995). One of the most characteristic aspects of the Neves effect is the relative enrichment in marine sediments of hinterland elements of which the source is furthest from the shore. Hinterland elements frequently include bisaccate pollen of gymnosperms. These palynomorphs may be dispersed into the marine environment by air-transport. In an onshore - offshore transect, the decrease of water-transported sporomorphs accounts for a relative increase in wind dispersed sporomorphs (e.g. Heusser, 1979; Traverse, 1988; Brinkhuis, 1994).

Effects of environmental change on SEG characteristics

The type of vegetation which is reflected by the SEGs is governed by two principal controls: geography and climate (e.g. Walter, 1973; Chapman, 1977; Grime, 1979; Bakker, 1985; Runhaar et al., 1987; Van der Maarel, 1993). Consequently, in successive palynological assemblages, shifts in (1) the relative abundance of SEGs, and (2) the quantitative composition of individual SEGs are expected to be indicative of changes in geography and/or climate. The major geographical factor inducing palaeoenvironmental changes is generally accepted to be sea-level fluctuations in the Jurassic - Early Cretaceous, taking a maximum temporal resolution of 50k years - 200k years into account (e.g. Brown, 1990; Partington et al., 1993a; Herngreen et al., 2000).

Sea-level fluctuations
Sea-level fluctuations are generally accepted to play a major role in basin infill and provide an important stratigraphic correlation tool, at least on a regional scale (e.g. Haq et al., 1988; Partington et al., 1993a; DeGraciansky, 1999). Within marginal marine to non-marine sediments (coastal/delta plain and upper shelf area), sea-level fluctuations are recorded by cyclic shifts of the shoreline (Galloway, 1989; Vail et al., 1991). A landward or seaward shift of the shoreline influences (1) the respective increase or decrease of the presence of salt water and salt spray and (2) the respective increase or decrease of the groundwater table and related deterioration or improvement of drainage patterns of rivers (Posamentier et al., 1988; Törnqvist, 1993).

The predominant effect of the increase in marine influence due to the invasion of the coastal/delta plain area by marine (salt) waters (sea-level rise) is thought to be an actual reduction of the spatial distribution of the area inhabited by the vegetation reflected by the Lowland SEG. Since this vegetation is not resistant against salt influence, it will need a 'buffer' zone. If the area is very flat, this zone may be formed by a tidally-influenced environment with corresponding vegetation. If the slope of area is slightly steeper or the sea-level rise more prominent, the coastal vegetation is forced back and partly replaces the lowland vegetation (compare Figure 2a and 2b). Similarly, during a sea-level fall the lowland area will expand and there will be a relative increase in the Lowland SEG relative to the Coastal or Tidally-influenced SEGs. Therefore in our model, sea-level causes changes between the SEGs. In particular the ratio of the Coastal SEG ver-

sus the Lowland SEG is deemed as a proxy for sea-level fluctuations. This implies that sea-level fluctuations can be recognised in fully non-marine environments.

By definition the boundary between the vegetation reflected by the Upland SEG and the Lowland SEG is relatively stable and occurs at or landward of the hinge point. However, since sea-level fluctuations cause changes in river drainage patterns, the abundances of palynomorphs of the Upland SEG (mainly alete bisaccates) are thought to be relatively high during a rising sea-level at the flooding surface. Since these palynomorphs are (also) air-transported, they form a constant input from the upland (Neves effect). The relative enrichment is due to a period of condensation, i.e. a decrease of sediment supply, including water-transported palynomorphs (e.g. Heusser, 1979; Loutit et al., 1988; Brinkhuis & Zachariasse, 1988). The Pioneer SEG is considered to have relatively higher abundances around the maximum of the transgression as can be expected for a colonising group of plants (ruderals sensu Grime, 1979).

Although sea-level fluctuations are suggested to predominantly cause changes between the SEGs, the changes of groundwater table and river drainage patterns will result in differences in fresh water availability. Whereas there is still an optimum in nutrients and water and a low stress level for plants in the lowland area, this optimum will convert to one with slightly less wet conditions. These changing conditions will have effect on competitive strategists and, therefore, primarily on the Lowland SEG. Our model suggests that because of declining drainage conditions and a higher groundwater table during a sea-level rise, a moderate increase in wetter elements within the Lowland SEG may be present. Comparably, a sea-level fall may show a slight increase in drier elements of the Lowland SEG.

