

Palynofloral patterns of terrestrial ecosystem change during the end-Triassic event – a review

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Abstract – A review of the palynofloral succession at the well-documented Triassic–Jurassic boundary sites – Kuhjoch (Austria), St Audrie’s Bay (UK), Stenlille (Denmark), Astartekløft (Greenland), Sverdrup Basin (Arctic Canada), Northern Carnarvon Basin (Western Australia), Southeast Queensland (eastern Australia) and New Zealand – show all sites experienced major to moderate re-organization of the terrestrial vegetation during the end-Triassic event. The changes led to subsequent taxonomic losses of between 17% and 73% of the Rhaetian pre-extinction palynoflora. The majority of the typical Rhaetian taxa that disappear are so far not known from *in situ* occurrences in reproductive structures of macrofossil plant taxa. From an ecological perspective, the most dramatic changes occurred in the Sverdrup Basin, Stenlille, Kuhjoch and Carnarvon Basin, where the pre- and post-extinction palynofloras were fundamentally different in both composition and dominance. These changes correspond to ecological severity Category I of McGhee *et al.* (2004), while the remaining sites are placed in their Subcategory IIa because there the pre-extinction ecosystems are disrupted, but recover and are not replaced post-extinction. Increased total abundances of spores on both hemispheres during the extinction and recovery intervals may indicate that environmental and/or climatic conditions became less favourable for seed plants. Such conditions may include expected effects of volcanism in the Central Atlantic Magmatic Province, such as acid rain, terrestrial soil and freshwater acidification due to volcanic sulfur dioxide emissions, fluctuating ultraviolet flux due to ozone depletion caused by halogens and halocarbon compounds, and drastic changes in climatic conditions due to greenhouse gas emissions.

Keywords: end-Triassic mass extinction, Triassic–Jurassic boundary, terrestrial palynology, ecological severity.

1. Introduction

In Late Triassic times the supercontinent Pangaea stretched from pole to pole, surrounded by Panthalassa and partly dissected by the Tethys Ocean (Fig. 1). A strong monsoonal atmospheric circulation is believed to have induced three non-zonal (non-latitudinal) climate regions with: (1) arid/semi-arid conditions in central Pangaea and along the western margin of the Tethys, (2) alternating wet and dry seasonal conditions along the eastern coasts of Laurasia and Gondwana as well as the western coasts of Pangaea, and (3) wet and warm conditions in the high latitudes (Preto, Kustatscher & Wignall, 2010). Towards the end of the Triassic Period, in late Rhaetian time, Triassic life suffered one of the five most severe crises during the Phanerozoic Eon (Sepkoski, 1996). These mass extinction events are characterized by global extinction rates and magnitudes greatly exceeding background levels. The end-Triassic mass extinction, or ETE, is particularly marked by such losses of marine organisms (Sepkoski, 1996). At the base of the marine food web, extinction of phyto- and zooplankton may have resulted in strongly reduced or highly altered primary production (Ward *et al.* 2001). Dinoflagellates and coccolithophor-

ids that had undergone rapid radiation during Late Triassic time experienced high extinction rates. Benthic organisms such as scleractinian corals, megalodont bivalves and calcareous algae were especially hard hit (Kießling *et al.* 2007). Ammonites, nektonic predators, also suffered high diversity losses and survivors were possibly energy-saving passive floaters (Whiteside & Ward, 2011). The end-Triassic event is temporally linked to extensive flood basalt volcanism with the formation of the large igneous province the Central Atlantic Magmatic Province (CAMP) (Schoene *et al.* 2010), and degassing from this volcanism is generally believed to have played a major part in the extinction scenario.

Much emphasis has been put on the marine record during this biotic crisis, and the terrestrial environment is generally considered to have been equally affected (McElwain & Punyasena, 2007). Some authors suggest that there is no distinctive floral mass extinction during the end-Triassic event, but rather that the terrestrial plant record only suffered disturbances, globally, rather than catastrophic losses (Bonis & Kürschner, 2012; Bond & Wignall, 2014). However, major palaeobotanical studies across the Triassic–Jurassic boundary (TJB) are lacking from most areas. The only macroplant record across the TJB that has been studied in detail and in higher resolution is that from

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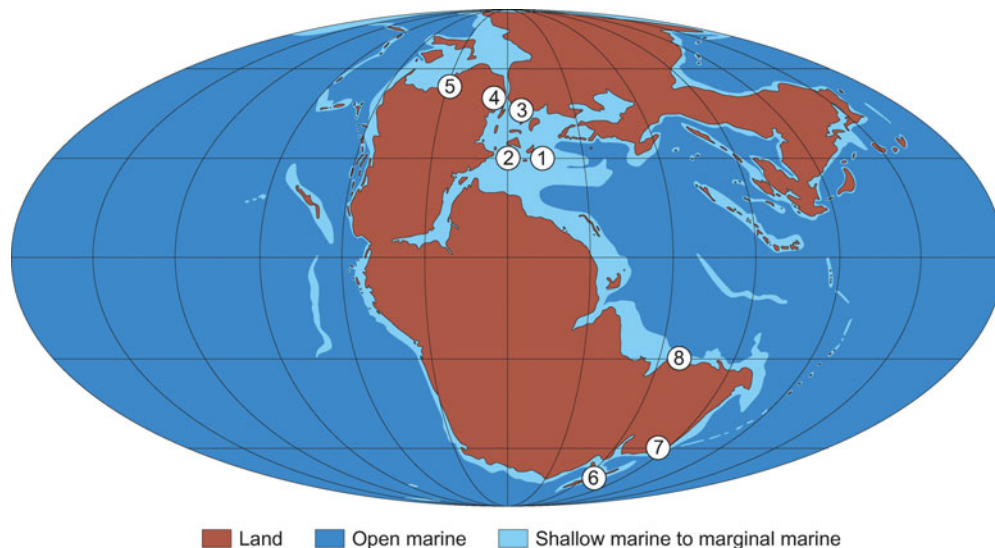


Figure 1. (Colour online) Palaeomap of Pangaea (after R. Blakey, 2014, <http://cpgeosystems.com/paleomaps.html>) showing the palaeogeographical location of localities discussed in the text: 1 – Kuhjoch, Austria; 2 – St Audrie's Bay, UK; 3 – Stenlille, Denmark; 4 – Astartekløft, Greenland; 5 – Sverdrup Basin, Arctic Canada; 6 – Northern Carnarvon Basin, Western Australia; 7 – Southeast Queensland, eastern Australia; 8 – New Zealand.

Greenland (Harris, 1937; McElwain *et al.* 2007). The Greenland macroplant record is considered autochthonous, and to reflect the vegetation locally, with very little input of regional floral elements. The well-preserved macroplant fossil assemblages from Greenland have provided a detailed insight into the terrestrial environment and the changes that occurred across the TJB in this particular area, and show an exceptionally high species turnover of >80%, while the extinction at genus level was considerably more moderate, ~17% (McElwain *et al.* 2007). On a global scale, possibly only one plant family became extinct, namely the Peltaspermaeaceae (McElwain & Punyasena, 2007).

However, taxonomic loss is not the only important factor when assessing the severity of a biotic crisis. Ecological factors, expressed as (1) magnitude of ecological disruption, and (2) ranking of ecological impact, have provided additional information on the severity of a biotic crisis (Droser *et al.* 2000; McGhee *et al.* 2004, 2013). McGhee *et al.* (2004) placed the terrestrial biotic crisis at the end-Triassic event in either their severity Category I: existent ecosystems collapse and are replaced by new post-extinction ecosystems, or IIa: disruption produces permanent loss of major ecosystem components (McGhee *et al.* 2004). However, they do state that the impact of the end-Triassic crisis on terrestrial biota is problematic in terms of ecological characterization (McGhee *et al.* 2004).

This review will focus solely on taxonomic and ecological changes in terrestrial palynology across the TJB. The terrestrial palynology of a number of well-documented TJB successions that provide quantitative or at least semi-quantitative palynological data are reviewed and compared. This is by no means a complete review of all published records so far, but the aim is to investigate palynofloral patterns that can provide an insight into if and how the terrestrial ve-

getation was affected on a global scale during the ETE.

2. Parent plant affinities and environmental and climatic preferences

In order to interpret the palynological record it is necessary to refer the dispersed fossil spores and pollen to parent plant taxa. Table 1 lists the known or probable plant affinities of common Rhaetian–Hettangian spore and pollen taxa. For many of these taxa the probable affinity is merely based on their general morphology and similarity to extant taxa. Others are known from *in situ* occurrences in macroplant fossils, and this provides us with more information on their habit and preferred environment. A few taxa remain of unknown affinity. Authors working on Triassic palynofloras often divide spores and pollen into hygrophytic (i.e. wet-loving) or xerophytic (i.e. drought tolerant), based primarily on the works of Visscher & van der Zwan (1981), Brugman, van Bergen & Kerp (1993) and Visscher *et al.* (1994). Several published papers have supplied more detailed information on possible ecological preferences of Jurassic fossil plants, which can be used to interpret the palynological record (e.g. Abbink, 1998; van Konijnenburg-van Cittert, 2002, 2008). Some authors have used the link between sedimentology and palynology, or multivariate statistical analyses to interpret environmental and climatic preferences (e.g. Hubbard & Boulter, 1997; Bonis & Kürschner, 2012). In some cases such studies can indicate differences in ecological or climatological preference of morphologically similar and probably closely related taxa.

3. Review of selected palynological TJB successions

The terrestrial palynological changes across the TJB interval from a selected number of sites are re-

Table 1. List of selected Triassic–Jurassic spore-pollen taxa and their probable parent plant affinities, and possible ecological and climatological preferences

	Known or probable parent plant affinity	Habit	Preferred environment	Climatic preferences
Pollen				
<i>Alisporites/Falcisporites</i> spp.	Seed fern, Corystospermales	canopy	Lowland	Xerophytic
<i>Araucariacidites australis</i>	Conifer, Auracariaceae	canopy	Coastal (Abbink, 1998)	Cooler (Abbink, 1998)
<i>Ashmoripollis reducta</i>	Unknown gymnosperm			
<i>Cerebropollenites thiergartii</i>	Conifer	canopy	?Pioneer	
<i>Cerebropollenites macroverrucosus</i>	Conifer	canopy	?Pioneer (Abbink, 1998)	
<i>Chasmatosporites apertus</i>	Cycads/Ginkgos	canopy	Lowland (Abbink, 1998)	Drier, cooler (Abbink, 1998)
<i>Chasmatosporites elegans</i>	Cycads/Ginkgos	canopy	Lowland (Abbink, 1998)	Drier, cooler (Abbink, 1998)
<i>Chasmatosporites hians</i>	Cycads/Ginkgos	canopy	Lowland (Abbink, 1998)	Drier, cooler (Abbink, 1998)
<i>Clavatipollenites hughesii</i>	Unknown gymnosperm		?Lowland (Abbink, 1998)	
<i>Classopollis meyerianus</i>	Conifer, Cheirolepidiaceae	canopy or shrubs	well drained, coastal	Warm conditions
<i>Classopollis torosus</i>	Conifer, Cheirolepidiaceae	canopy or shrubs	Coastal, sandy bars, coastal islands (Francis, 1983; Vakhrameev, 1991; Alvin, 1982)	Warm conditions although somewhat cooler than <i>C. meyerianus</i> (Bonis & Kürschner, 2012)
<i>Exesipollenites</i> spp.	Conifer, Cupressaceae/Taxodiaceae	canopy or shrub	Coastal (Abbink, 1998)	Warmer (Abbink, 1998)
<i>Eucommiidites</i> spp.	Erdtmanithecales	canopy	Lowland (Abbink, 1998)	Drier, warmer (Abbink, 1998)
<i>Geopollis zwolinskiae</i>	Conifer, Cheirolepidiaceae	canopy	Coastal	Warm conditions
<i>Granuloperculatipollis rudis</i>	Conifer, Cheirolepidiaceae	canopy	Coastal	Warm conditions
<i>Lunatisporites rhaeticus</i>	Conifer	canopy		Xerophytic
<i>Monosulcites minimus</i>	Bennettitales	canopy	Lowland, drier patches in mires	Drier, warmer (Abbink, 1998)
<i>Monosulcites</i> spp. (Others)	Cycads/Ginkgos/Bennettitales/Peltaspermales (Seed ferns)	canopy	Mire, drier patches	Drier, cooler (Abbink, 1998)
<i>Ovalipollis ovalis</i>	Conifer	?well drained, unknown habit		Xerophytic (Roghi, 2004)
<i>Perinopollenites elatoides</i>	Conifer, Cupressaceae/Taxodiaceae	canopy	Mire, river banks, lowland	Wetter, cooler (Abbink, 1998)
<i>Pinuspollenites minimus</i>	Conifer, Pinaceae	canopy	Upland, well drained	Xerophytic
<i>Protohaploxylinus</i> spp.	Conifer	canopy	Well drained	Xerophytic
<i>Quadraeculina anellaeformis</i>	Podocarpaceae (Boulter & Windle, 1993)	canopy	Upland, well drained	Xerophytic
<i>Rhaetipollis germanicus</i>	Unknown gymnosperm			
<i>Riccisporites tuberculatus</i>	Unknown gymnosperm			
<i>Spheripollenites</i> spp.	Conifer			
<i>Vitreisporites</i> spp.	Seed fern, Caytoniales	canopy	Lowland, mire, floodplains, deltaic (Abbink, 1998)	Hygrophytic, warm (Abbink, 1998)
Spores				
<i>Aratrisporites</i> spp.	Lycophyte, Pleuromeiaceae	ground cover	Coastal, mire	Xerophytic (Retallack, 1975).
<i>Baculatisporites comaumensis</i>	Fern, Osmundaceae	ground cover	Lowland, mire	Wetter, warmer (Abbink, 1998)
<i>Baculatisporites oppressus</i>	Fern, Osmundaceae	ground cover	Lowland, mire	Marsh, Wetter, warmer (Abbink, 1998)
<i>Calamospora tener</i>	Equisetales	ground cover	River banks, lake shores	Tropical to temperate (Abbink, 1998)
<i>Camarozonosporites</i> spp.				
<i>Cibotiumspora juriensis</i>	Fern	ground cover	Lowland	Hygrophytic
<i>Cingulizonates rhaeticus</i>	Lycophyte	ground cover	Lowland, mire	Hygrophytic
<i>Conbaculatisporites mesozoicus</i>	Fern	ground cover	Lowland	Hygrophytic
<i>Concavisporites</i> spp.	Fern, Dicksoniaceae, Dipteridaceae, Cyatheaceae	understory, ground cover	Lowland, drier environments	Hygrophytic
<i>Conbaculatisporites spinosus</i>	Fern	ground cover, mire	Lowland	Hygrophytic
<i>Converrucosisporites</i> spp.	Fern	ground cover, mire	Lowland	Hygrophytic
<i>Deltoidospora</i> spp.	Fern, Dipteridaceae, Dicksoniaceae	understory, ground cover	Pioneer, drier patches in mire	Drier, warmer (Abbink, 1998)

Table 1. Continued

	Known or probable parent plant affinity	Habit	Preferred environment	Climatic preferences
<i>Densoisporites</i> spp.	Lycophyte, Pleuromeiaceae	ground cover	Coastal or mire	Hygrophytic
<i>Densosporites</i> spp.	Lycophyte	ground cover, mire		Hygrophytic
<i>Dictyophyllidites</i> spp.	Fern, Dicksoniaceae, Dipteridaceae, Cyatheaceae	understory, ground cover	Pioneer. Lowland, drier environments	Drier, warmer (Abbink, 1998)
<i>Gleicheniidites</i> spp.	Fern, Gleicheniaceae	ground cover	Pioneer. Lowland, drier environments	Drier, warmer (Abbink 1998)
<i>Gordonispora fossulata</i>	Bryophyte	ground cover	Lowland, mires, river banks or wet environments	Hygrophytic
<i>Iraquispora laevigata</i>	Fern	ground cover	Lowland	Hygrophytic
<i>Ischyosporites</i> spp.	Fern, Schizaeaceae	ground cover	Lowland, mire or wet environments	Wetter, warmer (Abbink, 1998)
<i>Kraeuselisporites reissingerii</i>	Lycophyte	ground cover	Lowland	Hygrophytic
<i>Laevigatosporites</i> spp.	Fern, Marattiales	ground cover	Lowland	Hygrophytic
<i>Limbosporites</i> spp.	Lycophyte	ground cover	Lowland, mire or wet environments	Hygrophytic
<i>Lycopodiacidites rugulatus</i>	Fern	ground cover		Hygrophytic
<i>Marattisporites scabratus</i>	Fern, Marattiales	ground cover	Lowland, mire or wet environments	Hygrophytic
<i>Matonisporites</i> spp.	Fern, Matoniaceae	ground cover	Lowland, mire or wet environments	Hygrophytic
<i>Osmundacidites wellmanii</i>	Fern, Osmundaceae	ground cover	Lowland, mire or wet environments	Wetter, warmer (Abbink, 1998)
<i>Punctatisporites</i> spp.	Fern, Osmundaceae	ground cover	Lowland, mire or wet environments	Wetter, warmer (Abbink, 1998)
<i>Polycingulatisporites</i> spp.	Bryophyte	ground cover, mire	Lowland, mires, river banks or wet environments	Hygrophytic
<i>Polypodiisporites polymicroforatus</i>	Fern, Schizaeaceae	ground cover	Pioneer? (van de Schootbrugge et al. 2009), Lowland	Hygrophytic
<i>Polypodiisporites</i> spp.	Fern, Schizaeaceae, Polypodiaceae	ground cover, mire	Lowland	Hygrophytic
<i>Porcellispora longdonensis</i>	Bryophyte, liverwort	ground cover	Ephemeral lake margins	Xerophytic, drought tolerant (Reinhardt and Ricken, 2000; Roghi, 2004)
<i>Retitriteles</i> spp.	Fern	ground cover	Lowland, mire or wet environments	Hygrophytic
<i>Rogalskaisporites</i> spp.	Bryophyte	ground cover	Lowland, mires, river banks or wet environments	Hygrophytic
<i>Skarbysporites crassexina</i>	Fern	ground cover, mire		Hygrophytic
<i>Stereisporites</i> spp.	Bryophyte	ground cover	Lowland, mires, river banks or wet environments	Hygrophytic
<i>Striatella seebergensis</i>	Fern, Pteridaceae	ground cover, mire		Hygrophytic
<i>Thymospora</i> spp.	Fern, Marattiales	ground cover	Lowland, mire or wet environments	Hygrophytic
<i>Tigrisporites microrugulatus</i>	Fern	ground cover	Lowland	Hygrophytic
<i>Toripustulatisporites hokonuiensis</i>	Fern	ground cover	Lowland	Hygrophytic
<i>Trachysporites</i> spp.	Fern	ground cover	Lowland	Hygrophytic
<i>Triancoraesporites ancorae</i>	Lycophyte	ground cover	Lowland	Hygrophytic
<i>Uvaeosporites</i> spp.	Lycophyte, Selaginellales	ground cover	River banks, marshes	Hygrophytic
<i>Zebrasporites</i> spp.	Fern	ground cover	Lowland	Hygrophytic

viewed below. The major changes in spore-pollen taxa abundances at each locality are displayed in Figures 2, 3, 5–8, 11, where two reviewed sites at a time are compared. Five of the reviewed TJB successions are located in the northern hemisphere, while only three from the southern hemisphere have been found to contain sufficient palynological data to assess. The sites are put into a stratigraphical framework, where, if possible, independent dates obtained via invertebrate marine fossils or marine dinoflagellate cysts are used as

markers. The base of the Jurassic is defined by the first occurrence of the ammonite *Psiloceras spelae* (Hillebrandt *et al.* 2013). In addition to this traditional marine marker, the base of the Jurassic is also defined by an accessory marker, the pollen *Cerebropollenites thiergartii*, which at the GSSP (Global Stratotype Sections and Point) at Kuhjoch in Austria appears for the first time *c.* 3 m below the first occurrence of *P. spelae*.

