

Taxonomic resolution of the Triassic–Jurassic sporomorph record in East Greenland

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ABSTRACT – Sporomorphs (pollen and spores) provide valuable information about vegetation history over a range of temporal and spatial scales. However, sporomorphs can be morphologically invariant among species within genera, and among genera within certain families. In some cases, the parent plant of a sporomorph is unknown. These factors blur the relationship between sporomorph assemblages and the source vegetation, and reduce the taxonomic precision of vegetation reconstructions based on sporomorphs. This study investigates the taxonomic precision with which sporomorphs record vegetation across the Triassic–Jurassic transition (Tr–J) at Astartekløft, East Greenland. Results indicate that reconstructions of Tr–J vegetation at Astartekløft based on sporomorphs are hampered by considerable taxonomic imprecision. Something is known of the botanical affinity of almost all sporomorphs at Astartekløft at the class level, but just 50% of sporomorph taxa have a known botanical affinity at the family level. Additionally, ~23% of all sporomorph taxa at Astartekløft have affinities to more than one parent plant class, and ~36% of sporomorph taxa have affinities to more than one parent plant family. This taxonomic imprecision should be accounted for when interpreting percentage diagrams of sporomorph taxa across the Tr–J. *J. Micropalaeontol.* 30(2): 107–118, September 2011.

KEYWORDS: *palynology, taphonomy, Triassic, Jurassic, extinction*

INTRODUCTION

Following the seminal work of von Post (1916) the use of dispersed sporomorphs (pollen and spores) to reconstruct vegetation history is now commonplace. Sporomorphs have provided valuable information on vegetation from the Palaeozoic to the present day, and on spatial scales ranging from moss polsters (e.g. Domínguez-Vázquez *et al.*, 2004) to continents and biomes (e.g. Overpeck *et al.*, 1992; Mitchell, 2011). In some plant groups, such as liverworts (e.g. Schuster, 1992) and hornworts (e.g. Villarreal *et al.*, 2007), sporomorph morphology is an important character used to distinguish between different species. However, in other plant groups sporomorphs can be morphologically invariant among species within genera, such as the pollen of *Quercus* (oaks) (e.g. Liu *et al.*, 2007), and possibly morphologically invariant among many genera within certain families, such as the Poaceae (grasses) (e.g. Wodehouse, 1935). Thus, sporomorph identification can suffer from limited taxonomic resolution (e.g. Birks & Birks, 2000; Jackson & Booth, 2007). In some cases the parent plant of a dispersed sporomorph is unknown. This is often the case in studies of extinct plant groups in pre-Quaternary time, where the unequivocal linkage of dispersed sporomorphs to parent plants is reliant on the discovery of sporomorphs *in situ* in fossilized reproductive structures (e.g. Balme, 1995). Where a sporomorph has not been found *in situ*, its botanical affinity may be interpreted by morphological and/or ultrastructural comparison with other sporomorphs (e.g. Batten & Dutta, 1997).

Morphological invariance among sporomorphs, and the absence of reliable occurrences of dispersed sporomorph taxa *in situ* in fossilized reproductive structures or fertile foliage, together impart a degree of taxonomic imprecision to a vegetation reconstruction based on sporomorphs. This controls the taxonomic resolution of a sporomorph assemblage, which is the taxonomic level at which the source vegetation can be reconstructed from dispersed sporomorphs. The taxonomic resolution

of a sporomorph assemblage lies somewhere on a conceptual sliding scale. At one end of the scale, the identity of the parent plant of each and every sporomorph in an assemblage is known at the species level: everything is known of the botanical affinities of the sporomorphs and the taxonomic resolution of the assemblage is highest. At the opposite end of the scale, the identity of the parent plant of each and every sporomorph in an assemblage is completely unknown: nothing is known of the botanical affinities of the sporomorphs and the taxonomic resolution of the assemblage is lowest. Assemblages of dispersed sporomorphs lie somewhere between these two extremes, and contain a mixture of sporomorphs that are morphologically invariant at species, genus or family level, together with some sporomorphs whose affinities at low taxonomic levels, such as family or genus, are unknown.