Other geographic changes

Changes of the geographic setting include lateral shifts of rivers on a relatively small scale but may also involve on a much larger scale, changes in tectonic regime such as changes in basin subsidence or basin uplift. In particular the abundance of the River SEG in the palynological assemblages will be dependent on the geographical setting. This SEG mainly includes sporomorphs (notably spores) that are directly shed into the water. Hence, changes of river input into the depositional environment will probably be reflected through changes in abundances of sporomorphs of this group. Similarly, the geographic setting also influences the Tidally-influenced SEG. The differences in spatial distribution of tidally-influenced communities

along a steep (e.g. fault-controlled) coast, and along a shallow marine deltaic coast are apparent. The other SEGs are suggested not to be affected strongly by small-scale changes in the geographic setting. However, large-scale tectonic reorganisation or continental drift will evidently have rigorous effects on the vegetation.

Climate changes

Changing climate plays a key-role in reconstructing and understanding past environments. However, the existing palaeoclimatic data for the Jurassic is relatively scattered in time and space (e.g. Hallam, 1985, 1994; Frakes et al., 1992). Therefore, a need exists to establish a well-calibrated 'high resolution' climate curve. Quaternary studies show that the use of palynological data allows the reconstruction of the climate and recognition of climate changes which can be used to introduce such a 'high resolution' climate curve (e.g. Zagwijn & Hager, 1987; Van der Kaars, 1991; Morley & Richards, 1993; Targarona, 1997; Van der Zwan & Brugman, 1999).

Climate controls the level of humidity (precipitation/air-humidity) and temperature. Consequently, principally without a change in the geographical configuration, the availability of light, nutrients and/or water is altered significantly by a climate change. These variables have direct impact on the competitive strategy of plants. Thus, in our model climate changes are considered to significantly change the constituents of the SEGs or to cause dramatic changes of the abundances of the various constituents within a SEG. The plants attributed to the Lowland SEG only have a competitive strategy. Consequently, the Lowland SEG is most sensitive to climate change. In addition, a competitive strategy is followed by the plants within the recognised palaeovegetations reflected by the other SEGs. Therefore, climate changes are also thought to influence the contents of, in particular, the Coastal and Upland SEGs. The other SEGs are considered not to be influenced significantly by a climate change. If, for example, the vegetation producing a River SEG is compared with the present day situation along, for example, the Egyptian Nile, this Ecogroup is considered not to be affected significantly by a climate change, except under extreme conditions, e.g. if a constant water supply fails. Similarly, also the Tidally-influenced SEG is thought not be affected significantly by climate change (e.g. Walter, 1973). In summary, according to our model palaeoclimatic reconstruction and recognition of climatic changes may be achieved by, within a SEG, categorising and plotting the dry vs. wet elements (humidity) and warm vs. cold elements (temperature) (Abbink et al., 2001).

Ecologies of dominant Jurassic – Early Cretaceous plants

The Jurassic – Early Cretaceous SEGs are constrained by inferences on the ecologies of the parent plants of frequently occurring sporomorph taxa. A selection of common sporomorph taxa from Northwest Europe (Table 1) is based on an evaluation of published quantitative data sets by e.g. Batten (1978), Birkelund et al. (1978), Boulter & Windle (1993), Burger (1966), Couper (1958), Dörhöfer (1977), Döring (1965, 1966a and b, 1976), Fensome (1983), Filatoff (1975), Guy-Ohlson (1971, 1986), Herngreen (1971), Herngreen & de Boer (1974), Herngreen et al. (2000), Heunisch (1993), Hogg (1993), Norris (1969), Srivastava (1987), Tralau (1968), Vakhrameev (1991), Van Amerom et al. (1976), Weiss (1989) and unpublished information available at the Laboratory of Palaeobotany and Palynology. The botanical affinity of the palynological categories is mainly inferred from extensive information on fossil in situ spores and pollen (review by Balme, 1995; specific references in Table 1). Table 2 gives an overview of the common sporomorphs that are considered to be characteristic of the various SEGs.