In order to assess the ecological impact at each site, the spores and pollen at each site were placed

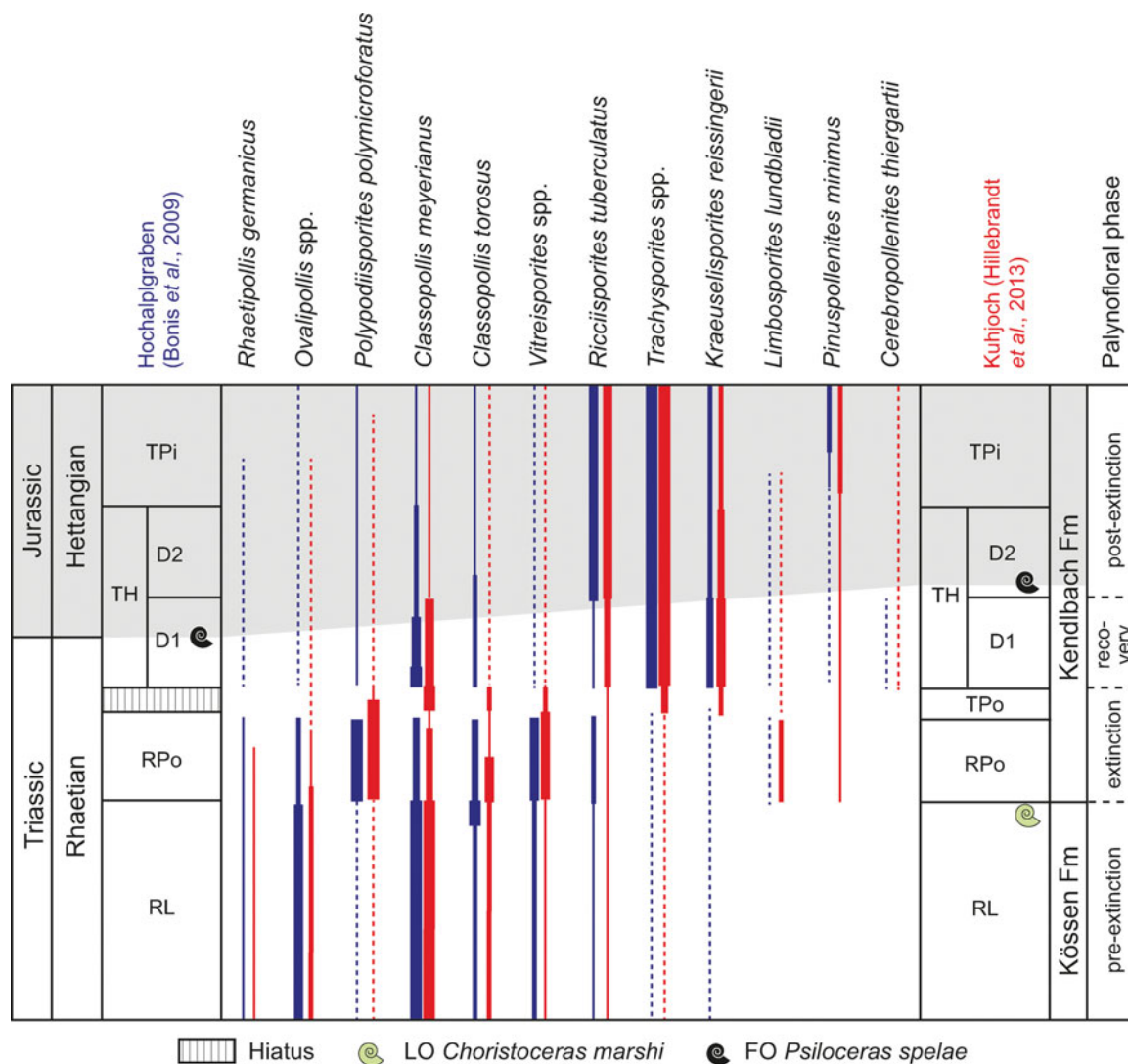


Figure 2. (Colour online) Selected palynological changes across the TJB at the GSSP locality Kuhjoch and Hochalplgraben in Austria (after Bonis *et al.* 2009; Hillebrandt *et al.* 2013). Grey-shaded area marks the Jurassic.

in groups according to their known or probable parent plant affinity (following information in Table 1). From previous palynological work on the end-Permian and the Cretaceous–Palaeogene mass extinction events (e.g. Sweet & Braman, 1992; Looy *et al.* 1999; Vajda, Raine & Hollis, 2001; Lindström & McLoughlin, 2007; Hermann *et al.* 2012) it is clear that palynofloral successions across such biotic crises can be divided into pre-extinction, extinction, recovery and post-extinction palynofloral phases. Pre-extinction and post-extinction palynofloras represent the stable pre- and post-vegetation, respectively. Extinction palynofloras are characterized by increased taxonomic losses and compositional changes. Recovery palynofloras may be characterized by rapidly changing assemblages, constituting not only surviving, but also lingering and new incoming taxa. This subdivision is applied to the palynological successions at the herein reviewed sites in order to assess taxonomic and ecological changes over the investigated time interval.

3.a. The GSSP locality Kuhjoch, and Hochalplgraben, Austria

At the TJB the Eiberg Basin, today located in the Northern Calcareous Alps, was an intraplatform on the northern margin of the Tethys (Hillebrandt *et al.* 2013). The GSSP locality consists of two sections, Kuhjoch West and East (Hillebrandt *et al.* 2013). The palynology of the TJB successions at Kuhjoch West and another section at Hochalplgraben were presented in Bonis, Kürschner & Krystyn (2009). In addition, Hillebrandt *et al.* (2013) published an update of the Kuhjoch West succession, complemented with data from Kuhjoch East. The palynofloral changes over the extinction interval at Kuhjoch are reviewed below (Fig. 2), and the palynofloral changes are summarized in Table 2.

3.a.1. Pre-extinction palynoflora (Rhaetian)

In the Eiberg Member (Kössen Formation) pre-extinction palynofloras are dominated by xerophytic conifer pollen: the cheirolepid pollen

Table 2. List of ecosystem changes, expressed as palynologically inferred parent plant group dominance across the TJB in the successions reviewed herein, as well as the taxonomic and ecological severity assessment of each site

Locality	Pre-extinction palynoflora	Extinction palynoflora	Recovery palynoflora	Post-extinction palynoflora	Taxonomic severity	Ecological severity
Sverdrup Basin, Arctic Canada	<i>Ricciisporites</i> dominant, lycophytes abundant. Cheirolepids abundant but decreasing upwards.	Poorly known. Lycophytes and/or tree ferns dominate. Caytoniales are common.	Caytoniales, tree ferns and Cupressaceae/Taxodiaceae dominate. Ginkgo/cycads and Equisetales are abundant.	Cupressaceae/Taxodiaceae and osmundaceous ferns dominate.	38–52 %	I
Astartekløft, Greenland	<i>Ricciisporites</i> dominant, cheirolepids present.	Lycophytes (Selaginellales) dominate, with alternating abundance of <i>Ricciisporites</i> , tree ferns and osmundaceous ferns.	Tree ferns dominate. Osmundaceous ferns are abundant.	Osmundaceous ferns dominate. Conifers (Pinaceae and <i>Cerebropollenites</i>) and corystosperms are common.	17 %	IIa
Stenlille, Denmark	Cheirolepidiaceae and Cupressaceae/Taxodiaceae dominate, <i>Ricciisporites</i> common.	<i>Ricciisporites</i> , tree ferns and schizaeacean ferns dominate.	Cupressaceae/Taxodiaceae and tree ferns dominate, with common bryophytes.	Cupressaceae/Taxodiaceae and Pinaceae and tree ferns dominate.	47 %	I
Kuhjoch, Austria	Cheirolepidiaceae and <i>Ovalipollis</i> -conifers dominate.	Schizaeacean ground ferns, caytonialeans and tree ferns dominate.	Ground ferns dominate. Tree ferns and lycophytes common.	Ground ferns dominate, <i>Ricciisporites</i> common. Pinacean conifers present.	26 %	I
St Audrie's Bay, UK	Cheirolepidiaceae and <i>Ricciisporites</i> dominate.	Cheirolepidiaceae dominate, Caytoniales and schizaeacean ferns are common. Part of zone probably missing owing to unconformity.	Cheirolepids and Selaginellales dominate. Tree ferns and ground ferns abundant.	Cheirolepids dominate. Lycophytes and Pinaceae are occasionally common to abundant.	35 %	IIa
N Carnarvon Basin, Western Australia	Corystosperms dominate, tree ferns are abundant	Corystosperms dominate. Tree ferns and osmundaceous, marattialean and schizaeacean ferns are common.	Possibly missing in section.	Cheirolepids dominate. Cupressaceae/Taxodiaceae and tree ferns are common.	73 %	I
SE Queensland, Australia	Corystosperms dominate, lycophytes are abundant	Corystosperms dominate, marattialean ferns are abundant. Ginkgo/cycads common.	Corystosperms dominate. Ginkgo/cycads abundant. Osmundaceous ferns, tree ferns and bryophytes common.	Corystosperms and Cheirolepids dominate. Cupressaceae/Taxodiaceae common.	19 %	IIa
New Zealand	Lycophytes dominate. Bryophytes and corystosperms are abundant	Bryophytes dominate. Tree ferns, osmundaceous and marattialean ferns are abundant. Corystosperms are decreasing in abundance.	Bryophytes dominate. Tree ferns and osmundaceous ferns are abundant.	Bryophytes dominate. Tree ferns, corystosperms and cheirolepids are abundant. Caytoniales occasionally abundant.	15 %	IIa

The ecological severity is estimated using category assessments of McGhee *et al.* (2004)

Classopollis and *Ovalipollis* of unknown coniferalean affinity (Bonis, Kürschner & Krystyn, 2009; Hillebrandt *et al.* 2013) (Fig. 2). These assemblages were assigned to the *Rhaetipollis–Limbosporites* (RL) Zone by Kürschner, Bonis & Krystyn (2007) and correlated with the *Rhaetipollis–Limbosporites* Zone of Lund (1977) (Fig. 2).

3.a.2. Extinction palynoflora (Rhaetian)

The first marine extinction pulse, where conodonts, Triassic ostracods and the Triassic ammonoid *Choristoceras marshi* occur for the last time, is located in the topmost bed of the Eiberg Member, ‘the T-bed’ (*sensu* Hillebrandt), a c. 1 cm thick black millimetre-laminated clay layer, interpreted as an anoxic event and a first marine regression (Hillebrandt *et al.* 2013). The succeeding Schattwald beds (lower Kendlbach Formation) represent the peak of the marine extinction (Hillebrandt & Krystyn, 2009; Hillebrandt *et al.* 2013). The extinction palynofloras of this interval differ substantially from pre-extinction ones (Fig. 2; Table 2), and were assigned to the *Rhaetipollis–Porcellispora* (RPo) Zone (Kürschner, Bonis & Krystyn, 2007; Bonis, Kürschner & Krystyn, 2009; Hillebrandt *et al.* 2013). Initially *Classopollis* pollen was abundant together with the caytonialean pollen *Vitreisporites bjuvensis* and fern spores *Deltoidospora* and *Polypodiisporites polymicroforatus*. Within the middle and upper part of the Schattwald beds cheirolepidacean conifer pollen almost disappeared completely, while the probable schizaeacean fern spore *P. polymicroforatus* continued to increase in abundance (Hillebrandt *et al.* 2013) (Fig. 2). At Kuhjoch East, assemblages assigned to the *Trachysporites–Porcellispora* (TPo) Zone (Kürschner, Bonis & Krystyn, 2007) show an initial continued dominance of *P. polymicroforatus* and *Deltoidospora*, together with common caytonialean *Vitreisporites* pollen, but with a gradual increase in *Classopollis*, and a temporary dominance of fern spores assigned to *Conbaculatisporites* in the upper part of the zone (Fig. 2). The RPo and TPo zones were both correlated with the *Ricciisporites–Polypodiisporites* Zone of Lund (1977) (Bonis, Kürschner & Krystyn, 2009).

3.a.3. Recovery palynoflora (latest Rhaetian)

At Kuhjoch East the succeeding D1 Subzone of the *Trachysporites–Heliosporites* (TH) Zone is dominated by *Classopollis meyerianus*, fern spores assigned to *Trachysporites fuscus* and lycopod spores *Kraeuselisporites reissingerii* (*Heliosporites reissingerii*) (Fig. 2). *Deltoidospora* is also common, but *P. polymicroforatus* is absent. At Kuhjoch West, the composition of the D1 Subzone palynoflora is similar; however, *Classopollis meyerianus* is less abundant and *Ricciisporites tuberculatus* is a common constituent. At Kuhjoch West, the accessory marker for the base of the Jurassic, *Cerebropollenites thiergartii*, occurs from the base of the D1 Subzone (Hillebrandt *et al.* 2013).

The palynoflora of the D1 Subzone is here regarded as representing the recovery phase.

3.a.4. Post-extinction palynoflora (Hettangian)

The D2 Subzone differs from the previous one only in that the abundance of *C. meyerianus* has declined further (Hillebrandt *et al.* 2013). *Ricciisporites* continues to be common to abundant and even increases in abundance upwards within the following *Trachysporites–Pinuspollenites* (TPi) Zone. The TPi Zone is marked by an incoming of the bisaccate pinacean conifer pollen *Pinuspollenites minimus*. *Trachysporites* remains the most abundant constituent, while *Kraeuselisporites reissingerii* (*Heliosporites reissingerii*) has decreased markedly (Fig. 2). At Hochalplgraben the palynofloral succession is similar (Bonis, Kürschner & Krystyn, 2009), but as in the Kuhjoch West section, the TPo Zone is missing owing to an unconformity (Fig. 2). At Kuhjoch the base of the Jurassic, i.e. the first occurrence of the ammonite *Psiloceras spelae*, is in the lower part of the D2 Subzone. However, at Hochalplgraben the first occurrence of *Psiloceras spelae* actually occurs lower, within the D1 Subzone of the TH Zone (Bonis, Kürschner & Krystyn, 2009; Hillebrandt *et al.* 2013) (Fig. 2). The implications of this were not discussed in Hillebrandt *et al.* (2013).

Hillebrandt *et al.* (2013) did not discuss the palynofloral turnover at Kuhjoch, but from their figures it is indicated that at least 12 out of 46 taxa at Kuhjoch West, i.e. 26%, may have disappeared over the TJB interval.

3.b. St Audrie’s Bay, UK

As one of the final candidates proposed as a GSSP for the base of the Jurassic (Warrington, Cope & Ivimey-Cook, 1994), several studies have focused on, or included, the palynology of the upper Blue Anchor, Westbury, Lilstock and Blue Lias formations at St Audrie’s Bay, including Orbell (1973), Warrington, Cope & Ivimey-Cook (1994), Hounslow, Posen & Warrington (2004), van de Schootbrugge *et al.* (2007) and most recently Bonis, Ruhl & Kürschner (2010). In the latter study the terrestrial palynoassemblages were divided into four informal zones, SAB1 to SAB4, briefly reviewed below (Fig. 3). The palynofloral changes over the extinction interval at St Audrie’s Bay are summarized in Table 2.

3.b.1. Pre-extinction palynoflora (Rhaetian)

Pre-extinction assemblages from the upper Blue Anchor Formation and the Westbury Formation are characterized by high abundances of *Classopollis*, *Ricciisporites tuberculatus* and *Ovalipollis* and assigned to the SAB1 Zone (Bonis, Ruhl & Kürschner, 2010). *Rhaetipollis germanicus* is common in the lower part of the zone, and *Ovalipollis* occurs in much lower numbers in its upper part (Fig. 3).

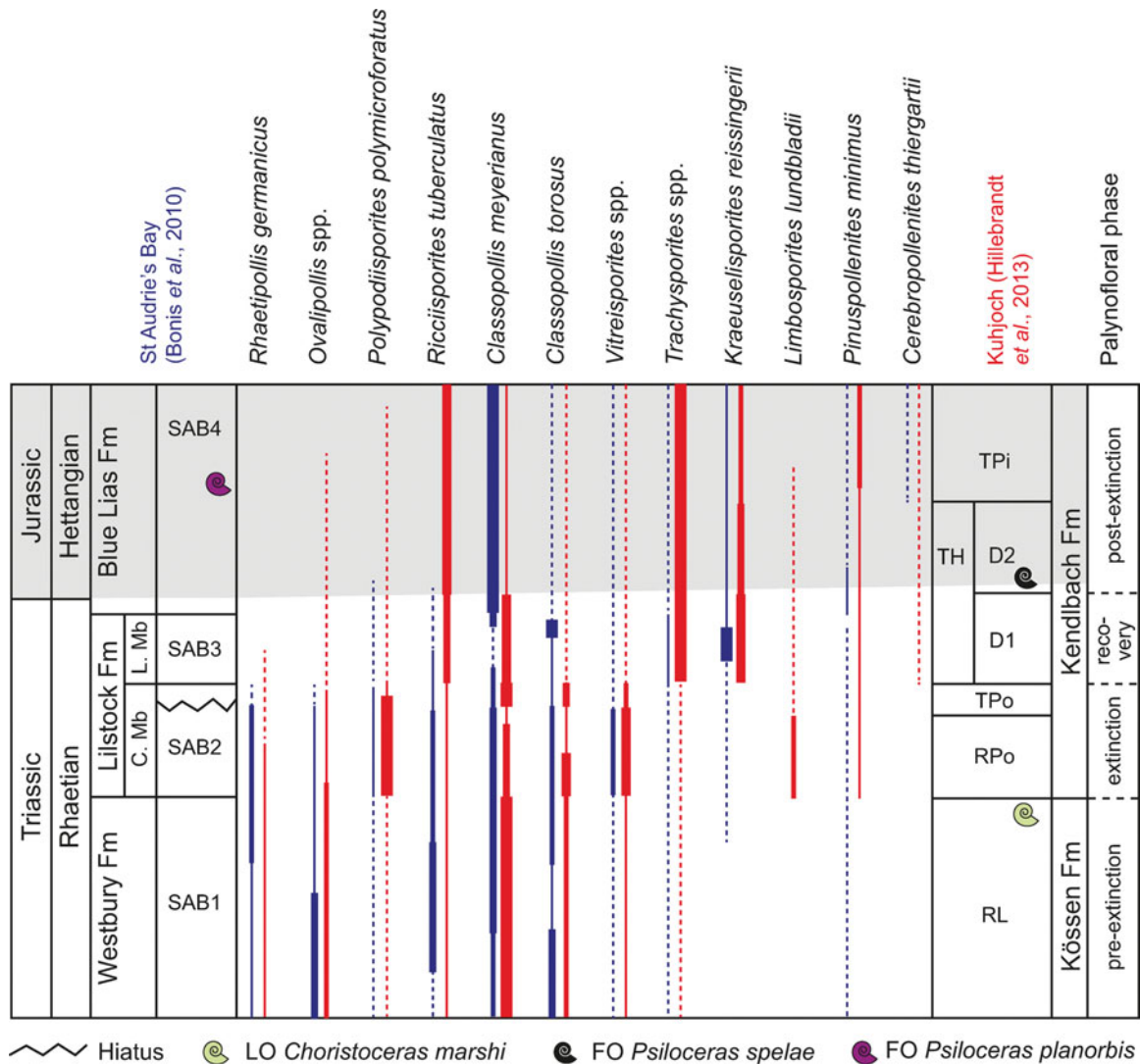


Figure 3. (Colour online) Selected palynological changes across the TJB at St Audrie's Bay, UK (after Bonis *et al.* 2010) in comparison with the GSSP at Kuhjoch, Austria (after Bonis *et al.* 2009; Hillebrandt *et al.* 2013). Grey-shaded area marks the Jurassic. C. Mb. – Cotham Member; L. Mb. – Langport Member.

3.b.2. Extinction palynoflora (Rhaetian)

Assemblages from the base of the Cotham Member (Lilstock Formation) to just below the initial negative C-isotope excursion of Hesselbo *et al.* (2002) were assigned to the SAB2 Zone (Bonis, Ruhl & Kürschner, 2010). In this zone the caytonialean pollen *Vitreisporites bjuvensis* and *V. pallidus* increase in abundance, while there is also an increase in spore abundance, in particular *Polypodiisporites polymicroforatus*, *Deltoidospora* spp. and the osmundaceous fern spores *Baculatisporites* and *Punctatisporites* (Fig. 3). *Classopollis torosus*, as well as *Ovalipollis*, *R. tuberculatus*, *V. bjuvensis* and *R. germanicus* all decrease markedly in the uppermost part of the zone (Bonis, Ruhl & Kürschner, 2010) (Fig. 3). The SAB2 Zone is herein considered to represent the extinction flora; however, it is important to note that the two uppermost samples from the SAB2 Zone were collected above the unconformity (Bonis, Ruhl & Kürschner, 2010), and that, owing to this, a part of the zone may be missing.

3.b.3. Recovery palynoflora (latest Rhaetian)

The succeeding SAB3 Zone, herein considered to represent the recovery flora, encompasses the uppermost Cotham Member and the entire Langport Member of the Lilstock Formation (Bonis, Ruhl & Kürschner, 2010). This zone should possibly be subdivided into two subzones, as the lower part of SAB3 is completely dominated by *C. meyerianus*, while the upper part of the zone contains abundant to dominant amounts of spores, primarily *Kraeuselisporites reissingerii*, *Deltoidospora* spp. and *Acanthotriletes varius*. Cheirolepid pollen assigned to *C. torosus* dominate one sample.