Taxonomic imprecision blurs the relationship between a sporomorph assemblage and the source vegetation. This hampers efforts to understand plant life during episodes of major environmental and biotic change, such as the Triassic–Jurassic mass extinction (Tr–J; ~200 Ma (Schoene *et al.*, 2010)). The Tr–J is one of the ‘Big Five’ mass extinction events of the Phanerozoic and resulted in the extinction of 23% of marine families and 22% of terrestrial families (Benton, 1995). However, the only confirmed global plant family extinction during this period of major global change, that of the Peltaspermales (a clade of seed-ferns; see McElwain & Punyasena, 2007), is masked in the sporomorph record because the pollen produced by this family (*Cycadopites*; Townrow, 1960) was also produced by at least four orders of plants (Cycadales, Ginkgoales, Bennettitales and Peltaspermales; Mander *et al.*, 2010). Additionally, detailed investigations of plant macrofossils (mostly leaves) at a Tr–J boundary section at Astartekløft in East Greenland have revealed that four cycad leaf genera (*Doratophyllum*, *Ctenis*, *Pseudoclenis* and *Nilssonina*) are present in Triassic sediments, but are absent from Jurassic rocks owing to their local extinction

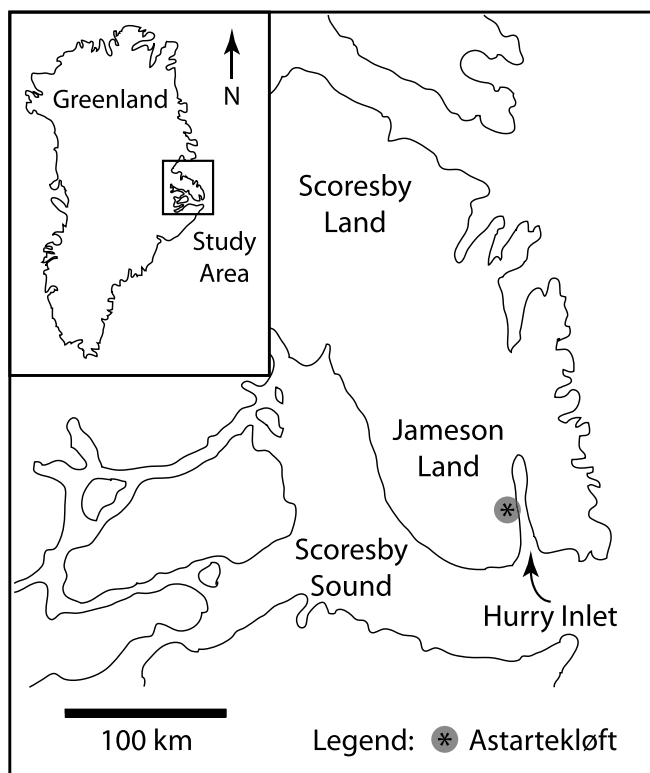


Fig. 1. Map showing the location of the Astartekløft section in Jameson Land, East Greenland (after McElwain *et al.*, 2007).

or emigration (McElwain *et al.*, 2007). This vegetation change is not recorded by sporomorphs at the same locality, partly because of morphological invariance among the ‘boat-shaped’ monosulcate pollen grains that were produced by most Mesozoic cycads (Balme, 1995; Mander *et al.*, 2010).

This study aims to investigate the taxonomic precision with which sporomorphs record the source vegetation across the Tr–J at Astartekløft by measuring: (1) the proportion of sporomorphs that have a known botanical affinity at Astartekløft; (2) the proportion of sporomorphs that have affinities to more than one parent plant at Astartekløft.

MATERIALS AND METHODS

Geological setting and stratigraphy

The material for this study was derived from rocks that crop out at Astartekløft in Jameson Land, East Greenland (Fig. 1). The rock succession at this locality comprises the fluvial–lacustrine Kap Stewart Group, which was deposited on the margins of the perennial hydrologically closed Kap Stewart Lake, situated in the south of the East Greenland rift basin (Dam & Surlyk, 1992). This locality has yielded exceptionally well-preserved plant macrofossils (e.g. Harris, 1937; McElwain *et al.*, 2007) that are restricted to a series of muddy and silty fossiliferous layers, hereafter referred to as ‘plant beds’ (Fig. 2). These plant beds are located in the sandy and shaley Primulaelv Formation, which was deposited in a delta plain setting (Dam & Surlyk, 1992, 1993; Surlyk, 2003; McElwain *et al.*, 2007). The absence of marine palynomorphs from the Kap Stewart Group at Astartekløft indicates that environments of deposition were

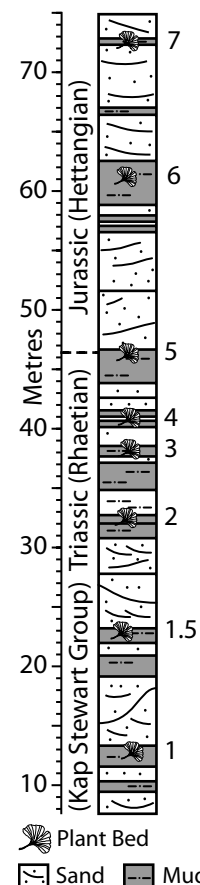


Fig. 2. Schematic sedimentary log of the Astartekløft section (adapted from Hesselbo *et al.*, 2002; McElwain *et al.*, 2007, and also shown in Belcher *et al.*, 2010 and Mander *et al.*, 2010). Plant beds numbered 1–7 and highlighted by schematic *Ginkgo* leaves. Plant beds 1–5 represent deposition by floodwaters into overbank environments, plant bed 6 represents a poorly developed coal swamp and plant bed 7 represents a shallow pool developed in a semi-abandoned abandoned channel (McElwain *et al.*, 2007). Position of Triassic/Jurassic boundary approximated by first appearance of the pollen grain *Cerebropollentites thiergartii*, following Kuerschner *et al.* (2007) and Bonis *et al.* (2009) (see Mander *et al.*, 2010).

exclusively terrestrial (Pedersen & Lund, 1980; Koppelhus, 1996; Mander *et al.*, 2010).