The ecology of the various groups of parent plants mentioned in Table 1 and 2 is mainly based on published palaeoecological information and partly on comparison with extant relatives of the plant groups (nearest living relatives). Early Cretaceous ecological interpretations are provided by e.g. Batten (1975), Pelzer (1984), Pelzer & Wilde (1987), Pelzer et al. (1992). Jurassic ecological interpretations are provided by e.g. Alvin (1982), Balme (1995), Filatoff (1975), Francis (1984), Manum et al. (1991), Mohr (1989), Retallack (1997), Reyre (1980), Skog & Hill (1992), Vakhrameev (1991), Van der Burgh & Van Konijnenburg-Van Cittert (1984), Van Konijnenburg-Van Cittert & Van der Burgh (1989, 1996), Wesley (1973), Yaroshenko (1985), and unpublished information available at the Laboratory of Palaeobotany and Palynology.

In the following paragraphs, presumed ecologies of parent plant categories are briefly discussed as a background for an inclusion of dispersed sporomorphs in the different SEGs. Conclusions are summarised in Table 2.

Bryophytes

Bryophyte spores are represented by *Stereisporites* and *Staplinisporites* (p.p.). Although mosses usually grow under more or less humid conditions, some grow in dry places and most can withstand long periods of drought. On the basis of the Jurassic spores, it is impossible to distinguish between mosses favouring humid or dry conditions. However, as the majority of mosses grow near water, we consider the Jurassic spores to belong to the River SEG or possibly to the humid vegetations of the Lowland SEG.

Lycopsids

Isospores and microspores of lycopsids are represented by the form-genera *Densoisporites*, *Leptolepidites*, *Lycopodiacidites*, *Neoraistrickia*, *Retitriletes*, *Sestrosporites* and *Staplinisporites* (p.p.). The majority of extant lycopsid species occur in tropical regions, but many species are common in temperate regions and lycopsids have even been found in polar areas. Similar to bryophytes, most Jurassic lycopsid spores can only be tentatively used in ecological interpretations. Based on extant occurrences the lycopsid species may be attributed to the Lowland, River or Tidally-influenced SEGs. Only *Densoisporites* may be used as a more precise ecological indicator.

Densoisporites is known in situ from Triassic and Early Jurassic Pleuromeiaceae, a heterosporous lycopsid family with a close relationship to the extant Isoetaceae (Raine et al., 1988). Although the family has not (yet) been recorded after the Early Jurassic (Raine et al., 1988; Balme, 1995), types of *Densoisporites* occurring in younger Jurassic and Cretaceous times (e.g. *D. velatus*) are morphologically closely related to the Triassic and Early Jurassic pleuromeiaceous microspores.

Some members of the Pleuromeiaceae appear to have been facultative coastal halophytes (Retallack, 1975, 1997). It has been suggested that the morphology of *Densoisporites* microspores is adapted to water dispersal (Yaroshenko, 1985). Furthermore, Couper (1958) reported relatively large amounts of *Densoisporites* from Jurassic/Cretaceous tidally-influenced sediments. We conclude, therefore, that *Densoisporites* could well represent an element of Tidally-influenced SEG.

Uvaesporites is known in situ from Selaginellaceae. As these plants are reported to grow under humid conditions, we tentatively assign *Uvaesporites* to the River SEG.

Table 1. Selected Late Jurassic and earliest Cretaceous spores and pollen and their botanical affinity