3.b.4. Post-extinction palynoflora (Hettangian)

Psiloceras spelae has so far not been encountered in the TJ-succession from the UK. The oldest psiloceratid ammonite from the UK is *Psiloceras erugatum* (bed 8, Doniford Bay) closely followed by *Psiloceras planorbis* (bed 13, St Audrie's Bay) (Bloos & Page, 2000;

Hillebrandt *et al.* 2013) (Fig. 3). Based on the succession of ammonites, Hillebrandt *et al.* (2013) suggested that the TJB should be placed within the lowest few metres of the Blue Lias Formation. This formation was assigned to palynological SAB4 Zone by Bonis, Ruhl & Kürschner (2010); hence, the TJB is placed within the lowermost part of this zone (Fig. 3). However, the shift in the palynofloras from SAB3 to SAB4 is very abrupt with a dramatic increase in the cheirolepid pollen *C. meyerianus* at the base of the Blue Lias Formation, perhaps owing to an unconformity. The post-extinction palynoflora, as expressed in SAB4, is completely dominated by *C. meyerianus*, with only minor abundance peaks in the pinaceous pollen *Pinuspollenites minimus* and *Kraeuselisporites reissingerii* (Bonis, Ruhl & Kürschner, 2010) (Fig. 3).

Bonis, Ruhl & Kürschner (2010) illustrated the ranges of 34 (but not all registered) spore and pollen taxa in the St Audrie's Bay succession. Twelve of these, including *Ovalipollis*, *Rhaetipollis germanicus*, *Lunatisporites rhaeticus*, *R. tuberculatus* and *P. polymicroforatus*, disappear over the TJB interval, thus indicating a 35% turnover.

3.c. Stenlille

The general palynological changes across the siliciclastic marine to shallow marine TJB succession at Stenlille in the Danish Basin were presented in Lindström *et al.* (2012), and a detailed palynological study will be presented elsewhere, but a brief review of the palynological succession is presented herein. A selection of representative Rhaetian–Hettangian spores and pollen from the Danish Basin are shown in Figure 4. The Stenlille palynozonation is correlated with that of Kuhjoch (Fig. 5) and St Audrie's Bay (Fig. 6), and the palynofloral changes over the extinction interval are further summarized in Table 2.

3.c.1. Pre-extinction palynoflora (Rhaetian)

The pre-extinction assemblages from the Gassum Formation and lowermost part (black shales at MFS7 by Nielsen, 2003) of the Fjerritslev Formation are dominated by almost equal amounts of cheirolepidiacean pollen (predominantly *Classopollis torosus* with common *C. meyerianus* and *Granuloperculatipollis rudis*) and *Perinopollenites elatoides*. *Ricciisporites tuberculatus* is common to abundant, but rarely dominant. *Deltoidospora* spp. and *Vitreisporites* spp. are common. Typical Rhaetian taxa such as *Ovalipollis* spp., *Rhaetipollis germanicus*, *Limbosporites lundbladii* and *Lunatisporites rhaeticus* are present. The assemblages are assigned to the informal *Granuloperculatipollis–Classopollis–Perinopollenites* (GCP) Zone (Figs 5, 6; Table 2). This indicates a terrestrial vegetation dominated by probable coastal cheirolepids that could tolerate dryer conditions, with moisture-loving taxodiacean/cupressacean conifers, caytonialean pteridosperms and tree ferns growing in forested mires on

the lowlands behind the coastal zone (Petersen & Lindström, 2012). Towards the top of the interval all cheirolepid pollen decline in abundance. *Perinopollenites elatoides* persists in high abundances towards the top of the zone, while *Deltoidospora* increases in abundance (Figs 5, 6).

3.c.2. Extinction palynoflora (Rhaetian)

There is a marked change to the *Polypodiisporites–Ricciisporites–Deltoidospora* (PRD) Zone, which encompasses the grey siltstone interval of the Fjerritslev Formation (Lindström *et al.* 2012). The extinction palynoflora is dominated by the tree fern spores *Deltoidospora* spp., schizaeacean fern spores *P. polymicroforatus* and *R. tuberculatus* (Figs 5, 6). Except for *Ricciisporites*, pollen of gymnosperms are few during this interval. Towards the top of the grey siltstone interval, rare specimens assigned to *Cerebropollenites thiergartii* appear for the first time (Figs 5, 6). There is a successive change in the palynoflora, as first *Deltoidospora*, then *P. polymicroforatus* and *R. tuberculatus* decline markedly in abundance. Instead, sphenopsid spores assigned to *Calamospora tener*, ground fern spores *Conbaculatisporites* spp. and monosulcate pollen increase in abundance within a brief interval referred to the *Calamospora–Conbaculatisporites–Monosulcites* (CCM) Zone (Figs 5, 6).

3.c.3. Recovery palynoflora (latest Rhaetian)

The succeeding interval, the *Perinopollenites–Deltoidospora–Stereisporites* (PDS) Zone, is marked by a massive increase in taxodiacean/cupressacean pollen (*P. elatoides*), and spores of putative tree ferns (*Deltoidospora*) as well as cheirolepid pollen are present but in low abundances (Figs 5, 6). This is interpreted as the onset of recovery of the terrestrial ecosystem after the end-Triassic event (Lindström *et al.* 2012).

3.c.4. Post-extinction palynoflora (Hettangian)

The succeeding *Deltoidospora–Perinopollenites–Pinuspollenites* (DPPi) Zone is marked by an increase in pinaceous bisaccate pollen assigned to *Pinuspollenites minimus*. The assemblages are otherwise dominated by *Deltoidospora* with a high abundance of *Perinopollenites*, but the latter has markedly decreased in abundance in comparison to the previous interval (Figs 5, 6).

No ammonites have been found in the Stenlille succession, but *Psiloceras planorbis* is present in the Rødby-1 well in Denmark (situated in the northernmost part of the German Basin), which can be correlated with the Stenlille succession based on palynology, C-isotopes and geophysical log-correlation (K. H. Hansen, unpub. M.Sc. thesis, Univ. Copenhagen, 2013). This correlation indicates that the level of the first occurrence (FO) of *Psiloceras planorbis*

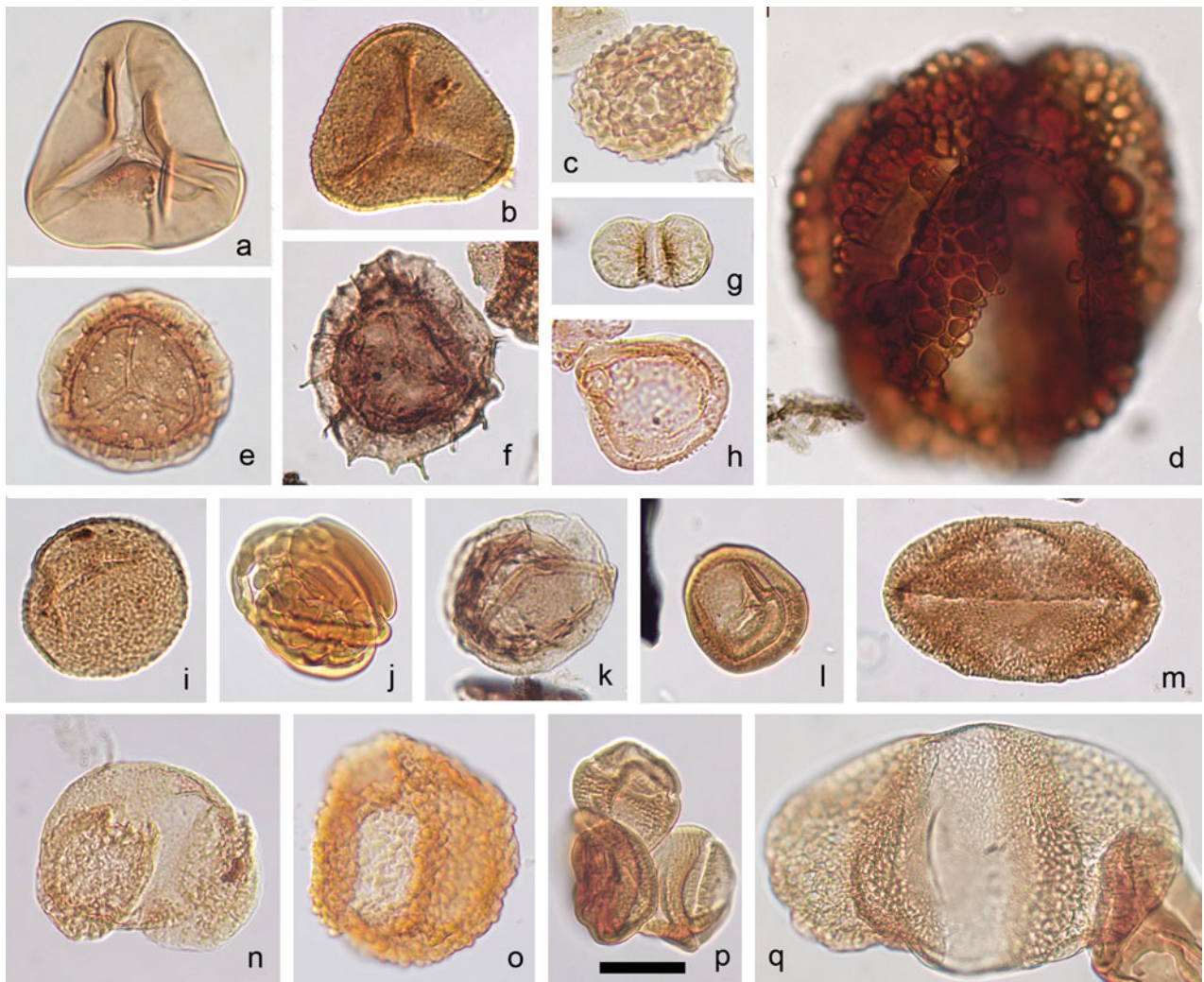


Figure 4. (Colour online) Photographs of some Rhaetian–Hettangian spores and pollen from the Danish Basin. Taxa names are followed by location, sample depth, slide number and England Finder coordinates. Scale bar is 20 μm . (a) *Deltoidospora toralis*, Höllviken-2, 1475.50 m: 4, J29/1. (b) *Trachysporites asper*, Stenlille-4, 1502.38 m: 4, O19/1. (c) *Thymospora ipsviciensis*, Höllviken-2, 1475.50 m: 2, O37/2. (d) *Ricciisporites tuberculatus*, Stenlille-1, 1506.74 m: 4, K24/1. (e) *Limbosporites lundbladii*, Höllviken-2, 1477.95 m: 1, J29/4. (f) *Kraeuselisporites reissingerii*, Stenlille-4, 1511.75 m: 3, N34/2. (g) *Vitreisporites pallidus*, Stenlille-4, 1500.51 m: 3, P42/4. (h) *Granuloperculatiipollis rudis*. (i) *Polypodiisporites polymicroforatus*, finely sculptured specimen, Höllviken-2, 1475.50 m: 4, K28/1. (j) *Rhaetipollis germanicus*, Höllviken-2, 1477.95 m: 1, G32/4. (k) *Perinopollenites elatoides*, Stenlille-4, 1501.42 m: 4, J26/1. (l) *Classopollis meyerianus*, Stenlille-4, 1502.15 m: 4, M31/2. (m) *Ovalipollis ovalis*, Stenlille-4, 1511.75 m: 3, H31/1. (n) *Pinuspollenites minimus*, Höllviken-2, 1372.95 m: 2, T41/4. (o) *Cerebropollenites thiergartii*, Höllviken-2, 1394.94 m: 1, H38/2. (p) *Classopollis torosus*, tetrad, Höllviken-2, 1372.95 m: 2, M30/4. (q) *Alisporites robustus*, Höllviken-2, 1422.2 m: 2, Q24/2.

should be placed within the lowermost part of the succeeding *Perinopollenites*–*Pinuspollenites* (PPI) Zone (Figs 5, 6); hence, the TJB is most probably placed in the lower DPPi Zone (Figs 5, 6). The PPI Zone differs from the previous one in that *Perinopollenites* dominates over *Deltoidospora*, which has declined markedly, while *Pinuspollenites* remains abundant. The DPPi and the PPI zones can both be correlated with the *Pinuspollenites*–*Trachysporites* Zone of Lund (1977) (Figs 5, 6).

Most of the typical Rhaetian taxa decrease markedly in abundance during the RPD Zone or disappear completely. Rare specimens of some taxa are still registered within the PDS and DPPi zones; however, it is difficult to assess whether these represent true occurrences or reworking. As much as 47% of the typical Rhaetian

taxa disappear at the top of the CCM Zone or prior to the PPI Zone (Table 2).

3.d. Astartekløft, Greenland

The palynological succession at Astartekløft was first described by Pedersen & Lund (1980), who divided it into two zones, Zone 1 and 2, which in turn were subdivided into three and two subzones, respectively. Subzones 1L (for lower) and 1M (for middle) equate to the *Lepidopteris* Zone of Harris (1937), while Subzone 1U (for upper) corresponds to the Transition Zone of Harris (1937). Subzones 2L and 2U both represent the *Taumatopteris* Zone (Pedersen & Lund, 1980). The exact stratigraphical positions of the samples analysed by Pedersen & Lund (1980) are difficult to relate to the

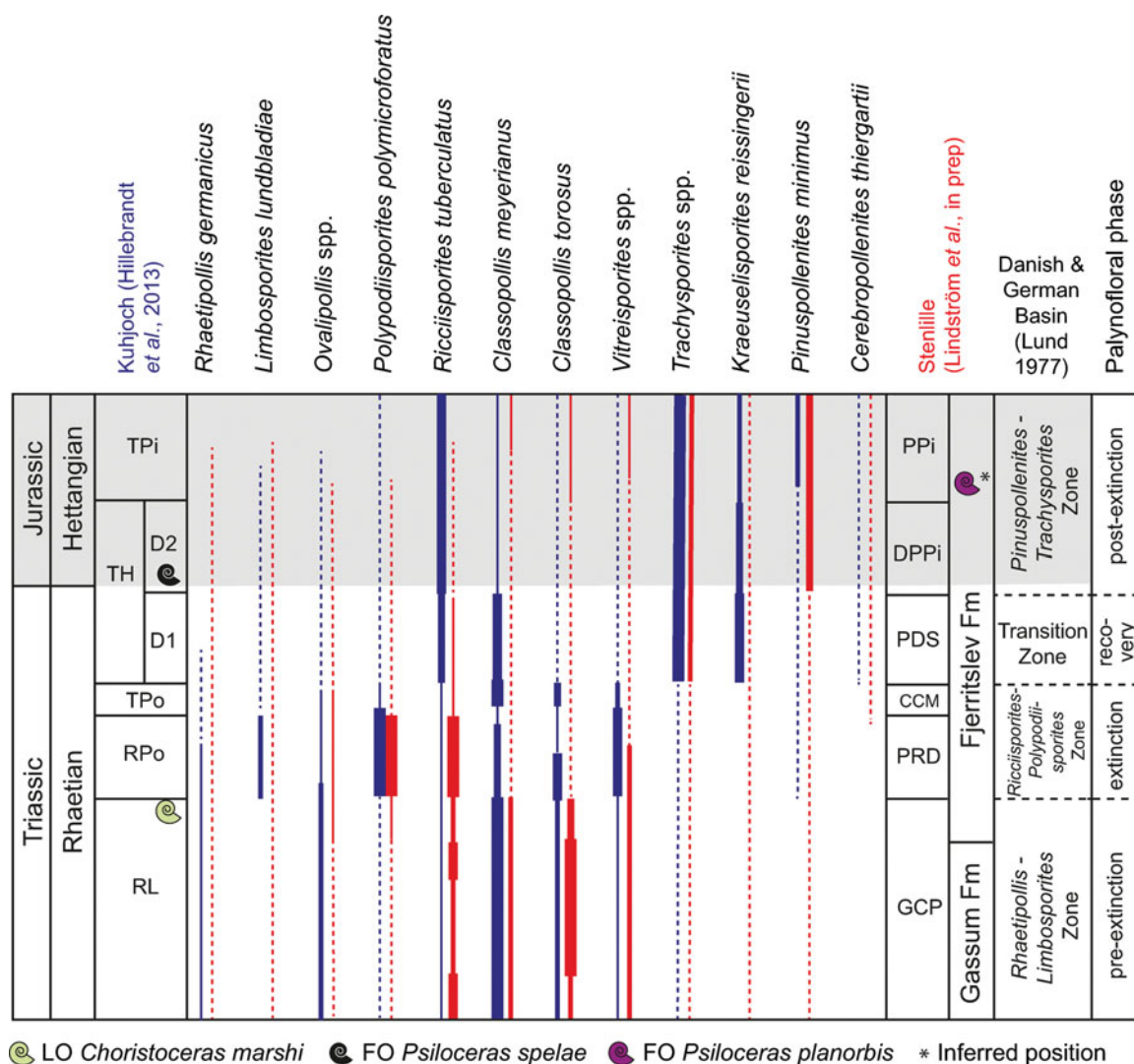


Figure 5. (Colour online) Selected palynological changes across the TJB succession at Stenlille, Denmark (after Lindström *et al.* 2012, this paper) in comparison with the GSSP at Kuhjoch, Austria (after Bonis *et al.* 2009; Hillebrandt *et al.* 2013). Grey-shaded area marks the Jurassic. Inferred position (*) of *Psiloceras planorbis* is from Lindström *et al.* (2015).

later published lithostratigraphic column of Hesselbo *et al.* (2002), but provide valuable information on the palynofloral changes in the succession. In a more recent palynological study of the Astartekløft succession, Mander, Kürschner & McElwain (2010, 2013) restricted their sampling and analyses to the seven macrofossil plant beds. Based on cluster analysis they divided the palynofloral succession into four zones, A1 to A4. Detailed palynological data for the latter can be found in Mander, Kürschner & McElwain (2010, supplementary dataset S2). There are some significant differences between the palynological record of Pedersen & Lund (1980) and that of Mander, Kürschner & McElwain (2013). The most prominent difference is found in the amounts of *Pinuspollenites minimus* registered in the succession. Mander, Kürschner & McElwain (2013) registered common to abundant *P. minimus* throughout the succession, without any significant changes in abundance. According to Pedersen & Lund (1980), *P. minimus* is only sporadically present in subzones 1L

and 1M, not registered in subzones 1U and 2L, and first becomes common in the uppermost assemblage of Subzone 2U. It is not clear whether these differences could be due to different sampling strategies. The palynofloral changes over the extinction interval at Astartekløft are briefly reviewed below (Fig. 7), and are summarized in Table 2.

3.d.1. Pre-extinction palynoflora (Rhaetian)

The lowest zone of Mander, Kürschner & McElwain (2013), A1 (plant beds 1, 1.5 and 2), is dominated by *Ricciisporites tuberculatus* with common osmundaceous fern spores (*Osmundacidites*, *Baculatisporites*, *Punctatisporites*) and lycopphyte spores, mainly *Uvaesporites reissingerii* (Fig. 7). Zone A2 (plant beds 3 and 4) is marked by a distinct increase in the abundance of tree fern spores (*Deltoideospora*), osmundaceous fern spores and lycopphyte spores, primarily *U. reissingerii*, but in the lowermost assemblage

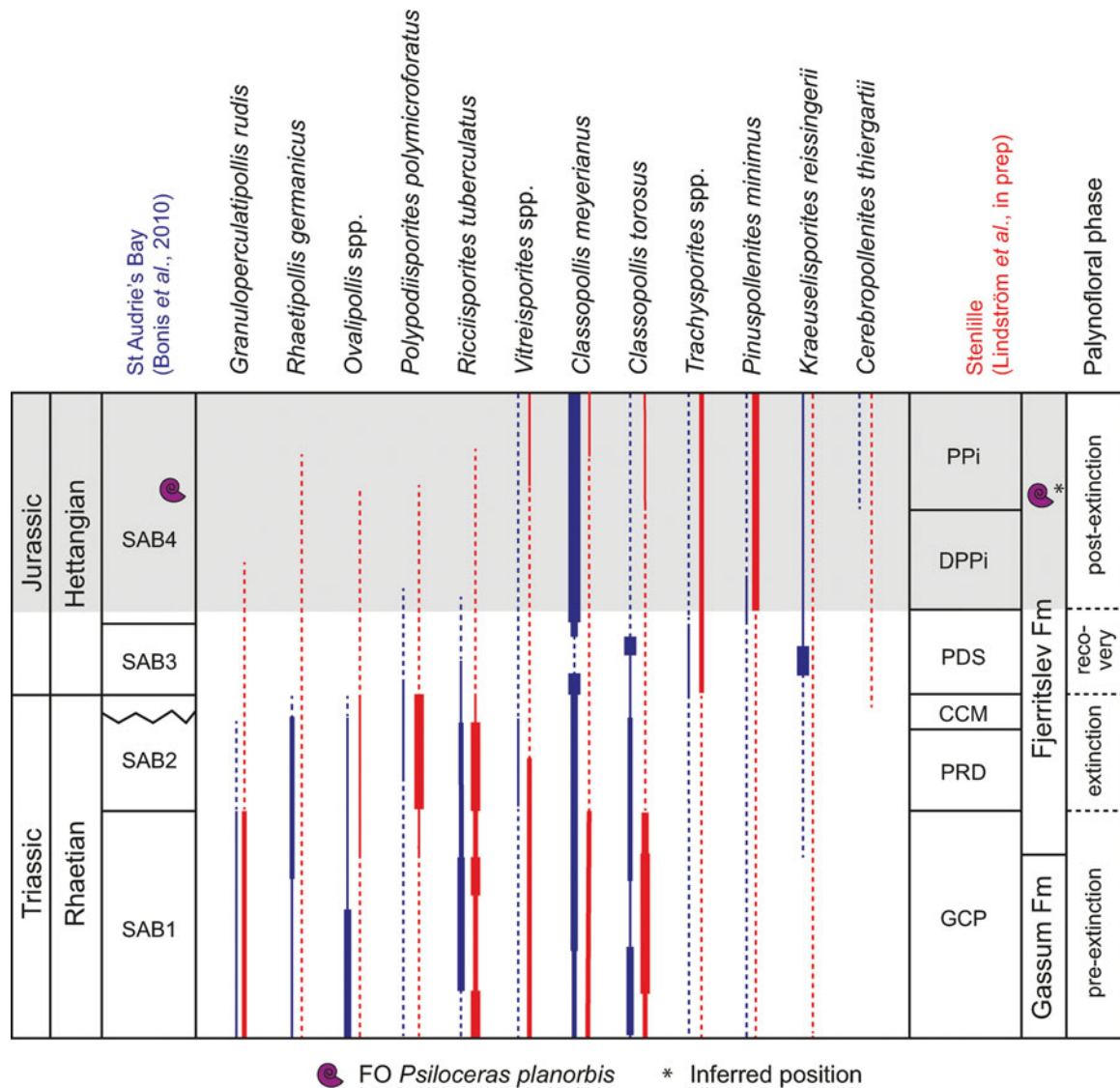


Figure 6. (Colour online) Selected palynological changes across the TJB succession at Stenlille, Denmark (after Lindström *et al.* 2012, this paper) in comparison with that at St Audrie's Bay, UK (after Bonis *et al.* 2010). Grey-shaded area marks the Jurassic. Inferred position (*) of *Psiloceras planorbis* is from Lindström *et al.* (2015).