Spore taxon	Botanical affinity
Calamospora mesozoica	Equisetales (Balme, 1995)
Cicatricosisporites spp.	Schizaeaceae (*Anemia/Mohria*-type) (Van Konijnenburg-Van Cittert, 1981, 1991)
Concavisporites spp.	Matoniaceae (Van Konijnenburg-Van Cittert, 1993).
Concavissimisporites spp	?Dicksoniaceae/Cyatheaceae (*Eboracia*; Potonié, 1970)
Contignisporites spp.	Pteridaceae (Filatoff and Price, 1988)
Cyathidites/Deltoidospora/ *Dictyophyllidites* spp.	Dicksoniaceae, Cyatheaceae, Dipteridaceae, Matoniaceae Van Konijnenburg-Van Cittert, 1989, 1993; Balme, 1995)
Densoisporites spp.	Lycopodiaceae (*Selaginella*)/Pleuromeiaceae (Knox, 1950; Lundblad, 1950)/(Raine *et al.*, 1988)
Duplexisporites problematicus (Striatella)	Pteridaceae (Filatoff, 1975; Filatoff and Price, 1988)
Gleicheniidites spp.	Gleicheniaceae (Potonié, 1967)
Impardecispora apiverrucata	?Dicksoniaceae (Venkatachala *et al.*, 1969)
Ischyosporites spp.	Schizeaceae (*Lygodium*-type) (Van Konijnenburg-Van Cittert, 1981, 1991)
Leptolepidites spp.	Lycopodiales (Filatoff, 1975)
Lycopodiacidites spp.	Lycopodiales (Filatoff, 1975)
Matonisporites spp.	Matoniaceae (Van Konijnenburg-Van Cittert, 1993)
Neoraistrickia spp.	Lycopodiales (Filatoff, 1975)
Osmundacidites wellmanii	Osmundaceae (*Osmunda*-type) (Van Konijnenburg-Van Cittert, 1978).
Plicatella spp.	Schizaeaceae (*Anemia/Mohria*-type) (Van Konijnenburg-Van Cittert, 1981, 1991)
Punctatisporites spp. / *Todisporites* spp.	Osmundaceae (*Todites*-type) (Van Konijnenburg-Van Cittert, 1978).
Retitriletes spp.	Lycopodiaceae (*Lycopodium*-type) (Potonié, 1967)
Sestrosporites pseudoalveolatus	?Lycopodiales
Staplinisporites spp.	Mosses and Lycopodiaceae (Potonié, 1967; Boulter & Windle, 1993)
Stereisporites spp.	Mosses (Filatoff, 1975; Boulter and Windle, 1993)
Striatella spp.	Pteridaceae (Filatoff and Price, 1988)
Trilobosporites spp.	?Dicksoniaceae (Venkatachala *et al.*, 1969)
Uvaesporites spp.	Selaginellaceae (Balme, 1995)
Varirugosisporites spp.	possibly Schizaeaceae, *Lygodium*-type (Filatoff, 1975)

Pollen taxon	Botanical affinity
Alete bisaccate pollengrains Boulter and Windle, 1993)	Pteridosperms, Conifers (Pinaceae, Podocarpaceae) (Van Konijnenburg-Van Cittert, 1971;
Alisporites thomasii	Pteridosperms (Corystospermales) (Van Konijnenburg-Van Cittert, 1971; Balme, 1995)
Araucariacites australis	Araucariaceae (Van Konijnenburg-Van Cittert, 1971)
Callialasporites spp.	Araucariaceae (Van Konijnenburg-Van Cittert, 1971; Boulter & Windle, 1993)
Cerebropollenites spp.	?Taxodiaceae (Van der Burgh and Van Konijnenburg-Van Cittert, 1989)
Chasmatosporites spp.	?Cycadales (Tralau, 1968)
Clavatipollenites spp.	?Angiospermae (Balme, 1995)
Corollina torosa	Cheirolepidiaceae (*Hirmeriella*-type) (Van Konijnenburg-Van Cittert, 1987; Balme, 1995)
Corollina echinatus	Cheirolepidiaceae (*Frenelopsis*-type) (Van Konijnenburg-Van Cittert, 1987; Balme, 1995
Eucommiidites minor	?; similar grains have a possible suggested relationship with anthophytes (Gnetales or early angiosperms (Pedersen *et al.*, 1989)
Eucommiidites troedsonii	Cycadales (Van Konijnenburg-Van Cittert, 1971; Balme, 1995)
Exesipollenites spp.	Bennettitales (Harris, 1969, 1974)
Monosulcites spp.	Cycadales, Bennettitales (Potonié, 1967; Van Konijnenburg-Van Cittert, 1971; Boulter & Windle, 1993)
Monosulcites minimus	Ginkgoales (Potonié, 1967; Van Konijnenburg-Van Cittert, 1971; Boulter & Windle, 1993)
Perinopollenites spp.	Taxodiaceae (Van Konijnenburg-Van Cittert, 1971)
Quadraeculina anellaeformis	Podocarpaceae (Boulter & Windle, 1993)
Spheripollenites spp.	inner bodies of Taxodiaceae, Cheirolepidiaceae etc.
Vitreisporites pallidus	Caytoniales (Pteridosperms) (Van Konijnenburg-Van Cittert, 1971)

Equisetales

Equisetales are represented by *Calamospora mesozoica*. Extant horsetails usually require a wet habitat (river bank, lowland marsh) and they occur both in (sub)tropical and temperate regions. This also applies to Jurassic representatives. Therefore, the spores are included in the River SEG.

Ferns

The majority of extant ferns (Filicales) prefer to grow in a shadowy, humid environment. Only a few taxa can bear full sunlight (e.g. Gleicheniaceae). Most ferns are tropical, but they can also be common in temperate forests. In general, therefore, the presence of fern spores indicates more or less humid condi-

Table 2 Schematic classification of the SEGs

SEG	SPECIES	REMARKS
Upland	Alete Bisaccate Pollengrains	A few alete bisaccate taxa may not be placed in this group, i.e. *Alisporites thomasii* and *Vitreisporites pallidus*.
	Quadraeculina anellaeformis	
Lowland	*Calamospora* spp.	marsh:'wetter'; 'warmer'
	Chasmatosporites spp.	'drier'; 'cooler'
	Cicatricosisporites spp.	marsh: 'wetter'; 'warmer'
	Clavatipollenites spp.	'drier'; 'warmer'; this taxon is questionably attributed to this SEG.
	Concavisporites spp.	'drier'; 'warmer'
	Concavissimisporites spp.	'drier'; 'warmer'
	Contignisporites spp.	'drier'; 'warmer'
	Cycadopites spp.	'drier'; 'warmer'
	Deltoidospora/Dictyophyllidites/ Cyathidites spp.	'drier'; 'warmer'
	Duplexisporites problematicus (*Striatella*)	'drier'; 'warmer'
	Eucommiidites troedsonii	'drier'; 'warmer'
	Exesipollenites spp.	'drier'; 'warmer'; due to the xerophytic character of the motherplant, this taxon may also be placed in the Coastal SEG.
	Gleicheniidites spp.	'drier'; 'warmer'
	Impardecispora apiverrucata	'drier'; 'warmer'
	Ischyosporites spp. marsh:	'wetter'; 'warmer'
	Matonisporites spp.	'drier'; 'warmer'
	Monosulcites minimus	'drier'; 'cooler'
	Monosulcites spp.	'drier'; 'warmer'
	Osmundacidites (B aculatisporites) spp. marsh:	'wetter'; 'warmer'
	Perinopollenites spp. marsh:	'wetter'; 'cooler'
	Plicatella spp.	'drier'; 'warmer'
	Punctatisporites/T odisporites spp. marsh:	'wetter'; 'warmer'
	Trilobosporites spp.	'drier'; 'warmer'
	Varirugosisporites spp.	'drier'; 'warmer'
River	*Leptolepidites* spp.	
	Lycopodiacidites spp.	
	Neoraistrickia spp.	
	Sestrosporites pseudoalveolatus	
	Staplinisporites spp.	
	Stereisporites spp.	
	Uvaesporites spp.	
	Vitreisporites pallidus	
Pioneer	*Cerebropollenites* spp.	This taxon is questionably attributed to this SEG.
Coastal	*Araucariacites* spp.	'cooler'
	Callialasporites spp.	'cooler'
	Corollina spp.	'warmer'
	Exesipollenites spp.	'warmer'; see under Lowland SEG.
Tidally-influenced	*Alisporites thomasii*	
	Densoisporites spp.	
	Retitriletes spp.	This taxon is questionably attributed to this SEG.
NOT ATTRIBUTED	*Eucommiidites minor*	
	Spheripollenites spp.	
REMARKS	Ferns spores are here placed in the Lowland SEG, but may also be attributed to the River SEG. Bryophyte spores are here attributed to the River SEG but may also be placed in the Lowland SEG. See text for further explanation.	

tions preferably in warm environments. Also the majority of ferns that have been found in European Jurassic floras are considered to be elements of moist lush vegetation (Harris, 1961; Van der Burgh & Van Konijnenburg-Van Cittert, 1984; Van Konijnenburg-Van Cittert & Van der Burgh, 1989) often occurring near river banks (Pelzer et al. 1992). Therefore, most fern spores may be characteristic for the Lowland (marsh) or River SEGs. This is particularly the case for spores of Osmundaceae (*Osmundacidites, Baculatisporites, Punctatisporites, Todisporites*), Schizaeaceae (*Cicatricosisporites, Plicatella* and to a lesser degree *Ischyosporites* and *Varirugosisporites*), Dicksoniaceae, Dipteridaceae and Cyatheaceae (*Cyathidites, Concavissimisporites, Deltoidospora, Impardecispora*) and Pteridaceae (*Contignisporites, Duplexisporites*).