Limbosporites lundbladii (Fig. 7). However, this lycophyte acme is only characteristic for the lower half of the zone (plant bed 3), with only common *R. tuberculatus*. Zone A1 and the lower part of A2 probably correspond to subzones 1L and 1M of Pedersen & Lund (1980) as they only register that *R. tuberculatus* is common and *U. reissingerii* is present within Subzone 1M. These assemblages are correlated with the *Rhaetipollis–Limbosporites* Zone of Lund (1977) by both Pedersen & Lund (1980) and Mander, Kürschner & McElwain (2013).

3.d.2. Extinction palynoflora (Rhaetian)

Both Pedersen & Lund (1980) and Mander, Kürschner & McElwain (2013) suggested that the *Ricciisporites–Polypodiisporites* Zone is absent in Greenland. However, the dominance of *R. tuberculatus* together with abundant *Deltoidospora* and common osmundacean fern spores in the upper half of Zone A2 (plant

bed 4) may correlate in part to the *Ricciisporites–Polypodiisporites* Zone (Mander, Kürschner & McElwain, 2010, 2013). Zone A3 of Mander, Kürschner & McElwain (2013) represents plant bed 5 and the 'Transition Zone' of Harris (1937) (Fig. 7). It is dominated by *U. reissingerii* and osmundaceous fern spores, mainly *Baculatisporites comaumensis*, while *R. tuberculatus* has decreased in abundance. There are also acmes in the equisetopsid spore *Calamospora tener* and the cupressacean/taxodiacean conifer pollen *Perinopollenites elatoides* in the upper part of the zone. The accessory marker for the base of the Jurassic, *Cerebropollenites thiergartii*, is registered for the first time within this zone (Fig. 7) (Mander, Kürschner & McElwain, 2010, 2013). These results are in accordance with those of Pedersen & Lund (1980), who likewise found common to frequent *U. reissingerii* and common *B. comaumensis* in the 'Transition Zone' (i.e. their Subzone 1U). However, they did not register any minor acmes in *P. elatoides* or *C. tener*. They also

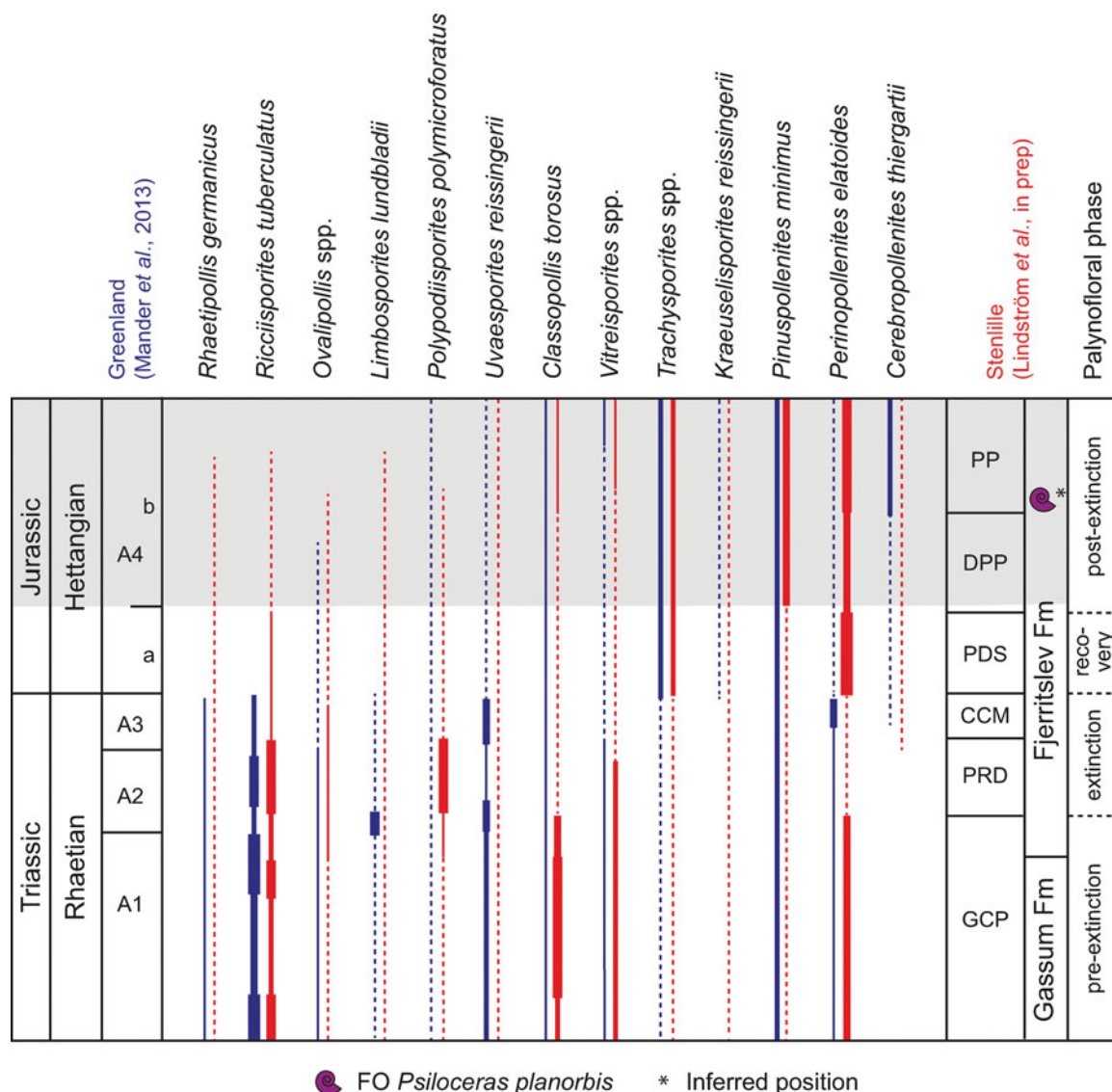


Figure 7. (Colour online) Selected palynological changes across the TJB succession at Astartekløft, Greenland (after Mander et al. 2010, 2013) in comparison with that at Stenlille, Denmark (after Lindström et al. 2012, this paper). Grey-shaded area marks the Jurassic. Inferred position (*) of *Psiloceras planorbis* is from Lindström et al. (2015).

registered a questionable specimen of *C. thiergartii* in their uppermost sample (Pedersen & Lund, 1980).

3.d.3. Recovery palynoflora (latest Rhaetian)

Mander, Kürschner & McElwain (2013) assigned plant beds 6 and 7 to Zone A4, which is characterized by common fern spores assigned to *Trachysporites*, while *U. reissingerii* has decreased markedly and only occurs sporadically. However, there is a major difference in the palynological composition of the two beds, which is why Zone A4 is subdivided into two subzones, a and b, herein. In the lower subzone, A4a (plant bed 6), probable tree fern spores constitute more than 45% of the assemblages. Total loss of *Ricciisporites* and lycophyte spores plus a marked decrease in conifer pollen in Subzone A4a (plant bed 6) indicate loss of tree-bearing vegetation. Instead spores from tree ferns (*Deltoidospora*) and osmundaceous ground ferns dom-

inate completely. The entire Zone A4 is correlated by Mander, Kürschner & McElwain (2013) with the *Pinuspollenites–Trachysporites* Zone of Lund (1977); however, Subzone A4a is herein considered to correlate better with the Transition Zone of Lund (1977).

3.d.4. Post-extinction palynoflora (Hettangian)

In the upper Subzone A4b (plant bed 7) *Deltoidospora* never makes up more than 9% of the assemblages. In addition, Subzone A4b contains higher abundances of corystosperm bisaccate pollen (*Alisporites*), and conifer pollen assigned to *C. thiergartii* is also common, indicating the establishment of forests. This is similar to the subdivision of Zone 2 by Pedersen & Lund (1980) into 2L and 2U, only, as mentioned earlier, *Pinuspollenites* was not registered as common until in their uppermost assemblage of Subzone 2U.

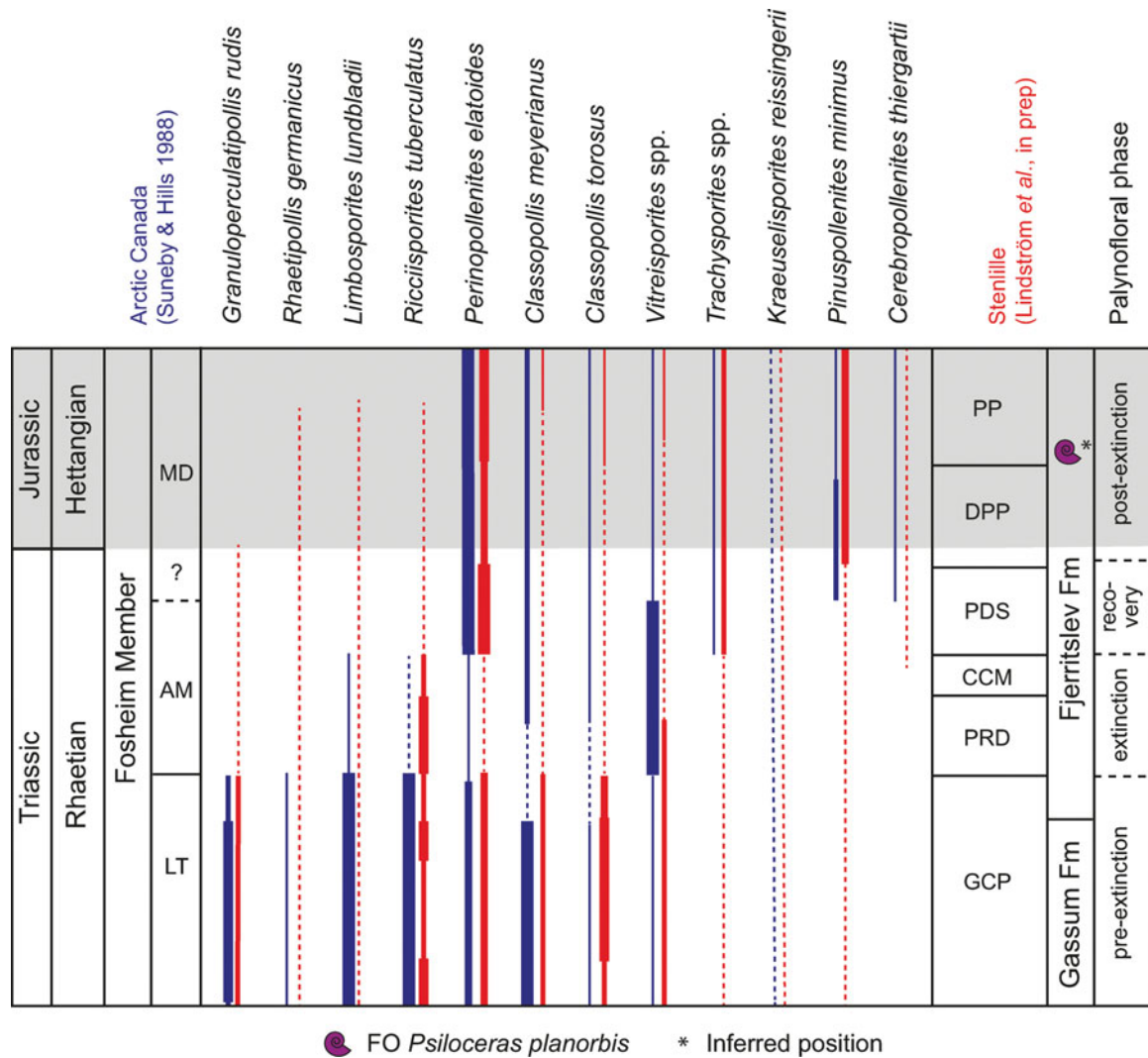


Figure 8. (Colour online) Selected palynological changes across the TJB succession in the Sverdrup Basin, Arctic Canada (after Suneby & Hills, 1988) in comparison with that at Stenlille, Denmark (after Lindström *et al.* 2012, this paper). Grey-shaded area marks the Jurassic. Inferred position (*) of *Psiloceras planorbis* is from Lindström *et al.* (2015).

Mander, Kürschner & McElwain (2013) considered single occurrences of typical Rhaetian taxa in their uppermost assemblages to be reworked. Out of 52 taxa present in the Rhaetian zones A4 and A5, nine disappear within this interval (Mander, Kürschner & McElwain, 2010, supplementary table S2), i.e. a palynofloral turnover of 17%.

3.e. Sverdrup Basin, Arctic Canada

The semi-quantitative palynology of the TJB succession encompassing the Fosheim Member of the Heiberg Formation indicates that the boundary between the Rhaetian and the Hettangian can be distinguished in the Sverdrup Basin (Suneby & Hills, 1988). Rhaetian–Hettangian palynofloras were recognized in two sections: McKinley Bay and Blackwelder Anticline (Suneby & Hills, 1988). The palynofloral changes across the TJB in the Sverdrup Basin are reviewed briefly below (Fig. 8), and are summarized in Table 2.

3.e.1. Pre-extinction palynoflora (Rhaetian)

Typical Rhaetian palynofloras dominated by *Ricciisporites tuberculatus* and *Limbosporites lundbladii*, together with common *Granuloperculatipollis rudis* characterize the *Limbosporites lundbladii* – *Ricciisporites tuberculatus* (LT) Biozone of Suneby & Hills (1988). Cheirolepid pollen decreases upwards. The cupressacean/taxodiacean pollen *Perinopollenites elatoides* is consistently present but never dominant (Table 2).

3.e.2. Extinction palynoflora (Rhaetian)

The succeeding *Retitriletes austroclavatidites* – *Chasmatosporites magnolioides* (AM) Biozone covers strata that are often barren of palynomorphs (Suneby & Hills, 1988). The few productive samples of this zone contain many of the species typical for the previous zone; however, these usually persist in lower abundances and disappear at the top of the zone including e.g.

R. tuberculatus, *L. lundbladii*, *Cingulizonates rhaeticus* and many other typical Rhaetian elements (Suneby & Hills, 1988). Assemblages from McKinley Bay are dominated by lycophyte spores (*Limbosporites*) and abundant tree fern spores, and common caytonialean bisaccates (*Vitreisporites*). The lower and middle AM Biozone is herein considered to represent the extinction flora, in which lycophytes dominate together with common tree ferns and caytonialean seed ferns (Fig. 8; Table 2).

3.e.3. Recovery palynoflora (latest Rhaetian)

The upper AM Biozone (known from Blackwelder Anticline) is dominated by caytonialean bisaccate pollen assigned to *Vitreisporites*. Tree ferns (*Deltoidospora*, *Dictyophyllidites*) and ginkgoalean/cycadalean monolete pollen assigned to *Chasmatosporites apertus* are common to abundant. The uppermost part of the AM Biozone is marked by a major increase in cupressacean/taxodiacean pollen (*Perinopollenites elatoides*) and abundant equisetalean spores (*Calamospora*) (Fig. 8).

3.e.4. Post-extinction palynoflora (Hettangian)

Assemblages of the Upper Fosheim Member are assigned a Hettangian to Sinemurian age, and are referred to the *Cerebropollenites macroverrucosus* – *Pityosporites divulgatus* (MD) Biozone (Suneby & Hills, 1988). This zone is characterized by common to abundant bisaccate pollen, and increased abundances of *Chasmatosporites*, *Perinopollenites* and osmundaceous fern spores (*Baculatisporites*, *Osmundacidites*). *Cerebropollenites thiergartii* appears at the base of the zone in one locality, but at the other two localities it first appears in the middle of the zone together with *C. macroverrucosus*, a NW European marker for the Hettangian–Sinemurian boundary (Dybckjær, 1991). Only the lowermost part of the MD Biozone, below the FO of *C. macroverrucosus*, is herein considered to represent Hettangian strata (Fig. 8).

Forty-two out of 79 of the taxa present within the Rhaetian LT and AM biozones in the McKinley Bay section are not present in the overlying MD Biozone, indicating a turnover of 53% (Table 2). In the Blackwelder Anticline section the similar turnover is 38% (23/61 taxa) (data from Suneby & Hills, 1988).

3.f. New Zealand

In New Zealand identification of the TJB is based on marine invertebrates, and is probably located near the FO of the bivalve *Otapiria marshalli*, while the first psiloceratid ammonites correlated with the Pacificum Horizon appear higher up in the Aratauran succession (Stevens, 2012). Late Triassic to Early Jurassic palynofloras from New Zealand have been described by De Jersey & Raine (1990) and Zhang & Grant-

Mackie (2001), and were recently reviewed in De Jersey & McKellar (2013) and Bomfleur *et al.* (2014). As an example, the palynofloral succession at Kawhia coast encompasses the Ngutunui, Arataura, Rewarewa and Arawhero formations and includes palynofloras assigned to assemblages II to IV by Zhang & Grant-Mackie (2001), and these are reviewed briefly below (Fig. 9), and the palynofloral changes are summarized in Table 2.

3.f.1. Pre-extinction palynoflora (Rhaetian)

Rhaetian (Otapirian) pre-extinction palynofloras occur in Assemblage II from the lower Ngutunui Formation and are dominated by the lycophyte spores *Densoisporites psilatus* and *Uvaesporites* spp., and corystosperm pollen assigned to *Alisporites* (Zhang & Grant-Mackie, 2001).

3.f.2. Extinction palynoflora (Rhaetian)

The boundary between assemblages II and III is marked by a dramatic decline in the abundance of the characteristic Triassic taxa, *Alisporites* spp. and *Densoisporites psilatus*, from 60% in Assemblage II to 5% in Assemblage III (De Jersey & McKellar, 2013). At Kawhia coast productive samples representing each zone are separated by *c.* 14 m of strata. Assemblage III commonly contains high abundances of spores, in particular bryophyte spores (*Polycingulatisporites*, *Rogalskiasporites*, *Stereisporites*), and laevigate trilete spores that may represent tree ferns (*Deltoidospora* and *Dictyophyllidites*) are also common (Zhang & Grant-Mackie, 2001). The lower boundary of Assemblage III is further marked by the FOs of *Toripustulatisporites hokonuiensis* and *Retitriletes semimuris*. At Kawhia coast this biozone can possibly be subdivided into an older and a younger subzone, herein referred to subzones A and B, respectively. Subzone A encompasses palynofloras recovered from strata of the upper Ngutunui Formation that still contain the Triassic bivalve *Otapiria dissimilis* (Akikuni *et al.* 2010). Hence, the earliest part of Assemblage III in New Zealand and its eastern Australian equivalent the *Toripustulatisporites hokonuiensis* Assemblage Zone of De Jersey & McKellar (2013; see Section 3.g below) is actually late Rhaetian in age. The lowermost assemblage in Subzone A is dominated by bryophyte and tree fern spores, and abundant osmundaceous fern spores. Corystosperms have decreased in abundance and are partly replaced by caytonialeans. It may represent the extinction palynoflora, but there is also a possibility that the extinction palynoflora is not represented owing to the low sampling resolution across the formation boundary.