Extant Matoniaceae are restricted to mountain slopes in the Malaysian Archipelago, where they are exposed to cold nights and humid, warm days. They protect themselves against these conditions by having a resistant cuticle, a feature that is unknown in other ferns. Most Mesozoic matoniaceous ferns also demonstrate a thick epidermis or a cuticle (Van Konijnenburg-Van Cittert, 1993) and, therefore, we consider them to have grown under somewhat harsh but probably warm/humid conditions. We include their spores (*Concavisporites, Deltoidospora,* and *Matonisporites*) in the Lowland SEG.

Extant sun-tolerant Gleicheniaceae grow in vast areas in (sub)tropical regions. Macro-remains of gleicheniaceous ferns (producing *Gleicheniidites*) were common during Late Jurassic and Cretaceous times, and they may have covered vast lowland areas during these times as well (Harris, 1981: savannah or bracken-covered heath). The spores are included in the Lowland SEG.

Pteridosperms

The majority of Late Jurassic alete pollen grains represent conifers and belong to the Upland SEG. There are a few exceptions: *Vitreisporites pallidus* and some species of *Alisporites*.

Vitreisporites pallidus belongs to the Caytoniales. The Caytoniales are considered to have grown in a deltaic environment during warm Jurassic/Cretaceous times (Harris, 1964). Pelzer (1984) believed that they grew on the transition between the floodplain and backswamp peats, while Van Konijnenburg-Van Cittert & Van der Burgh (1989) believed them to be plants of moist lush vegetation. Anyway, they indicate a warm and rather wet environment. We include the pollen in the River SEG.

*Alisporites (*especially *A. thomasii*) has been record-ed in situ from *Pachypteris*-type of pteridosperms that belong to the Corystospermales. The subtropical genus *Pachypteris* was widespread during Middle and Late Jurassic times, and disappeared in the Early Cretaceous (Vakhrameev, 1991). Some species, e.g. *P. papillosa*, have probably been large-sized bushes that formed mangrove thickets along river mouths inundated by tides (Harris, 1964, 1983). Therefore, we include *Alisporites thomasii* in the Tidally-influenced SEG.

Ginkgoales, Cycadales, Bennettitales

Most fossil pollen grains of the Ginkgoales and the Cycadales belong to *Monosulcites* and/or *Cycadopites*. The pollen can usually only be distinguished under SEM or TEM (Hill, 1990), although in general ginkgoalean pollen grains are slightly smaller than those of cycads (Van Konijnenburg-Van Cittert, 1971).

Ginkgo biloba is the only extant representative of the Ginkgoales. It is a deciduous tree that lives in temperate regions and can withstand severe frost. In Mesozoic times, the Ginkgoales were a more diverse group that was mainly restricted to temperate regions, but occasionally representatives were found in the subtropical belt. Pollen grains from these Mesozoic Ginkgoales are usually rather small and can be included in *Monosulcites minimus* Cookson (Van Konijnenburg-Van Cittert, 1971).

Extant Cycadales occur in tropical regions and are usually adapted to withstand droughts (thick leathery leaves with thick cuticles and protected stomata), although a few species occur in rain forests. In the Mesozoic, cycads were more diverse and certain extinct taxa, such as the Nilsoniaceae, were lowland plants in subtropical areas with warm and frost-free weather (Van Konijnenburg-Van Cittert & Van der Burgh, 1989; Vakhrameev, 1991). Pollen of some of the Mesozoic cycads may occasionally correspond to *Monosulcites minimus*, but the majority can be included in larger species of *Chasmatosporites, Monosulcites* or *Cycadopites*.

Many pollen grains of the extinct Bennettitales also belong to *Monosulcites/Cycadopites*, but are distinguished by their large size and a more spindle-like shape (elongate-elliptical outline; Couper, 1958; Harris, 1969; Van Konijnenburg-Van Cittert, 1971). Bennettitaleans grew, like the Mesozoic cycads, mainly in the subtropical belts with warm and frost-free weather (Vakhrameev, 1991). Some taxa yielding *Monosulcites* were probably restricted to deltaic areas (Harris, 1969; Van Konijnenburg-Van Cittert & Van der Burgh, 1989), others preferred a drier microclimate

and grew on slopes adjoining marine basins (Vakhrameev, 1991) or in upland vegetation (Van Konijnenburg-Van Cittert & Van der Burgh, 1989). Their thicker cuticles with protected stomata also indicate that they were adapted to withstand periods of drought or salt influence. Also in Cretaceous sediments there is evidence for occurrences in upland areas (Watson & Sincock, 1992) or even in dry savannahs (Harris, 1973).

Despite the possibility of other habitats, we consider that most Late Jurassic to Early Cretaceous *Monosulcites/Cycadopites* pollen grains have originated from Ginkgoales, Cycadales, and Bennettitales that grew in lowland vegetation. Consequently, this pollen is included in the Lowland SEG.

Apart from *Monosulcites/Cycadopites*, some bennettitalean plants also produced pollen corresponding to *Exesipollenites* (plants with the bisexual *Williamsoniella* flowers and *Nilssoniopteris* leaves; Harris, 1969, 1974; Van Konijnenburg-Van Cittert, 1971). It is likely that these plants preferred a dry microclimate even with some salt influence (Batten, 1976; Watson & Sincock, 1992). Therefore, we include *Exesipollenites* in the Lowland SEG, with a possible extension to the Coastal SEG.

Conifers

Apart from some pteridosperms, genera of several conifer families, e.g. (extant) Pinaceae and Podocarpaceae, are characterised by alete bisaccate pollen grains. Because of a general lack of identifying characters among Mesozoic coniferalean alete bisaccates, it is usually difficult to indicate their botanical affinity at a family level.

Podocarpaceae, which also produce *Quadraeculina anellaeformis* pollen, occur nowadays only in (sub)tropical areas of the southern hemisphere, often on mountain slopes. In the Mesozoic they were common on the northern hemisphere as well, again restricted to (sub)tropical belts. Most extant Pinaceae occur in temperate zones in relatively dry environments, and many taxa can withstand severe cold. In general one may say that also in the Mesozoic these conifer families inhabited relatively dry areas of upland forest (Vakhrameev, 1991). A high frequency of alete bisaccates of the type produced by Pinaceae and Podocarpaceae can therefore be considered to be indicative of Upland SEGs.

Callialasporites and *Araucariacites* species (e.g. *A. australis*) may be associated with the Araucariaceae (Van Konijnenburg-Van Cittert, 1971; Boulter & Windle, 1993). Practically all large types of Late Jurassic and Early Cretaceous *Inaperturopollenites*

pollen are also considered to have araucarian affinities (Balme, 1995). Extant Araucariaceae are often a dominant element in forests in Australia and South America. Their leathery leaves and thick cuticles are an adaptation to long periods of drought and cold conditions. They frequently grow near shores as they can withstand the influence of salt wind.

In Jurassic/Cretaceous times, a high frequency of *Araucariacites/Callialasporites* is, in general, correlated with a warm climate without large seasonal amplitudes (Reyre, 1980; Mohr, 1989). Evidence from macrofossils indicates that araucarian trees often grew in forests not far from the coast (Harris, 1979; Barale & Flamand, 1982; Vakhrameev, 1991). Therefore, large quantities of *Callialasporites* and *Araucariacites* pollen may be indicative of Coastal SEGs.

Species of *Corollina* have been recorded in situ from various representatives of Jurassic and (Early) Cretaceous Cheirolepidiaceae. Within this family, two subfamilies can be distinguished: the Hirmeriellae or *Hirmeriella* – group (mainly but not exclusively occurring in the Jurassic), and the Frenelopsidae or *Frenelopsis* – group (common in the Cretaceous). Although the pollen grains of both groups belong to *Corollina*, they can be distinguished at a species level. *Corollina torosus* belongs to the Hirmeriellae, while *Corollina echinatus* belongs to the Frenelopsidae. The ecology of this palynologically important family (*Corollina* often forms a major part of palynological assemblages), has long been subject of debate. In general, one can conclude that Cheirolepidiaceae were drought resistant, thermophilous shrubs and trees that required at least a subtropical climate (Francis, 1983; Vakhrameev, 1991). They were never dominant in cold climatic regions. Most authors agree that the Jurassic *Hirmeriella* species were probably coastal plants (Vakhrameev, 1970, 1991; Batten, 1973, 1975; Jung, 1974; Alvin, 1982; Watson, 1988), either growing on sandy bars and coastal islands or even as mangroves. During the Cretaceous, the Cheirolepidiaceae probably occupied a whole range of warm habitats (Batten, 1976; Alvin, 1982; Francis, 1983), from river banks for some *Hirmeriella* species, to arid, even desert conditions for most *Frenelopsis* and *Pseudofrenelopsis* species. Especially the latter two taxa show many xeromorphic stem and cuticle characters indicative of an adaptation to (seasonal) arid habitats (Broutin & Pons, 1975; Alvin, 1982; Watson, 1988). Although most authors believe that these xeromorphic characters are related to real xerophytism rather than halophytism (e.g. Alvin, 1982), others favour coastal habitats for at least some *Frenelopsis* species (Doludenko & Reymanowna, 1978; Pons & Broutin,

1978; Pons, 1979). In conclusion, we consider the presence of large numbers of *Corollina torosus* (or morphologically related species) to be indicative of Coastal SEGs, while in Cretaceous times *Corollina echinatus* (and related species) should be placed either in the Coastal or in the Lowland SEG.