3.f.3. Recovery palynoflora (latest Rhaetian)

The upper assemblage of Subzone A is dominated by bryophyte spores. Corystosperms, tree ferns and osmundaceous ferns are abundant. The caytonialean

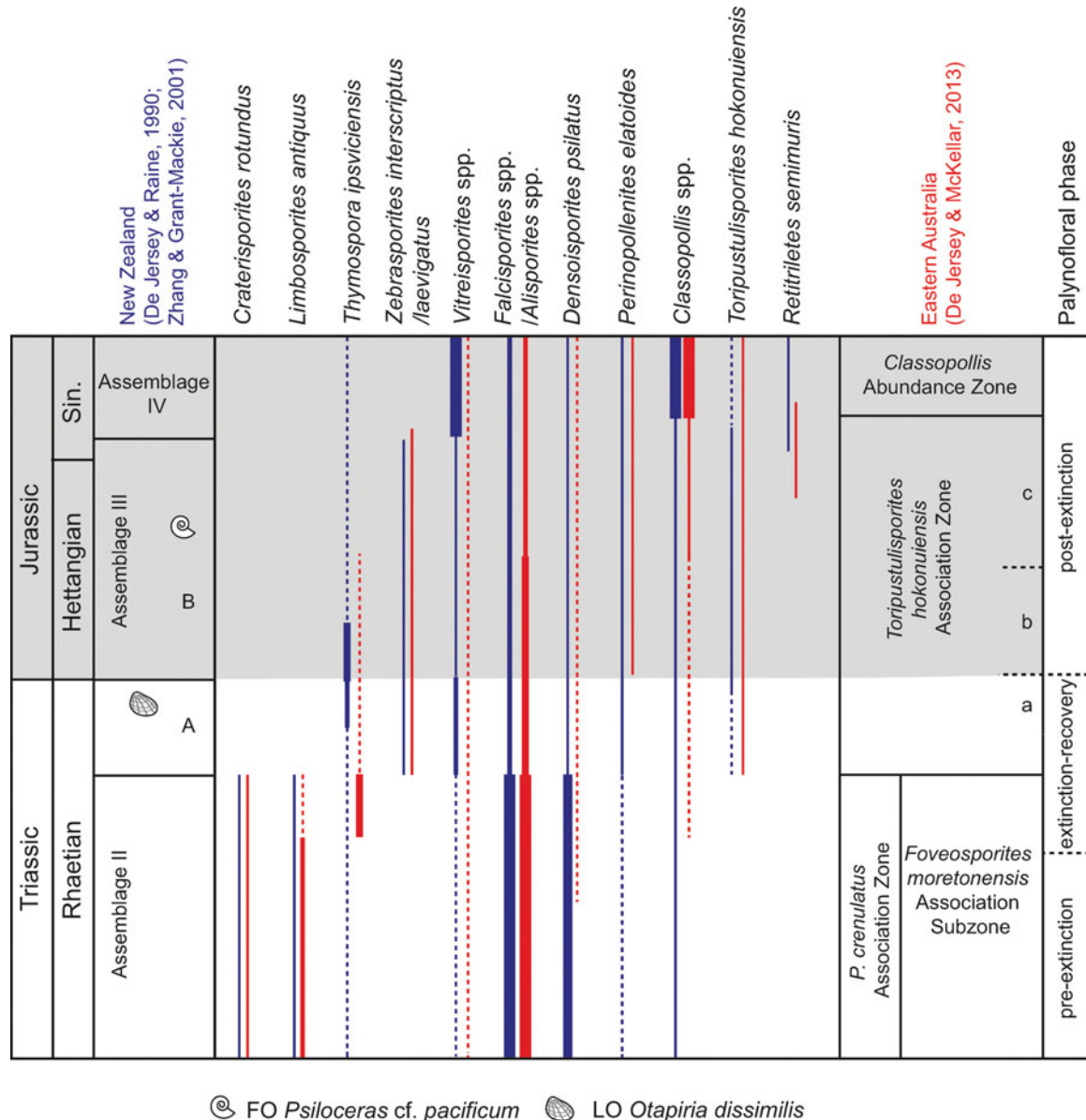


Figure 9. (Colour online) Selected palynological changes across the TJB succession at SW Kawhia, New Zealand (after Zhang & Grant-Mackie, 2001) in comparison with that from Queensland, Australia (after De Jersey, 1971; De Jersey & McKellar, 2013). Grey-shaded area marks the Jurassic. Sin. – Sinemurian.

bisaccate pollen *Vitreisporites pallidus* (as *V. signatus*) and marattialean fern spores are common.

3.f.4. Post-extinction palynoflora (Hettangian–Sinemurian)

The typical early Hettangian bivalve *Otapiria marshalli* has not been recovered from the Kawhia coast section, and because early Sinemurian ammonites have been recovered from the lower part of the Arataura Formation at Kawhia coast the Hettangian succession is either condensed or parts of it are missing (Akikuni *et al.* 2010; Stevens, 2012). However, *O. marshalli* has been recovered from the Awakino Gorge section, where it occurs some 23 m above the last occurrence of *O. dissimilis* (Akikuni *et al.* 2010). Hence, the younger Subzone B of Assemblage III (recognized herein) en-

compasses only one Hettangian palyno-sample, while the remaining two are early Sinemurian in age (Zhang & Grant-Mackie, 2001; Akikuni *et al.* 2010). In Subzone B caytonialean bisaccates (*Vitreisporites*) are present but in low numbers, while osmundaceous fern spores assigned to *Osmundacidites* and *Baculatisporites* are more abundant. The Sinemurian Assemblage IV from the Rewarewa and Arawhero formations is characterized by abundant cheirolepid pollen assigned to *Classopollis* and an increasing abundance of caytonialean *Vitreisporites* (Zhang & Grant-Mackie, 2001).

Only 6 of 39 taxa, i.e. 15%, disappear at the boundary between assemblages II and III, but the major change is in the composition of the palynoflora (Table 2).

3.g. Queensland, eastern Australia

De Jersey & McKellar (2013) presented new palynological data across the TJB in the terrestrial succession of the Clarence-Moreton Basin in southeastern Queensland. TJB palynology of this area has previously been presented in De Jersey (1971). The recognition of the boundary was based on the first appearances of five taxa that are also present in the independently dated (by ammonites and bivalves) TJB succession in New Zealand (see Section 3.f above). Like the New Zealand record, the eastern Australian record is of low resolution, but still displays some major and characteristic changes across the TJB (Table 2), and these are reviewed briefly below (Fig. 9). A selection of Rhaetian–Hettangian spores and pollen from Australia are shown in Figure 10.

3.g.1. Pre-extinction flora (Rhaetian)

Pre-extinction assemblages from the Raceview Formation were assigned to the *Polycingulatisporites crenulatus* Zone, which is characterized by a dominance of corystospermous bisaccate pollen assigned to *Alisporites/Falcisporites*. From the study by De Jersey (1971) it is evident that there are palynofloral changes within the uppermost Raceview Formation. In the cored GSQ Ipswich 4 well, assemblages from this formation are first dominated by bisaccate pollen with common lycophyte spore *Limbosporites antiquus*.

3.g.2. Extinction palynoflora (Rhaetian)

Towards the top of the Raceview Formation and the *P. crenulatus* Association Zone there is a slight decrease in bisaccates. *Limbosporites antiquus* becomes rare while instead marattialean (*Thymospora ipsviciensis*) and osmundaceous (*Osmundacidites*) fern spores become abundant (De Jersey, 1971). De Jersey & McKellar (2013) showed rare *Limbosporites antiquus* and abundant *Thymospora ipsviciensis* in their Raceview Formation samples from GSQ Ipswich 25. These assemblages may represent the extinction palynoflora; however, studies with a higher resolution are needed to assess the palynofloral changes across the formation boundary.

3.g.3. Recovery palynoflora (latest Rhaetian)

Assemblages from the succeeding Ripley Road Sandstone are assigned to the *Toripustulatisporites hokonuiensis* Association Zone, the lower limit of which is marked by the FO of the nominate taxon (De Jersey & McKellar, 2013). In the lowermost part of this zone, corystospermous bisaccate pollen (*Alisporites*) continues to dominate, although it has declined slightly in abundance compared to the previous zone. Further, osmundaceous fern spores, probable tree fern spores and bryophyte spores are common to abundant. This lowermost part of the *Toripustulatisporites*

hokonuiensis Association Zone, herein referred to as subzone a, is correlated with Assemblage IIIa in New Zealand, which suggests a latest Rhaetian age for this part of the zone (Fig. 9). It may represent the recovery palynoflora.

3.g.4. Post-extinction palynoflora (Hettangian–Sinemurian)

Alisporites continues to dominate in the middle part of the *Toripustulatisporites hokonuiensis* Association Zone, but there is also a marked increase in monosulcate pollen (*Ginkgo*, cycads). The middle part of the zone, herein referred to as subzone b, is further marked by the incoming of *Perinopollenites elatoides*. In the upper part of the zone, here referred to as subzone c (Fig. 8), cheirolepidiacean conifer pollen becomes common while there is a marked decrease in corystosperm pollen. In the succeeding Sinemurian *Classopollis* Abundance Zone, cheirolepids and corystosperm pollen dominate, together with common monosulcate pollen and osmundaceous fern spores (data from De Jersey & McKellar, 2013).

In general, the eastern Australian TJB record is similar to that of New Zealand; however, in the latter, spores generally dominate the palynofloras during Rhaetian and early Hettangian times, while the former contains much higher abundances of pollen. De Jersey & McKellar (2013) correlated their assemblages from the *P. crenulatus* Zone with the uppermost Assemblage II of New Zealand (Zhang & Grant-Mackie, 2001) based on the co-occurrence of *Limbosporites antiquus*, *Densoisporites psilatus* and *Classopollis meyerianus*. One interesting trend observed in both the New Zealand and the eastern Australian records is an abundance of marattialean fern spores, which post-dates the Rhaetian lycophyte abundance. This lycophyte abundance is not apparent in the record of De Jersey & McKellar (2013), but is evident in that of De Jersey (1971) where sampling probably includes older strata.

The palynological records of GSQ Ipswich 25 (De Jersey & McKellar, 2013) and GSQ Ipswich 3 and 4 (De Jersey, 1971) both indicate that 19% of the typical Rhaetian palynoflora disappears across the TJB.

3.h. Northern Carnarvon Basin, Western Australia

In the Carnarvon Basin, Western Australia, the TJB transition has been sampled in two cored wells, North Rankin 6 and Keast 2 (Backhouse & Balme, 2002). The sedimentary succession belongs to the upper Brigadier Formation and is without any apparent unconformity, but the sharp shift from Rhaetian to Hettangian palynofloras suggest there may be a part of the section missing (Backhouse & Balme, 2002). The characteristics of the palynofloral changes across the TJB in Western Australia are summarized in Table 2, and are briefly reviewed below (Fig. 11).

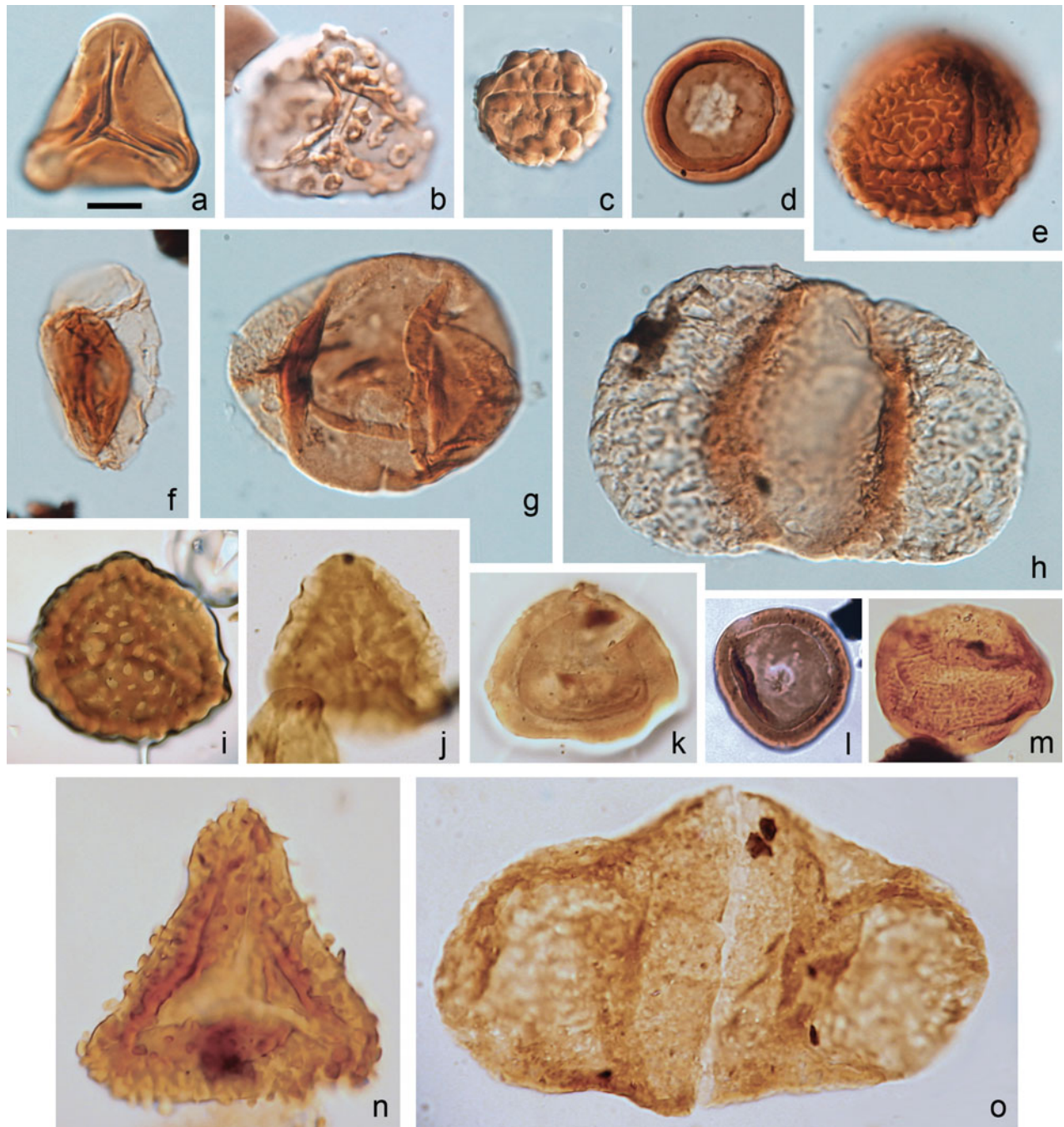


Figure 10. (Colour online) Photographs of selected Rhaetian–Hettangian spores and pollen from the southern hemisphere. (a–h) Carnarvon Basin, Western Australia (from Backhouse & Balme, 2002; reproduced with permission of MRIWA). (i–o) Queensland, eastern Australia (from De Jersey & McKellar, 2013; reproduced with permission of the State of Queensland). Taxa names are followed by location, sample depth, slide number and (for the Queensland specimens) England Finder coordinates. Scale bar is 10 μ m. (a) *Dictyophyllidites harrisii*, Dailey-1, 1400 m. (b) *Craterisporites rotundus*, North Rankin-5, 2925.76 m. (c) *Thymospora ipsviensis*, Dailey-1, 1400 m. (d) *Classopollis meyerianus*, Keast-2, 3015.44 m. (e) *Leschikisporis* sp. B, Keast-2, 3016.15 m. (f) *Perinopollenites elatoides*, Keast-2, 3015.44 m. (g) *Ashmoripollis reducta*, Dockerell-2, 2999.85 m. (h) *Falcisporites australis*, North Rankin-5, 2922.29 m. (i) *Limbosporites antiquus*, GSQ Ipswich 25, 313.43.39 m, S9622, S43/0. (j) *Zebrasporites interscriptus*, GSQ Ipswich 1, 147.39 m, S1780, D39/1. (k) *Densoisporites psilatus*, GSQ Ipswich 25, 320.61 m, S9619, M36/3. (l) *Classopollis meyerianus*, GSQ Ipswich 25, 88.68 m, 1630874, L27/2. (m) *Classopollis* sp. cf. *C. chateaunovi*, GSQ Ipswich 25, 78.68 m, A 480/1, K33/0. (n) *Toripustulatisporites hokonuiensis*, GSQ Ipswich 1, 117.19 m, S1819, O37/4. (o) *Falcisporites australis*, DME Ipswich NS 272, 368.14 m, S2135, L35/0.

3.h.1. Pre-extinction palynoflora (Rhaetian)

Rhaetian assemblages belong to the *Ashmoripollis reducta* Zone, which is dominated by the corytospermous pollen *Falcisporites australis*, the probable gym-

nospermous pollen *Ashmoripollis reducta*, as well as common fern spores assigned to *Thymospora ipsviensis*. The zone is subdivided into three subzones: the lower, the middle and the upper subzone, in ascending order (Backhouse & Balme, 2002). The lower and the

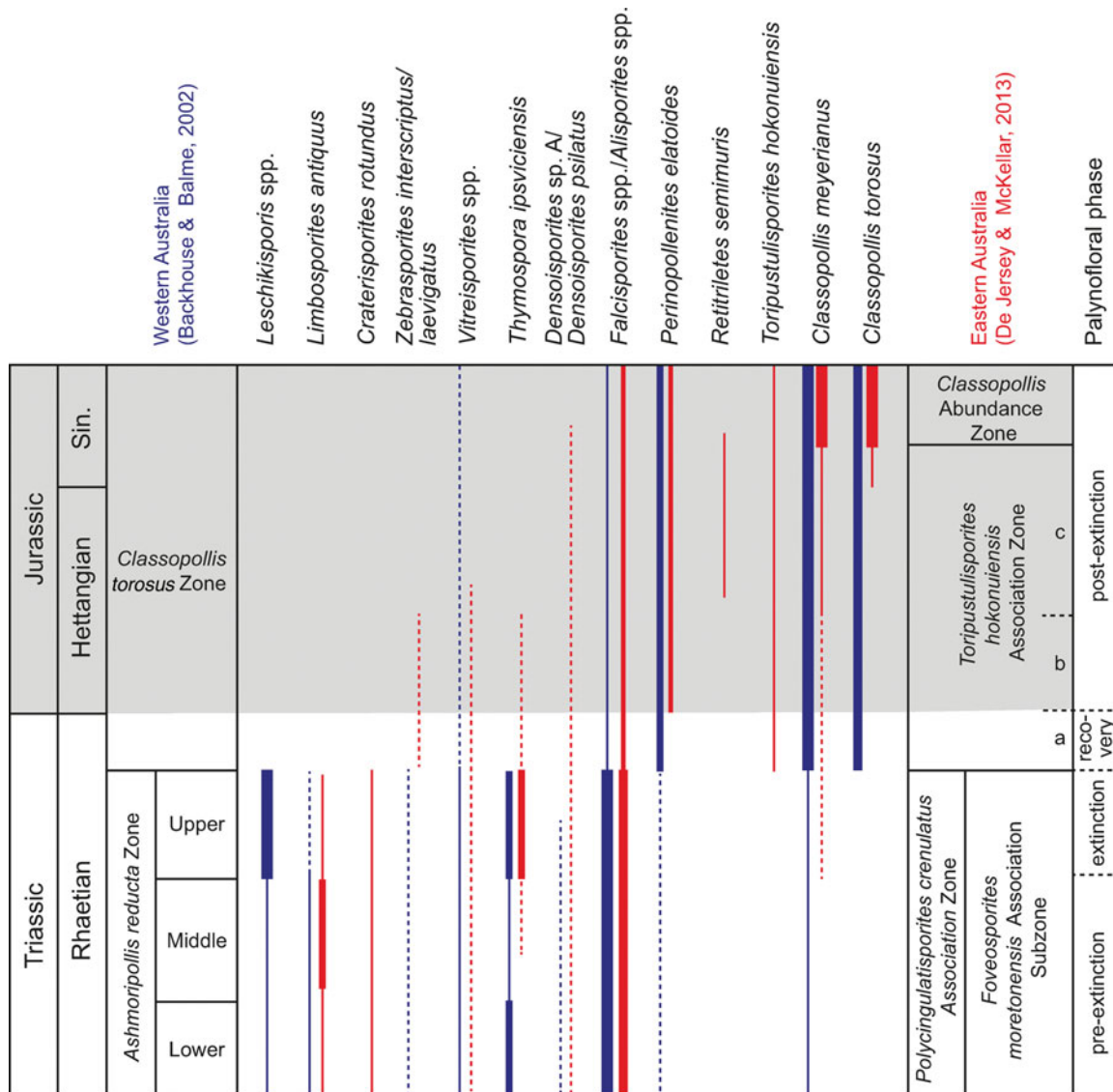


Figure 11. (Colour online) Selected palynological changes across the TJB succession in the Carnarvon Basin, Western Australia (after Backhouse & Balme, 2002) in comparison with that from Queensland, Australia (after De Jersey, 1971; De Jersey & McKellar, 2013). Grey-shaded area marks the Jurassic. Sin. – Sinemurian.

middle subzones are dominated by crustosperm seed ferns, with common to abundant tree fern spores, and are herein considered to represent the pre-extinction palynoflora.