Perinopollenites has been recorded from *Elatides,* an extinct representative of the Taxodiaceae (Van Konijnenburg-Van Cittert, 1971; Harris, 1979; Van Konijnenburg-Van Cittert & Van der Burgh, 1989; Balme, 1995). These thermophilic (Vakhrameev, 1991) conifers are well known from Late Jurassic and Early Cretaceous (Wealden) deposits, that are associated with wet lowlands with repeated marine transgressions (Pelzer *et al.,* 1992). Species of *Elatides* were also found in Middle Jurassic sediments were they are considered to be plants of lush vegetation (Harris, 1979). Also some extant members of the Taxodiaceae prefer humid environments. We therefore place *Perinopollenites* in the Lowland SEG.

Cerebropollenites has been found in situ (Van Konijnenburg-Van Cittert & Van der Burgh, 1989), in a polliniferous cone of unknown affinities although there are certain similarities to *Elatides* cones. Therefore, a taxodiaceous nature is a possibility. Other authors recognise similarities with *Tsuga*-like pollen (Balme, 1995), and thus point to an affinity with the Pinaceae. Despite this taxonomic uncertainty, the fact that *Cerebropollenites* occurs in large quantities immediately after a regression (Couper, 1958; Abbink, personal observation), could well be evidence of a pioneer nature of the parent plants. We therefore place *Cerebropollenites* in the Pioneer SEG.

Although the form-genus *Spheripollenites* may also include completely preserved palynomorphs, Jurassic forms identified as *Spheripollenites* are likely to be inner (nexine) bodies of coniferous pollen such as *Corollina* and *Perinopollenites.* Several authors even believe that the presence of large numbers of *Spheripollenites* together with large numbers of *Corollina,* indicate a more strongly developed annual dry season (Alvin, 1982; Mohr, 1989). Hence the forms might be added to the Lowland SEG. However, because of the taxonomic and ecological uncertainties of incomplete pollen, we refrain from applying *Spheripollenites* in the SEG model.

Eucommiidites

Eucommiidites minor has never been recorded in situ. However, the species has been found in dispersed Jurassic and Cretaceous pollen organs and seeds (Van Konijnenburg-Van Cittert, 1971; Pedersen *et al.,* 1989). The precise botanical affinity of these pollen organs and seeds is uncertain. The seeds suggest a close relationship with the Antophytes, a broad category comprising Bennettitales, Pentoxylales, Gnetales and Angiospermae. On the other hand, Jurassic cones containing *Eucommiidites troedsonii* grains are thought to have Cycadalean affinities (Van Konijnenburg-Van Cittert, 1971). No precise ecological conclusions can be drawn from the presence of this species.

Possible angiosperms

Clavatipollenites is thought to be related to the first angiosperms (Pedersen *et al.,* 1991, 1994). Although not much is known about the ecology of the plants, we questionably assign this species to the Lowland SEG, based on the sedimentary evidence (Brenner, 1963; Pedersen *et al.,* 1991).

Conclusions

The presented SEG model is considered to allow the identification of palaeoenvironmental changes, in particular sea-level fluctuations and climate changes based on quantitative distribution patterns of Jurassic – Early Cretaceous sporomorph assemblages. Variations between the various SEGs permit the recognition of sea-level fluctuations. Significant shifts within the SEGs, especially within the Lowland SEG are considered to reflect climate changes.

The SEG model provides the possibility to recognise depositional sequences in Jurassic - Early Cretaceous shallow marine to even non-marine settings exclusively on the basis of palynology. Hence, the model may provide a new and powerful tool for correlation between non-marine to shallow marine sequences and marine (standard) sequences (Abbink *et al.,* this volume). In addition, this approach allows detailed understanding of the palaeoenvironment and a glance at the Jurassic Earth System (Abbink *et al.,* 2001).

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