3.h.2. Extinction palynoflora (Rhaetian)

Crustosperms continue to dominate in the upper subzone of the *Ashmoripollis reducta* Zone, and ferns, especially marattialean and osmundaceous ferns and tree ferns, are also abundant, and schizaeacean fern spores are common. During the upper subzone, 12 out of 48 taxa disappear, and an additional 25 taxa disappear at the top of the zone (Backhouse & Balme, 2002). Most typical Rhaetian taxa that disappeared at the TJB in Western Australia were ferns or fern allies, e.g. schizaeacean, polypodiacean and marattialean fern spores (*Leschikisporis*, *Polypodiisporites*, *Thymospora*). Some of the undescribed forms

of *Leschikisporis* reported by Backhouse & Balme (2002) are morphologically similar, possibly even in part identical to variants of *Polypodiisporites polymicroforatus* from the northern hemisphere.

3.h.3. Recovery palynoflora (latest Rhaetian)

The boundary between the *Ashmoripollis reducta* Zone and the succeeding *Classopollis torosus* Zone is marked by a simultaneous abrupt decline in *Falcisporites* spp. and an increase in *Classopollis*, as well as a marked loss of taxa (Backhouse & Balme, 2002). The probable gymnosperm pollen *Ashmoripollis reducta* and polypodiacean/marattialean fern spores assigned to *Thymospora ipsviciensis*, which were common constituents during the upper *Ashmoripollis reducta* Zone, disappear along with many other fern spores. It should be noted that in these wells the typical Rhaetian dinoflagellate cysts *Rhaetogonyaulax rhaetica* and

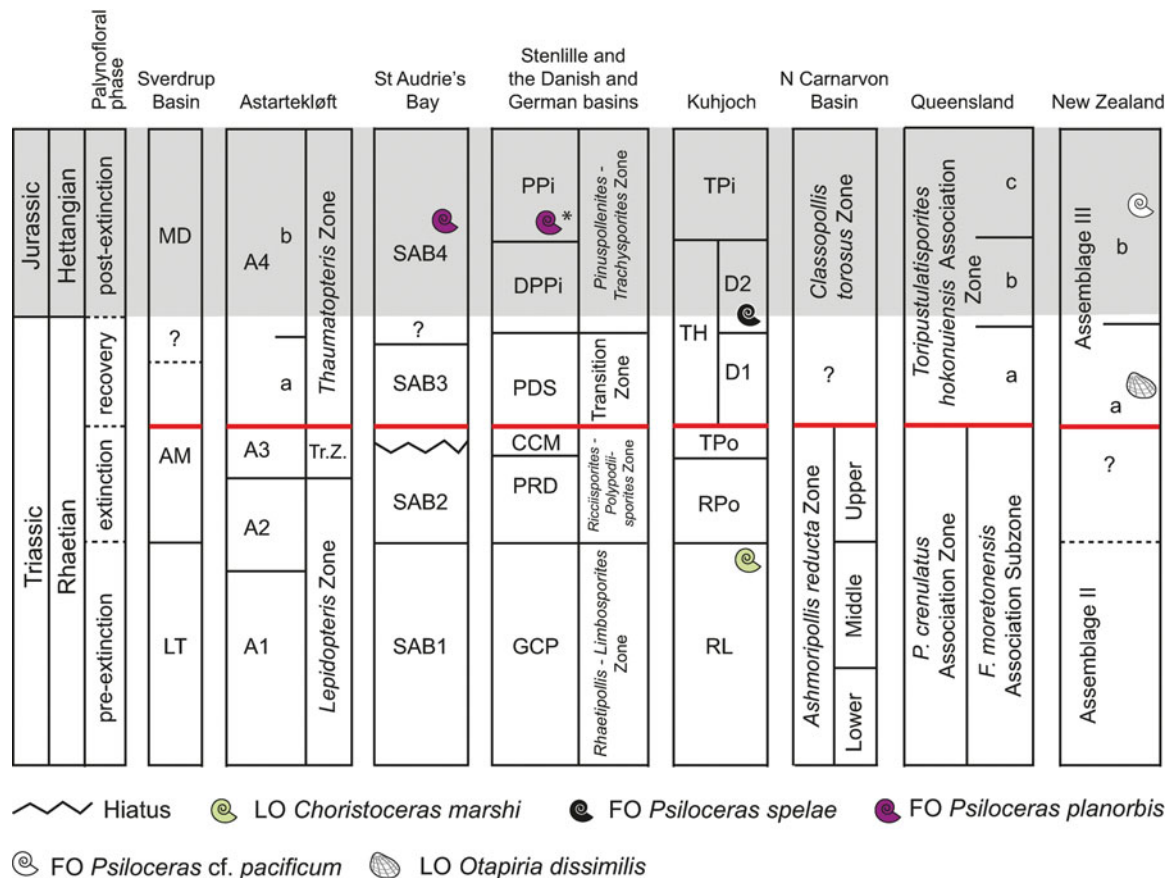


Figure 12. (Colour online) Global correlation of the palynofloral successions reviewed herein (Figs 2, 3, 5–9, 11). Grey-shaded area marks the Jurassic. Inferred position (*) of *Psiloceras planorbis* is from Lindström *et al.* (2015). Tr. Z. – Transition Zone; thick (red) horizontal line – top of extinction interval.

Suessia swabiana have their last records within the upper *A. reducta* Zone and at the top of it, respectively. Backhouse & Balme (2002) discussed the possibility of a hiatus at the TJB in their wells, even though there is no obvious unconformity present. This probably means that there is no record of the recovery palynoflora in this succession.

3.h.4. Post-extinction palynoflora (Hettangian–Sinemurian)

The post-extinction palynofloras are dominated by the cheirolepidiacean pollen *Classopollis meyerianus* and *C. torosus*, together with common cupressacean/taxodiacean pollen (*Perinopollenites elatoides*) and fern spores assigned to *Dictyophyllidites harrisii* (Backhouse & Balme, 2002).

The continued presence of the dinoflagellate cyst *Dapcodinium priscum* in the succeeding *Classopollis torosus* Zone (Backhouse & Balme, 2002) indicates that the *Classopollis torosus* Zone in these wells is not younger than early Sinemurian (Riding, Mantle & Backhouse, 2010).

Only 11 of the 48 taxa present in latest Rhaetian time are also present within the post-extinction palynoflora, which gives a turnover of 77% (data from Backhouse & Balme, 2002).

4. Discussion

4.a. Correlation

All the herein reviewed successions can be correlated fairly well palynologically in each hemisphere. The palynological correlations are supported by independent dating with marine invertebrates (Fig. 12). In particular, the GSSP locality Kuhjoch provides several useful markers for correlation, both marine and non-marine ones (Hillebrandt *et al.* 2013). A compilation of late Rhaetian–Hettangian important biotic marine and terrestrial events in NW Europe is presented in Figure 13. This shows that the extinction and recovery palynofloras identified herein correlate with the marine extinction interval, dead zone and initial recovery (Mander, Twitchett & Benton, 2008) (Fig. 13). In the southern hemisphere, the New Zealand succession plays an important role in long-distance correlations across the former southeastern parts of Pangaea by the combination of marine invertebrate faunas (Akikuni *et al.* 2010; Stevens, 2012) and palynology (Zhang & Grant-Mackie, 2001). Correlation of the New Zealand palynoflora, supported by marine invertebrate markers, allows recognition of the extinction interval and palynoflora also in the southern hemisphere (Fig. 12).

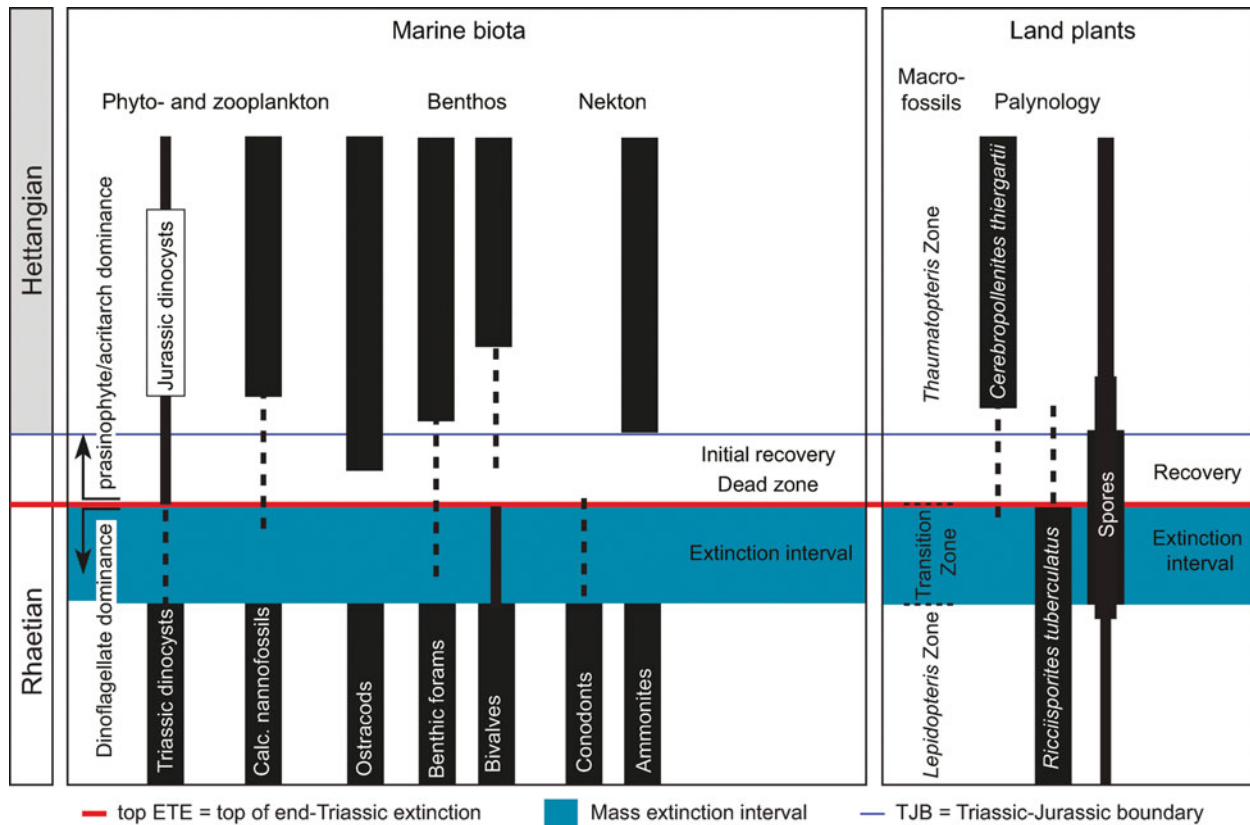


Figure 13. (Colour online) Comparison of NW European marine biotic events with terrestrial plant events. The marine biotic events are compiled from Hillebrandt *et al.* (2013), Mander *et al.* (2008), Clémence *et al.* (2010a, b) and Richoz *et al.* (2012). The terrestrial plant events are compiled from McElwain *et al.* (2007), Lund (1977) and data from the palynological sites reviewed herein.

4.b. Taxonomic and ecological severity

At all sites terrestrial ecosystem changes occur primarily prior to the TJB (Table 2; Fig. 12). Although, the taxonomic and ecological severity of these changes varies between areas, it appears that all areas experienced ecosystem disturbances during late Rhaetian time. These disturbances led to re-organization of the vegetation with major changes in abundances and loss of taxa as a consequence. The loss of taxa occurs over a time interval that primarily encompasses the marine extinction interval. As an example, at Kuhjoch an initial major change in the terrestrial ecosystem, from conifer-dominated to fern- and caytonialean-dominated vegetation, more or less coincides with the first marine extinction pulse (Hillebrandt *et al.* 2013). The marine extinctions continue while this new flora dominated by schizaeacean ferns, caytonialean seed ferns and tree ferns proliferates (Fig. 2; Table 2). Similarly, during this interval some typical Rhaetian taxa disappear completely, e.g. *Rhaetipollis germanicus*, and probably also *Triancoraesporites reticulatus*. Others decrease markedly in abundance, e.g. *Lunatisporites rhaeticus*, *Polypodiisporites polymicroforatus*, *Limboisporites lundbladii*, *Cingulizonates rhaeticus* and *Ovalipollis* spp., and are found as sporadic rare occurrences in the succeeding zones before disappearing completely. It can be difficult to assess whether such lingering taxa are *in situ* or simply reworked, as reworking of older material can seemingly extend the ranges of taxa. How-

ever, this pattern is similar in almost all of the herein reviewed sites. It is especially pronounced in the Danish (Lindström *et al.* 2012; Petersen & Lindström, 2012) and German basins (Lund, 1977; van de Schootbrugge *et al.* 2009; Heunisch *et al.* 2010).

The western Australian palynological succession is an exception, with its staggering 73 % of the Rhaetian taxa ending abruptly within or at the top of the upper *Ashmoripollis reducta* Zone (Backhouse & Balme, 2002). However, although Backhouse & Balme (2002) discussed the possibility of an unconformity separating the upper *Ashmoripollis reducta* Zone from the *Classopollis torosus* Zone, the taxonomic turnover is still a fact. Correlation between the western Australian TJB record and that of eastern Australia, and especially the abundance pattern of cheirolepid pollen (*Classopollis*), definitely suggests that there is an unconformity (Fig. 11). However, an earlier onset of *Classopollis*-abundance in Western Australia may have been an effect of palaeogeography and palaeoclimatic zones. At the TJB, the Northern Carnarvon Basin was situated approximately 30° S of the Equator, while south-central Queensland was located much further south, at c. 55° S (Fig. 1). The lowest taxonomic losses are registered in New Zealand (15%), Queensland (19%) and Greenland (17%) (Table 2), all of which are sites located in high latitudes (Fig. 1). The Sverdrup Basin was situated further north than Astartekløft, at c. 55° N (Fig. 1), but there the taxonomic losses are estimated at

38–52 % depending on locality (Suneby & Hills, 1988). In the Greenland case, the low spore-pollen turnover may be an effect of a change in fluvial regime as plant bed 5 (TJB of Mander, Kürschner & McElwain, 2010, 2013) is sharply overlain by a succession of upward-fining fluvial units, conglomerates and coarse-grained sandstones, reflecting strong erosion and badland development (Steinhorsdottir *et al.* 2012), indicating that reworking of Rhaetian strata could be an issue at this site.

The ecological impact for each site is estimated according to McGhee *et al.* (2004) and shown in Table 2. Sites categorized as ecological impact Category I are the Sverdrup Basin, Stenlille, Kuhjoch and Northern Carnarvon Basin. At these sites the pre- and post-extinction palynofloras are fundamentally different in composition and dominance, and have also experienced major losses of palynofloral elements from the pre-extinction palynoflora (Table 2). The remaining sites (Astartekløft, St Audrie's Bay, SE Queensland and New Zealand) are all placed in ecological impact Category II, Subcategory IIa following McGhee *et al.* (2004). Here, the existent ecosystems are disrupted, but recover and are not replaced post-extinction, but the disruption has also produced permanent losses of major ecosystem components. The New Zealand and SE Queensland sites are those that are least affected by the reorganizations (Table 2).

4.c. The northern hemisphere *Ricciisporites* enigma

The enigmatic fused pollen-tetrad *Ricciisporites tuberculatus* is often common to abundant in Rhaetian strata in parts of the northern hemisphere, and a well-known casualty of the ETE. In the Rhaetian it is a prominent component of the five northern hemisphere sites reviewed herein. It has also been registered in Rhaetian successions in France (Rauscher *et al.* 1995), the Netherlands (Herngreen & De Boer, 1974), Germany (Achilles, 1981; Heunisch *et al.* 2010), Luxembourg (Schuurman, 1977), Poland (Orłowska-Zwolinska, 1983; Pieńkowski, Niedźwiedzki & Waksmundzka, 2012), Hungary (Götz *et al.* 2009), Slovakia (Ruckwied & Götz, 2009), Georgia (Yaroshenko, 2007) and China (Yong *et al.* 2003); is absent or sporadic in Spain (Barrón *et al.* 2006; Gómez, Goy & Barrón, 2007); and appears to be absent from Italy (Galli *et al.* 2007) and sites further to the west and south. It basically appears to be confined to mid-latitude (30° N to 60° N) locations. So far, the affinity of the parent plant remains unknown, but its exine ultrastructure most closely resembles that of gymnosperms (Pedersen, 1983) and clearly shows that it is constructed as a permanent pollen tetrad (Mander *et al.* 2012). Kürschner, Mander & McElwain (2014) speculated that it was a herbaceous gymnosperm and that this would explain the absence of macrofossil remains. In most sites *Ricciisporites* disappears at the top of the extinction interval or decreases dramatically in abundance and only lingers on for a short interval in the succeeding zones (Figs 2, 3, 5–8).

The Austrian records differ from this pattern. The continued high abundance of *Ricciisporites tuberculatus* in the Austrian sections (Kürschner, Bonis & Krystyn, 2007; Bonis, Kürschner & Krystyn, 2009) is remarkable, and may suggest that this area may have acted as a refugia for a population of the parent plant taxon after the biotic crisis.

4.d. A global spore spike?

A global 'fern spike' or 'spore spike' has been described from palynofloral successions as a consequence of the environmental changes after the Cretaceous–Palaeogene (KPg) event (see e.g. Schulte *et al.* 2010 and references therein). Fowell & Olsen (1993) described a spore spike from the TJB succession of the Newark Basin, and as this coincided with an iridium anomaly, Olsen *et al.* (2002) suggested an impact scenario as a cause for the ETE. Both the location of the TJB based on the palynofloral turnover and the associated fern spike below the CAMP basalts in the eastern North American basins (Fowell & Olsen, 1993) was questioned by Cirilli *et al.* (2009), who found Rhaetian palynomorphs in sediments above the oldest basalts. In NW Europe late Rhaetian proliferation of ferns and fern allies during the extinction interval was described by van de Schootbrugge *et al.* (2009) and interpreted as establishment of pioneering vegetation after widespread deforestation caused by volcanic degassing from the CAMP. The deforestation scenario as well as the fern spike was questioned by Bonis & Kürschner (2012), the latter primarily because there is no stratigraphic consensus that the Newark spore spike and the NW European one are contemporaneous. However, regardless of the age of the Newark spore spike, it is evident from the sites reviewed herein that in contrast to most pre-extinction palynofloras, spores from ferns (tree ferns, schizaeacean, osmundacean and marattialean ferns), bryophytes and lycophytes became dominant components of the extinction palynofloras (Table 2), indicating that the environmental changes that took place generally favoured spore-producing plants over seed plants on both hemispheres. However, there is no indication of a global short-lived spore spike such as those reported from the KPg event (Schulte *et al.* 2010). In many sites spore-producing plants continue to play a dominant part in the recovery and post-extinction vegetation after the ETE (Table 2), and latitudinal differences are evident.

Very few of the typical Rhaetian to Hettangian spore taxa are considered to be xerophytic (Table 1), which means increased relative amounts of spores could be interpreted as signalling wetter conditions. When analysing the total relative abundances of spores in TJB records from the northern hemisphere it is important to remember that many authors have classified *Ricciisporites tuberculatus* as a bryophyte spore instead of a gymnosperm pollen. In this review this applies to the records from Greenland (Mander, Kürschner &

Table 3. Palaeolatitudinal position and total relative spore abundance for each site within each palynofloral phase (except Sverdrup Basin for which only semi-quantitative data exist)

Locality	Palaeo-latitude	Pre-extinction palynoflora	Extinction palynoflora	Recovery palynoflora	Post-extinction palynoflora
Sverdrup Basin, Arctic Canada	55° N	Only semi-quantitative data	Only semi-quantitative data	Only semi-quantitative data	Only semi-quantitative data
Astartekløft, Greenland	50° N	10–55%. Later 25–80%	50–80%	85–95%	60–85%
Stenlille, Denmark	45° N	>20%. Later 30–50%	30–70%	10–50%	30–70%. Later 20–30%.
Kuhjoch, Austria	30° N	<5%	30–70%	50–70%	50–70%
St Audrie's Bay, UK	30° N	<5%	5–60%. Fluctuating strongly	20–95%. Fluctuating strongly	<5%, rarely higher
N Carnarvon Basin, Western Australia	30° S	20–30%	25–55%	Possibly missing in section	<20%
SE Queensland, Australia	55° S	35%	35–75%	35%	15–25%
New Zealand	70° S	65–70%	85–90%	50–65%	40–55%

McElwain, 2010, 2013), St Audrie's Bay (Bonis, Ruhl & Kürschner, 2010) and Kuhjoch (Bonis, Kürschner & Krystyn, 2009; Hillebrandt *et al.* 2013), and the relative abundances of spores have been adjusted accordingly herein.

In pre-extinction palynofloras, those from high latitudes, i.e. New Zealand and Greenland, contain the highest relative abundances of spores (Table 3), which may then indicate more humid conditions in these areas. The records from St Audrie's Bay and Kuhjoch display the lowest relative abundances of spores, <5% (Table 3), suggesting terrestrial conditions near these two areas were not humid enough to sustain a vegetation rich in spore-producing plants.

It should be noted that in both the Astartekløft and Stenlille records the relative amounts of spores begin to increase just prior to the extinction interval (Table 3). This may be interpreted as an onset of more humid conditions in these two areas, at least. In Greenland, the total relative amount of spores was exceptionally high during the recovery phase (up to 95%; data from Mander, Kürschner & McElwain, 2010), and still continued to be dominating in the post-extinction palynoflora, up to 85%. At Stenlille, spores make up as much as 50% to 70%, respectively, of the recovery and initial post-extinction palynofloras, but later decrease to relative abundances around below 30% of the post-extinction assemblages (Lindström *et al.* 2012). This is in accordance with decreasing stomatal and canopy transpiration data for both ginkgos and Bennettitales already in plant bed 4 and continuing through plant beds 5 and 6, i.e. the extinction and recovery intervals, with transpiration first returning to pre-extinction levels in plant beds 7 and 8 (Steinhorsdottir *et al.* 2012). This is interpreted as a response in the plants to increased pCO_2 in the atmosphere (Steinhorsdottir *et al.* 2012). Suppressed transpiration may lead to increased runoff because surplus precipitation is not taken up by plant roots, and could potentially explain the increased total relative abundance of spores from plant bed 4

and upsection (Table 3), as increased soil water availability due to ponding and/or waterlogging may favour spore-producing plants (Steinhorsdottir *et al.* 2012). The increased runoff hypothesis is further supported by sedimentological evidence of the fluvial regime shifting from low-energy sluggish rivers to high-energy braided rivers (Steinhorsdottir *et al.* 2012). However, although slightly decreased, the spore abundance remains high also in plant bed 7 (post-extinction phase) even though transpiration had returned to pre-extinction levels.

Regionally widespread wildfires may also have affected the vegetation pattern through deforestation, increased erosion and badland development. Increased frequency of wildfires at the TJB has been reported from Poland, Greenland and the Danish Basin (Marynowski & Simoneit, 2009; Belcher *et al.* 2010; Petersen & Lindström, 2012).

However, the total relative abundance of spores increased dramatically at all sites during the extinction interval, and the increase is most dramatic in St Audrie's Bay and Kuhjoch (Table 3). At St Audrie's Bay, spores fluctuated markedly over the extinction and recovery interval, with peaks between 60% and 90%, with higher values within the recovery interval, but decrease to generally below 5% in the post-extinction palynoflora (Bonis, Ruhl & Kürschner, 2010). At Kuhjoch, the relative abundance of spores increases over the extinction interval, and fluctuates between *c.* 50% and 70%, in both the recovery and post-extinction palynofloras (Bonis, Kürschner & Krystyn, 2009; Hillebrandt *et al.* 2013). A global first-order sea-level rise at the base of the Jurassic, especially prominent in European marine and marginal successions, but also evident in successions from the Panthalassa Ocean (Hallam, 1997; Hallam & Wignall, 1999, 2000), may have affected the ground-water levels in coastal areas during earliest Jurassic time, favouring wet-loving vegetation. However, this does not explain the proliferation of spores during latest Rhaetian time when a short-lived but

Table 4. Palaeolatitudinal position (according to Fig. 1) and total relative abundance of cheirolepid pollen (*Geopollis*, *Granuloperculatipollis*, *Classopollis*)

Locality	Palaeo-latitude	Pre-extinction palynoflora	Extinction palynoflora	Recovery palynoflora	Post-extinction palynoflora
Sverdrup Basin, Arctic Canada*	55° N	Very common at base of zone. Very rare in upper part.	Rare	Common	Common
Astartekløft, Greenland	50° N	<2 %	<2 %	<2 %	<2 %
Stenlille, Denmark	45° N	10–60 %, mostly 20–40 %	<5 %	<10 %	<10 %.
Kuhjoch, Austria	30° N	45–95 %	15–40 %	90 % to 10 %, declining upwards	1–10 %
St Audrie's Bay, UK	30° N	15–90 %. Fluctuating strongly	15–75 %. Fluctuating strongly	5–95 %. Fluctuating strongly	75–100 %.
N Carnarvon Basin, Western Australia	30° S	<1 %	<1 %	Possibly missing in section	70 %
SE Queensland, Australia	55° S	<1 %	<1 %	<1 %	5–35 %
New Zealand	70° S	0 %	<2 %	<2 %	5–20 %

* For Sverdrup Basin the semi-quantitative data is from the Blackwelder Anticline (Suneby & Hills, 1988).

significant sea-level fall is registered (Hallam & Wignall, 2000).

4.e. Cheirolepidiacean conifers pre- and post-extinction

In general, cheirolepids are considered to have been xerophytic, i.e. drought tolerant, shrubs or trees (Vakhrameev, 1991), that were wind pollinated plants which produced large amounts of pollen (Ziaja, 2006). Vakhrameev (1991) suggested that low abundances of *Classopollis* would indicate temperate conditions, high abundances subtropical or tropical conditions, and ultrahigh abundances arid conditions. However, at least some cheirolepids appear to have been adapted to coastal environments (Batten, 1974; Alvin, 1982; Abbink, 1998). Abbink (1998) classified *Classopollis* as a coastal element signalling warm conditions. While some cheirolepids were coastal plants that could tolerate both seasonal droughts and a saline influence on the environment (Francis, 1984), others probably preferred less harsh environments. Mussard, Ducazeaux & Cugny (1997) found some differences in preferred environment for *Classopollis torosus* and *C. meyerianus*, suggesting that the latter probably preferred wetter environments. Based on principal components analysis ordination diagrams of assemblages from Austria and St Audrie's Bay, Bonis & Kürschner (2012) suggested that these two cheirolepidacean taxa have slightly different environmental preferences, with *C. meyerianus* being a more warm-loving taxon than *C. torosus*. Bonis & Kürschner (2012) suggested that *C. torosus* could tolerate lower temperatures, as it is present in the Greenland records (Pedersen & Lund, 1980; Mander, Kürschner & McElwain, 2010). However, according to Suneby & Hills (1988), *C. meyerianus* was much more common in the more northerly TJB succession of the Sverdrup Basin record than *C. torosus*. In Upper Jurassic semi-arid to arid successions *C. torosus* is sometimes overwhelmingly dominant (Batten, 1996), indicating that the differences in ecological preference

between *C. torosus* and *C. meyerianus* may not only be reliant on temperature.

In NW Europe, cheirolepid conifers were often a prominent part of the Rhaetian vegetation (Table 2). At Kuhjoch and Stenlille, cheirolepids suffered severe temporary decline during the extinction interval (Table 4). At Kuhjoch and St Audrie's Bay, cheirolepids were still occasionally prominent during the extinction interval (Figs 2, 3), and this has also been registered in Mingolsheim from southern Germany (van de Schootbrugge *et al.* 2009). At least two cheirolepid pollen taxa are known to have gone extinct at the ETE, *Granuloperculatipollis rudis* and *Geopollis zwolinskai* (see e.g. Lund, 1977). At Kuhjoch and Stenlille, cheirolepids returned after the extinction interval, but generally in much lower abundances than during the pre-extinction phase, down to around 10 % (Table 4; Lindström *et al.* 2012), while at St Audrie's Bay cheirolepids, and especially *C. torosus*, became totally dominating, often constituting almost monotypic assemblages (Bonis, Ruhl & Kürschner, 2010) (Table 4). In the interior of Pangaea (Newark Basin) *Classopollis* occurred sporadically in high abundances below the inferred TJB, but first became consistently dominant during Hettangian time (Whiteside *et al.* 2007).

In the southern hemisphere, in Australia, *C. meyerianus* first becomes a consistent presence from the base of the Rhaetian (Backhouse & Balme, 2002). Cheirolepids do not become prominent palynofloral elements until Early Jurassic time (Hettangian to Sinemurian) when *C. torosus* becomes dominant and widespread in Australia and New Zealand (Table 2). It is also known to be dominant in the Sinemurian of Antarctica (Bomfleur *et al.* 2014).

Considering the total relative spore abundance data of the reviewed sites (Table 3), it seems plausible that increased humid conditions during the extinction, and often also recovery interval, were unfavourable to cheirolepid conifers. Some cheirolepids, like the mother plants of *Granuloperculatipollis rudis* and

Geopollis zwolinskae, suffered extinction at the ETE, while other taxa were successful survivors that continued to thrive during the remainder of the Mesozoic Era. However, many spore-producing plants, especially ferns, can be opportunistic and act as pioneers and invaders of newly formed habitats (Page, 2002). This was especially true prior to the diversification of angiosperms. Many ferns can tolerate stressful habitats, including low-light conditions and low-nutrient soils, as long as they have enough water available to reproduce (Page, 2002). Hence, the increased total abundances of spores in both hemispheres during the extinction (and recovery) interval may only reflect environmental or climatic conditions that were less favourable for seed plants, as suggested by van de Schootbrugge *et al.* (2009). Such conditions may include expected effects of CAMP volcanism: acid rain and terrestrial soil and freshwater acidification due to volcanic sulfur dioxide emissions and fluctuating ultraviolet flux due to ozone depletion caused by halogens and halocarbon compounds, in combination with drastically changing climatic conditions due to greenhouse gas emissions. Such a scenario is similar to that recently proposed by Black *et al.* (2014) for the terrestrial end-Permian mass extinction.

5. Conclusions

This review shows that during latest Rhaetian time the terrestrial vegetation on both the northern and southern hemispheres was affected by environmental changes which led to taxonomic losses and the re-organization of the flora in all areas. Palynostratigraphic correlations between the different sites, supported by independent invertebrate fossil events (when present), show that the extinction and recovery phases occurred prior to the TJB. Extirpation/extinction of typical Rhaetian taxa generally follows a pattern of major decline in abundance during the extinction phase, followed by rare continued occurrences (lingering) during the recovery phase and sometimes even into the post-extinction phase. From a palynological point of view it can be difficult to assess whether these lingering occurrences are *in situ* or reworked.

Most of the typical Rhaetian or Triassic spore and pollen taxa that go extinct during the ETE are so far not known from *in situ* occurrences in reproductive structures of fossil plant taxa. The highest taxonomic turnover is registered in the N Carnarvon Basin, where 73% of the Rhaetian taxa disappear at the top of the extinction interval. Sverdrup Basin and Stenlille also exhibit high turnovers, with 38–52% and 47% of the Rhaetian taxa disappearing in each area, respectively.

The Rhaetian pre-extinction palynofloras of all sites appear to have been relatively stable. The northern hemisphere sites were dominated by either the enigmatic gymnosperm tetrad *Ricciisporites tuberculatus*, cupressacean/taxodiacean (*Perinopollenites elatoides*) pollen and/or cheirolepidiacean conifer pollen (*Granuloperculatipollis*, *Classopollis*). Total relative spore

abundances indicate drier environments in the low-latitude sites (Kuhjoch, St Audrie's Bay), while spore abundances appear to increase further north and south. The relative abundances of cheirolepid conifer pollen seem to corroborate this pattern, although they are during the pre-extinction phase only abundant in the northern hemisphere, where they are most abundant in the low-latitude sites (Kuhjoch and St Audrie's Bay) and seem to decrease in abundance towards the north. *Ricciisporites tuberculatus* appears to be confined to the northern hemisphere and more or less to the mid-latitude belt. In the southern hemisphere, the pre-extinction palynofloras were dominated by crustosperm pollen and lycophyte and/or bryophyte spores. The xerophytic crustosperms are most abundant in the N Carnarvon Basin, while lycophyte spores increase in abundance towards the south.

The extinction phase is characterized at all sites by major to moderate structural changes in the palynofloral composition. From an ecological perspective, the palynofloral changes at the Sverdrup Basin, Stenlille, Kuhjoch and Carnarvon Basin, are classified as ecological severity Category I of McGhee *et al.* (2004). At these sites the pre- and post-extinction palynofloras are fundamentally different in composition and dominance, and major losses of palynofloral elements from the pre-extinction palynoflora occurred. The remaining sites are placed in Subcategory IIa of McGhee *et al.* (2004), because their pre-extinction ecosystems are disrupted, and although this produced permanent losses of major ecosystem components, the ecosystems recover and are not replaced post-extinction. The eastern Australian and New Zealand sites are considered least affected by the ETE.

Increased total abundances of spores on both hemispheres during the extinction and recovery intervals may indicate that environmental and/or climatic conditions became less favourable for seed plants, as suggested by van de Schootbrugge *et al.* (2009), resulting in proliferation of spore-producing plants in all areas. High abundances of spores often continue during the recovery phase. This may reflect wetter conditions at all sites during the extinction and recovery phases. Alternatively, such conditions may include expected effects of CAMP volcanism such as acid rain, terrestrial soil and freshwater acidification due to volcanic sulfur dioxide emissions, fluctuating ultraviolet flux due to ozone depletion caused by halogens and halocarbon compounds, and drastic changes in climatic conditions due to greenhouse gas emissions.

The terrestrial ecosystem appears to have recovered by late Hettangian time in all areas, with the return of common to abundant woody plants. Although cheirolepid conifers suffered during the ETE, with at least two pollen taxa disappearing (*Granuloperculatipollis rudis*, *Geopollis zwolinskae*), they became important components of Early Jurassic palynofloras both on the northern and southern hemispheres.

In conclusion, this review indicates that the terrestrial vegetation was affected on a global scale during

the end-Triassic event, but further studies are needed. Future research on the causes and effects of the end-Triassic event, and the response of the terrestrial vegetation, would benefit from complementary and additional high-resolution palynological studies from TJB sites globally.

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References

- ABBINK, O. A. 1998. *Palynological Investigation in the Jurassic of the North Sea Region*. LPP Contribution Series 8. LPP Foundation, University of Utrecht, 192 pp.
- ACHILLES, H. 1981. Die rhaetische und liassische Mikroflora Frankens. *Palaeontographica Abteilung B* **179**, 1–86.
- AKIKUNI, K., HORI, R. S., VAJDA, V., GRANT-MACKIE, J. A. & IKEHARA, M. 2010. Stratigraphy of Triassic–Jurassic boundary sequences from the Kawhia coast and Awakino gorge, Murihiku Terrane, New Zealand. *Stratigraphy* **7**, 7–24.
- ALVIN, K. L. 1982. Cheirolepidiaceae: biology, structure and palaeoecology. *Review of Palaeobotany and Palynology* **37**, 71–98.
- BACKHOUSE, J. & BALME, B. E. 2002. *Late Triassic Palynology of the Northern Carnarvon Basin*. Minerals and Energy Research Institute of Western Australia Report 226, 168 pp.
- BARRÓN, E., GOMEZ, J. J., GOY, A. & PIEREN, A. P. 2006. The Triassic–Jurassic boundary in Asturias (northern Spain): palynological characterization and facies. *Review of Palaeobotany and Palynology* **138**, 187–208.
- BATTEN, D. J. 1974. Wealden palaeoecology from the distribution of plant fossils. *Proceedings of the Geologists' Association* **85**, 433–58.
- BATTEN, D. J. 1996. 20E – Upper Jurassic and Cretaceous miospores. In *Palynology: Principles and Applications* (eds J. Jansonius & D. C. McGregor), pp. 807–30. American Association of Stratigraphical Palynologists Foundation 2.
- BELCHER, C. M., MANDER, L., REIN, G., JERVIS, F. X., HAWORTH, M., HESSELBO, S. P., GLASSPOOL, I. J. & MCELWAIN, J. C. 2010. Increased fire activity at the Triassic/Jurassic boundary in Greenland due to climate driven floral change. *Nature Geoscience* **3**, 426–9.
- BLACK, B. A., LAMARQUE, J.-F., SHIELDS, C. A., ELKINSTANTON, L. T. & KIEHL, J. T. 2014. Acid rain and ozone depletion from pulsed Siberian Traps magmatism. *Geology* **42**, 67–70.
- BLOOS, G. & PAGE, K. N. 2000. The basal Jurassic ammonite succession in the North-West European Province: review and new results. *GeoResearch Forum* **6**, 27–40.
- BOMFLEUR, B., SCHÖNER, R., SCHNEIDER, J. W., VIERECK, L., KERP, H. & MCKELLAR, J. L. 2014. From the Transantarctic Basin to the Ferrar Large Igneous Province – new palynostratigraphic age constraints for the Triassic–Jurassic sedimentation and magmatism in East Antarctica. *Review of Palaeobotany and Palynology* **207**, 18–37.
- BOND, D. P. G. & WIGNALL, P. B. 2014. Large igneous provinces and mass extinctions: an update. In *Volcanism, Impacts, and Mass Extinctions: Causes and Effects* (eds G. Keller & A. C. Kerr), pp. 29–55. Geological Society of America, Special Paper no. 505.
- BONIS, N. R. & KÜRSCHNER, W. M. 2012. Vegetation history, diversity patterns, and climate change across the Triassic/Jurassic boundary. *Paleobiology* **38**, 240–64.
- BONIS, N. R., KÜRSCHNER, W. M. & KRISTYN, L. 2009. A detailed palynological study of the Triassic–Jurassic transition in key sections of the Eiberg Basin (Northern Calcareous Alps, Austria). *Review of Palaeobotany and Palynology* **156**, 376–400.
- BONIS, N. R., RUHL, M. & KÜRSCHNER, W. M. 2010. Milankovitch-scale palynological turnover across the Triassic – Jurassic transition at St. Audrie's Bay, SW UK. *Journal of the Geological Society, London* **167**, 877–88.
- BOULTER, M. C. & WINDLE, T. 1993. A reconstruction of some Middle Jurassic vegetation in northern Europe. *Special Papers in Palaeontology* **49**, 125–54.
- BRUGMAN, W. A., VAN BERGEN, P. F. & KERP, J. H. F. 1993. A quantitative approach to Triassic palynology, the Lettenkeuper of the Germanic Basin as an example. In *Sedimentation of Organic Particles* (ed. A. Traverse), pp. 409–29. Cambridge: Cambridge University Press.
- CIRILLI, S., MARZOLI, A., TANNER, L., BERTRAND, H., BURATTI, N., JOURDAN, F., BELLIENI, G., KONTAK, D. & RENNE, P. R. 2009. Latest Triassic onset of the Central Atlantic Magmatic Province (CAMP) volcanism in the Fundy Basin (Nova Scotia): new stratigraphic constraints. *Earth and Planetary Science Letters* **286**, 514–25.
- CLÉMENCE, M.-E., BARTOLINI, A., GARDIN, S., PARIS, G., BEAUMONT, V. & PAGE, K. N. 2010a. Early Hettangian benthic-planktonic coupling at Doniford (SW England): palaeoenvironmental implications for the aftermath of the end-Triassic crisis. *Palaeogeography, Palaeoclimatology, Palaeoecology* **295**, 102–15.
- CLÉMENCE, M. E., GARDIN, S., BARTOLINI, A., PARIS, G., BEAUMONT, V. & GUÉX, J. 2010b. Benthic-planktonic evidence from the Austrian Alps for a decline in sea-surface carbonate production at the end of the Triassic. *Swiss Journal of Geosciences* **103**, 293–315.
- DE JERSEY, N. J. 1971. *Early Jurassic Miospores from the Helidon Sandstone*. Geological Survey of Queensland, Publication 351, Palaeontological Papers 25, 53 pp.
- DE JERSEY, N. J. & MCKELLAR, J. L. 2013. The palynology of the Triassic–Jurassic transition on southeastern Queensland, Australia, and correlation with New Zealand. *Palynology* **37**, 77–114.
- DE JERSEY, N. J. & RAINE, J. I. 1990. *Triassic and Earliest Jurassic Miospores from the Murihiku Supergroup, New Zealand*. Geological Survey, Paleontological Bulletin 62, 164 pp.
- DYBKJÆR, K. 1991. Palynological zonation and palynofacies investigation of the Fjerritslev Formation (Lower Jurassic–basal Middle Jurassic) in the Danish Subbasin. *Danmarks Geologiske Undersøgelse Serie A* **30**, 1–22.
- DROSER, M. L., BOTTJER, D. J., SHEEHAN, P. M. & MCGHEE, G. R. 2000. Decoupling of taxonomic and ecologic

- severity of Phanerozoic marine mass extinctions. *Geology* **28**, 675–8.
- FOWELL, S. J. & OLSEN, P. E. 1993. Time calibration of Triassic/Jurassic microfossil turnover, eastern North America. *Tectonophysics* **222**, 361–9.
- FRANCIS, J. E. 1983. The dominant conifer of the Jurassic Purbeck Formation, England. *Palaeontology* **26**, 277–94.
- FRANCIS, J. E. 1984. The seasonal environment of the Purbeck (Upper Jurassic) fossil forests. *Palaeogeography, Palaeoclimatology, Palaeoecology* **48**, 285–307.
- GALLI, M. T., JADOUL, F., BERNASCONI, S. M., CIRILLI, S. & WEISSERT, H. 2007. Stratigraphy and palaeoenvironmental analysis of the Triassic–Jurassic transition in the western Southern Alps (Northern Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology* **244**, 52–70.
- GÓMEZ, J. J., GOY, A. & BARRÓN, E. 2007. Events around the Triassic–Jurassic boundary in northern and eastern Spain: a review. *Palaeogeography, Palaeoclimatology, Palaeoecology* **244**, 89–110.
- GÖTZ, A. E., RUCKWIED, K., PÁLFY, J. & HAAS, J. 2009. Palynological evidence of synchronous changes within the terrestrial and marine realm at the Triassic/Jurassic boundary (Csovár section, Hungary). *Review of Palaeobotany and Palynology* **156**, 401–9.
- HALLAM, A. 1997. Estimates of the amount and rate of sea-level change across the Rhaetian–Hettangian and Pliensbachian–Toarcian boundaries (latest Triassic to early Jurassic). *Journal of the Geological Society, London* **154**, 773–9.
- HALLAM, A. & WIGNALL, P. B. 1999. Mass extinction and sea-level change. *Earth-Science Reviews* **48**, 217–58.
- HALLAM, A. & WIGNALL, P. B. 2000. Facies change across the Triassic–Jurassic boundary in Nevada USA. *Journal of the Geological Society, London* **157**, 49–54.
- HARRIS, T. M. 1937. The fossil flora of Scoresby Sound, East Greenland, Part 5. Stratigraphic relations of the plant beds. *Meddelelser om Grønland* **112**, 1–112.
- HERMANN, E., HOCHULI, P. A., BUCHER, H. & ROOHL, G. 2012. Uppermost Permian to Middle Triassic palynology of the Salt Range and Surghar Range, Pakistan. *Review of Palaeobotany and Palynology* **169**, 61–95.
- HERNGREEN, G. F. W. & DE BOER, K. F. 1974. Palynology of Rhaetian, Liassic and Dogger strata in the Eastern Netherlands. *Geologie en Mijnbouw* **53**, 343–68.
- HESSELBO, S. P., ROBINSON, S. A., SURLYK, F. & PIASECKI, S. 2002. Terrestrial and marine extinction at the Triassic–Jurassic boundary synchronized with major carbon-cycle perturbations: a link to initiation of massive volcanism? *Geology* **30**, 251–4.
- HEUNISCH, C., LUPPOLD, F. W., REINHARDT, L. & RÖHLING, H.-G. 2010. Palynofazies, bio- und lithostratigraphie im Grenzbereich Trias/Jura in der Bohrung Mariental 1 (Lappwaldmulde, Ostniedersachsen). *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften* **161**, 51–98.
- HILLEBRANDT, A. V. & KRZYSTYN, L. 2009. On the oldest Jurassic ammonites of Europe (Northern Calcareous Alps, Austria) and their global significance. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **253**, 163–95.
- HILLEBRANDT, A. V., KRZYSTYN, L., KÜRSCHNER, W. M., BONIS, N. R., RUHL, M., RICHOSZ, S., SCHOBEN, M. A. N., URLICHS, M., BOWN, P. R., KMENT, K., MCROBERTS, C. A., SIMMS, M. & TOMÁŠOVÝCH, A. 2013. The Global Stratotype Sections and Point (GSSP) for the base of the Jurassic System at Kuhjoch (Karwendel Mountains, Northern Calcareous Alps, Tyrol, Austria). *Episodes* **36**, 162–98.
- HOUNSLOW, M. W., POSEN, P. E. & WARRINGTON, G. 2004. Magnetostratigraphy and biostratigraphy of the Upper Triassic and lowermost Jurassic succession, St. Audrie's Bay, UK. *Palaeogeography, Palaeoclimatology, Palaeoecology* **213**, 331–58.
- HUBBARD, R. N. L. B. & BOULTER, M. C. 1997. Mid Mesozoic floras and climates. *Palaeontology* **40**, 43–70.
- KIESSLING, W., ABERHAN, M., BRENNEIS, B. & WAGNER, P. J. 2007. Extinction trajectories of benthic organisms across the Triassic–Jurassic boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* **244**, 201–22.
- KÜRSCHNER, W. M., BONIS, N. R. & KRZYSTYN, L. 2007. Carbon-isotope stratigraphy and palynostratigraphy of the Triassic–Jurassic transition in the Tiefengraben section – Northern Calcareous Alps (Austria). *Palaeogeography, Palaeoclimatology, Palaeoecology* **244**, 257–80.
- KÜRSCHNER, W. M., MANDER, L. & MCELWAIN, J. C. 2014. A gymnosperm affinity for *Ricciisporites tuberculatus* Lundblad: implications for vegetation and environmental reconstructions in the Late Triassic. *Palaeobiodiversity and Palaeoenvironments* **94**, 295–305.
- LINDSTRÖM, S. & MCLOUGHLIN, S. 2007. Synchronous palynofloristic extinction and recovery after the end-Permian event in the Prince Charles Mountains, Antarctica: implications for palynofloristic turnover across Gondwana. *Review of Palaeobotany and Palynology* **145**, 89–122.
- LINDSTRÖM, S., PEDERSEN, G. K., VAN DE SCHOOTBRUGGE, B., HANSEN, K. H., KUHLMANN, N., THEIN, J., JOHANSSON, L., PETERSEN, H. I., ALWMARK, C., DYBKJÆR, K., WEIBEL, R., ERLSTRÖM, M., NIELSEN, L. H., OSCHMANN, W. & TEGNER, C. 2015. Intense and widespread seismicity during the end-Triassic mass extinction due to emplacement of a large igneous province. *Geology* **43**, 387–90.
- LINDSTRÖM, S., VAN DE SCHOOTBRUGGE, B., DYBKJÆR, K., PEDERSEN, G. K., FIEBIG, J., NIELSEN, L. H. & RICHOSZ, S. 2012. No causal link between terrestrial ecosystem change and methane release during the end-Triassic mass-extinction. *Geology* **40**, 531–4.
- LOOY, C. V., BRUGMAN, W. A., DILCHER, D. L. & VISSCHER, H. 1999. The delayed resurgence of equatorial forests after the Permian–Triassic ecological crisis. *Proceedings of the National Academy of Sciences USA* **96**, 13857–62.
- LUND, J. J. 1977. Rhaetic to Lower Liassic palynology of the onshore south-eastern North Sea Basin. *Danmarks Geologiske Undersøgelse II Række* **109**, 1–129.
- MANDER, L., COLLINSON, M. E., CHALONER, W. G., BRAIN, A. P. R. & LONG, D. G. 2012. The ultrastructure and botanical affinity of the problematic mid-Mesozoic palynomorph *Ricciisporites tuberculatus* Lundblad. *International Journal of Plant Sciences* **173**, 429–40.
- MANDER, L., KÜRSCHNER, W. M. & MCELWAIN, J. C. 2010. An explanation for conflicting records of Triassic – Jurassic plant diversity. *Proceedings of the National Academy of Sciences USA* **107**, 15351–6.
- MANDER, L., KÜRSCHNER, W. M. & MCELWAIN, J. C. 2013. Palynostratigraphy and vegetation history of the Triassic – Jurassic transition in East Greenland. *Journal of the Geological Society, London* **170**, 37–46.
- MANDER, L., TWITCHETT, R. J. & BENTON, M. J. 2008. Palaeoecology of the Late Triassic extinction event in the SW UK. *Journal of the Geological Society, London* **165**, 319–32.

- MARYNOWSKI, L. & SIMONEIT, B. R. T. 2009. Widespread Upper Triassic to Lower Jurassic wildfire records from Poland: evidence from charcoal and pyrolytic polycyclic aromatic hydrocarbons. *Palaios* **24**, 785–98.
- MCELWAIN, J. C., POPA, M. E., HESSELBO, S. P., HAWORTH, M. & SURLYK, F. 2007. Macroecological responses of terrestrial vegetation to climatic and atmospheric change across the Triassic/Jurassic boundary in East Greenland. *Paleobiology* **33**, 547–73.
- MCELWAIN, J. C. & PUNYASENA, S. W. 2007. Mass extinction events and the plant fossil record. *Trends in Ecology and Evolution* **22**, 548–56.
- MCGHEE, G. R., CLAPHAM, M. E., SHEEHAN, P. M., BOTTJER, D. J. & DROSER, M. L. 2013. A new ecological-severity ranking of major Phanerozoic biodiversity crises. *Palaeogeography, Palaeoclimatology, Palaeoecology* **370**, 260–70.
- MCGHEE, G. R., SHEEHAN, P. M., BOTTJER, D. J. & DROSER, M. L. 2004. Ecological ranking of Phanerozoic biodiversity crises: ecological and taxonomic severities are decoupled. *Palaeogeography, Palaeoclimatology, Palaeoecology* **211**, 289–97.
- MUSSARD, J.-M., DUCAZEUX, J. & CUGNY, P. 1997. Statistical analyses of palynomorph assemblages in Middle Jurassic deposits (Lower to Middle Bathonian, Brent Group, Norway). *Bulletin du Centre de Recherches Elf Exploration Production* **18**, 265–77.
- NIELSEN, L. H. 2003. Late Triassic–Jurassic development of the Danish Basin and the Fennoscandian Border Zone, southern Scandinavia. *Geological Survey of Denmark and Greenland Bulletin* **1**, 459–526.
- OLSEN, P. E., KENT, D. V., SUES, H.-D., KOEBERL, C., HUBER, H., MONTANARI, A., RAINFORTH, E. C., FOWELL, S. J., SZAJNA, M. J. & HARTLINE, B. W. 2002. Ascent of dinosaurs linked to an iridium anomaly at the Triassic–Jurassic boundary. *Science* **296**, 1305–7.
- ORBELL, G. 1973. Palynology of the British Rhaeto–Liassic. *Bulletin of the Geological Survey of Great Britain* **44**, 1–44.
- ORLOWSKA-ZWOLINSKA, T. 1983. Palynostratigraphy of the upper part of the Triassic epicontinental sediments in Poland. *Prace Instytutu Geologicznego* **104**, 1–89.
- PAGE, C. N. 2002. Ecological strategies in fern evolution: a neopteridological overview. *Review of Palaeobotany and Palynology* **119**, 1–33.
- PEDERSEN, K. R. 1983. Ultrastructure of *Ricciisporites*, an upper Triassic pollen tetrad. *Abstracts of the European Palaeobotanical Conference, 11–16 July 1983, Montpellier, France*.
- PETERSEN, H. I. & LINDSTRÖM, S. 2012. Synchronous wildfire activity rise and mire deforestation at the Triassic–Jurassic boundary. *PLoS One* **7**, e47236.
- PEDERSEN, K. R. & LUND, J. J. 1980. Palynology of the plant-bearing Rhaetian to Hettangian Kap Stewart Formation, Scoresby Sund, East Greenland. *Review of Palaeobotany and Palynology* **31**, 1–69.
- PIEŃKOWSKI, G., NIEDŹWIEDZKI, G. & WAKSMUNDZKA, M. 2012. Sedimentological, palynological and geochemical studies of the terrestrial Triassic–Jurassic boundary in northwestern Poland. *Geological Magazine* **149**, 308–22.
- PRETO, N., KUSTATSCHER, E. & WIGNALL, P. B. 2010. Triassic climates – state of the art and perspectives. *Palaeogeography, Palaeoclimatology, Palaeoecology* **290**, 1–10.
- RAUSCHER, R., HILLY, J., HANZO, M. & MARCHAL, C. 1995. Palynologie des couches de passage du Trias supérieur au Lias dans l’est du bassin Parisien: problèmes de datation du “Rhétien” de Lorraine. *Sciences Géologiques Bulletin* **48**, 159–85.
- REINHARDT, L. & RICKEN, W. 2000. Climate cycles documented in a playa system: comparison of geochemical signatures derived from subbasins (Triassic, Middle Keuper, Germany). *Zentralblatt für Geologie und Paläontologie* **1**, 315–40.
- RESTALLACK, G. 1975. The life and times of a Triassic lycopod. *Alcheringa* **1**, 3–29.
- RICHOZ, S., van DE SCHOOTBRUGGE, B., PROSS, J., PÜTTMANN, W., QUAN, T. M., LINDSTRÖM, S., HEUNISCH, C., FIEBIG, J., MAQUIL, R., SCHOUTEN, S., HAUZENBERGER, C. A. & WIGNALL, P. B. 2012. Hydrogen sulphide poisoning of shallow seas following the end-Triassic extinction. *Nature Geoscience* **5**, 662–7.
- RIDING, J. B., MANTLE, D. J. & BACKHOUSE, J. 2010. A review of the chronostratigraphical ages of Middle Triassic to Late Jurassic dinoflagellate cyst biozones of the North West Shelf of Australia. *Review of Palaeobotany and Palynology* **162**, 543–75.
- ROGHI, G. 2004. Palynological investigations in the Carnian of the Cave del Predil area (Julian Alps, NE Italy). *Review of Palaeobotany and Palynology* **132**, 1–35.
- RUCKWIED, K. & GÖTZ, A. E. 2009. Climate change at the Triassic/Jurassic boundary: palynological evidence from the Furkaska section (Tatra Mountains, Slovakia). *Geologica Carpathica* **60**, 139–49.
- SCHOENE, B., GUEX, J., BARTOLINI, A., SCHALTEGGER, U. & BLACKBURN, T. 2010. Correlating the end-Triassic mass extinction and flood basalt volcanism at the 100 ka level. *Geology* **38**, 387–90.
- SCHULTE, P., ALEGRET, L., ARENILLAS, I., ARZ, J. A., BARTON, P. J., BOWN, P. R., BRALOWER, T. J., CHRISTESON, G. L., CLAEYS, P., COCKELL, C. S., COLLINS, G. S., DEUTSCH, A., GOLDIN, T. J., GOTO, K., GRAJALES-NISHIMURA, J. M., GRIEVE, R. A. F., GULICK, S. P. S., JOHNSON, K. R., KIESSLING, W., KOEBERL, C., KRING, D. A., MACLEOD, K. G., MATSUI, T., MELOSH, J., MONTANARI, A., MORGAN, J. V., NEAL, C. R., NICHOLS, D. J., NORRIS, R. D., PIERAZZO, E., RAVIZZA, G., REBOLLEDO-VIEYRA, M., REIMOLD, W. U., ROBIN, E., SALGE, T., SPEIJER, R. P., SWEET, A. R., URRUTIA-FUCUGAUCHI, J., VAJDA, V., WHALEN, M. T. & WILLUMSEN, P. S. 2010. The Chicxulub asteroid impact and mass-extinction at the Cretaceous–Paleogene boundary. *Science* **327**, 1214–8.
- SCHURMAN, W. M. L. 1977. Aspects of late Triassic palynology. 2. Palynology of the “Grès et Schiste à Avicula contorta” and “Argiles de Vallois” (Rhaetian) of north-eastern France and southern Luxembourg. *Review of Palaeobotany and Palynology* **23**, 159–69.
- SEPKOSKI, J. J. 1996. Patterns of Phanerozoic extinction: a perspective from global data bases. In *Global Events and Event Stratigraphy in the Phanerozoic* (ed. O. H. Waliser), pp. 35–51. Berlin: Springer.
- STEINTHORSÐOTTIR, M., WOODWARD, F. I., SURLYK, F. & MCELWAIN, J. C. 2012. Deep-time evidence of a link between elevated CO₂ concentrations and perturbations in the hydrological cycle via drop in plant transpiration. *Geology* **40**, 815–8.
- STEVENS, G. R. 2012. Otapirian and Aratauran sequences (latest Triassic and earliest Jurassic) along the northern Marokopa coast (SW Auckland, New Zealand) and observations on the Triassic/Jurassic boundary in New Zealand. *New Zealand Journal of Geology and Geophysics* **55**, 37–51.

- SUNEBY, L. B. & HILLS, L. V. 1988. Palynological zonation of the Heiberg Formation (Triassic–Jurassic) eastern Sverdrup Basin, Arctic Canada. *Bulletin of Canadian Petroleum Geology* **36**, 347–61.
- SWEET, A. R. & BRAMAN, D. R. 1992. The K–T boundary and contiguous strata in western Canada: interactions between paleoenvironments and palynological assemblages. *Cretaceous Research* **13**, 31–79.
- VAJDA, V., RAINE, J. I. & HOLLIS, C. J. 2001. Indication of global deforestation at the Cretaceous–Tertiary boundary by New Zealand fern spike. *Science* **294**, 1700–2.
- VAKHRAMEEV, V. A. 1991. *Jurassic and Cretaceous Floras and Climates of the Earth*. Cambridge: Cambridge University Press, 318 pp.
- VAN DE SCHOOTBRUGGE, B., QUAN, T. M., LINDSTRÖM, S., PÜTTMANN, W., HEUNISCH, C., PROSS, J., FIEBIG, J., PETSCHICK, R., RÖHLING, H.-G., RICHOS, S., ROSENTHAL, Y. & FALKOWSKI, P. G. 2009. Floral changes across the Triassic/Jurassic boundary linked to flood basalt volcanism. *Nature Geoscience* **2**, 589–94.
- VAN DE SCHOOTBRUGGE, B., TREMOLADA, F., ROSENTHAL, Y., BAILEY, T. R., FEIST-BURKHARDT, S., BRINKHUIS, H., PROSS, J., KENT, D. V. & FALKOWSKI, P. G. 2007. End-Triassic calcification crisis and blooms of organic-walled “disaster species”. *Palaeogeography, Palaeoclimatology, Palaeoecology* **244**, 126–41.
- VAN KONIJNENBURG-VAN CITTERT, J. H. A. 2002. Ecology of some Late Triassic to Early Cretaceous ferns in Eurasia. *Review of Palaeobotany and Palynology* **119**, 113–24.
- VAN KONIJNENBURG-VAN CITTERT, J. H. A. 2008. The Jurassic fossil plant record of the UK area. *Proceedings of the Geologists’ Association* **119**, 59–72.
- VISSCHER, H. & VAN DER ZWAN, C. J. 1981. Palynology of the Circum-Mediterranean Triassic: phytological and palaeoclimatological implications. *Geologische Rundschau* **70**, 625–34.
- VISSCHER, H., VAN HOUTE, M., BRUGMAN, W. A. & POORT, R. J. 1994. Rejection of Carnian (late Triassic) “pluvial event” in Europe. *Review of Palaeobotany and Palynology* **83**, 217–26.
- WARD, P. D., HAGGART, J. W., CARTER, E. S., WILBUR, D., TIPPER, H. W. & EVANS, T. 2001. Sudden productivity collapse associated with the Triassic–Jurassic boundary mass-extinction. *Science* **292**, 1148–51.
- WARRINGTON, G., COPE, J. C. W. & IVIMEY-COOK, H. C. 1994. St. Audrie’s Bay, Somerset, England: a candidate Global Stratotype Section and Point for the base of the Jurassic. *Geological Magazine* **131**, 191–200.
- WHITESIDE, J. H., OLSEN, P. G., KENT, D. V., FOWELL, S. J. & ET-TOUHAMI, M. 2007. Synchrony between the Central Atlantic Magmatic Province and the Triassic–Jurassic mass-extinction event? *Palaeogeography, Palaeoclimatology, Palaeoecology* **244**, 345–67.
- WHITESIDE, J. H. & WARD, P. D. 2011. Ammonoid diversity and disparity track episodes of chaotic carbon cycling during the early Mesozoic. *Geology* **39**, 99–102.
- YAROSHENKO, O. P. 2007. Late Triassic palynological flora from Western Ciscaucasia. *Palaeontological Journal* **41**, 1190–7.
- YONG, L., ALLEN, P. A., DENSMORE, A. L. & QIANG, X. 2003. Evolution of the Longmen Shan foreland basin (Western Sichuan, China) during the Late Triassic Indosinian Orogeny. *Basin Research* **15**, 117–38.
- ZHANG, W. & GRANT-MACKIE, J. A. 2001. Late Triassic–Early Jurassic palynological assemblages from Murihiku strata of New Zealand, and comparisons with China. *Journal of the Royal Society of New Zealand* **31**, 575–683.
- ZIAJA, J. 2006. Lower Jurassic spores and pollen grains from Odrowąż, Mesozoic margin of the Holy Cross Mountains, Poland. *Acta Palaeobotanica* **46**, 3–83.