Collection of samples and palynological techniques

Rock samples were collected at 10 cm intervals from within each plant bed at Astartekløft (Fig. 2). Samples from plant bed 6 consist of coaly mudstone, and samples from all other plant beds consist of dark grey mudstones and siltstones. Between 15 g and 20 g of each sample was washed and crushed and dried for 24 hours at 60°C. Each sample was treated twice alternately with cold HCl (30%) to remove carbonate minerals and with cold HF (38%) to remove silicate minerals. The residue from each sample was washed with water until pH neutral, then sieved with 250 µm and 15 µm polypropylene mesh. Finally, organic and inorganic residues were separated using ZnCl₂. No oxidation techniques were used during the preparation of sporomorphs. Two slide preparations were made in glycerine jelly and these are available upon request.

A total of 40 rock samples were productive for sporomorphs from plant beds 1–7. A count of between 350 and 400 sporomorphs was made but where one morphotype dominated the sporomorph assemblage, counts were increased until at least 150 sporomorphs of the non-dominant types were recorded. Slides were counted in complete transects and included the centre and edges of the slides. A total of 14 579 sporomorphs were recorded from the 40 productive samples. Sporomorph identification was based on Morbey (1975), Lund (1977) and Pedersen & Lund (1980). A full data matrix showing occurrences of sporomorphs within samples from each plant bed at Astartekløft is available in Mander *et al.* (2010).

Measuring the taxonomic resolution of the Tr–J sporomorph record at Astartekløft

In order to measure the taxonomic resolution of the sporomorph record at Astartekløft, it was necessary to interpret the botanical affinities of each sporomorph taxon. Accordingly, the published literature was searched for sporomorphs found *in situ* in reproductive structures of fossil plant taxa. Most *in situ* occurrences are recorded in the annotated catalogue of fossil *in situ* spores and pollen grains of Balme (1995), but additional references have been consulted where this catalogue was found to be deficient or outdated. The botanical affinities of spores recovered from Astartekløft are shown in Table 1 and the botanical affinities of pollen grains recovered from Astartekløft are shown in Table 2. The parent plants of sporomorphs recovered from Astartekløft have been placed into a classification scheme comprising family, order and class. Where possible, each classification is supported by a published reference. In cases where no published information on the botanical affinity of a particular sporomorph was available, the sporomorph in question has either been classified to a parent plant class by analogy with other representatives of that class, or has been left unassigned to a parent plant.

The proportion of sporomorphs that have a known botanical affinity within each sample was calculated by dividing the total number of sporomorph taxa that have a known botanical affinity in a given sample by the total number of sporomorph taxa in that sample. Samples containing a higher proportion of sporomorphs with a known botanical affinity offer a more taxonomically precise picture of the source vegetation than samples having a lower proportion of sporomorphs with a known botanical affinity.

Certain sporomorphs are morphologically invariant among certain parent plant taxa and thus have affinities to more than one parent plant (Tables 1, 2). The abundance of these multi-affinity sporomorphs has been reported as a proportion of those sporomorphs that have a known botanical affinity. This proportion was calculated by dividing the total number of sporomorph taxa with affinities to more than one parent plant in a given sample by the total number of sporomorph taxa that have a known botanical affinity in that sample. Samples with a higher proportion of multi-affinity sporomorphs offer a less taxonomically precise picture of the source vegetation than samples with a lower proportion of multi-affinity sporomorphs. In this study proportions are reported as percentages and all statistical tests were performed in R (R DCT, 2007).

RESULTS

Known botanical affinities

Fifty-six sporomorph taxa were recorded from the 40 productive samples at Astartekløft (Table 3). Of these, exactly 50% have a known botanical affinity at the family level, 64% have a known botanical affinity at the order level and 86% at the class level (Table 3).

There is considerable variation in the proportion of sporomorphs that have a known botanical affinity between individual samples at Astartekløft. Some samples have a smaller proportion of sporomorphs that have a known botanical affinity, and some samples have a larger proportion of sporomorphs that have a known botanical affinity than might be expected based on the total pooled sample set (56 taxa from 40 samples). Within individual samples from Astartekløft, between 48% and 68% of sporomorph taxa were produced by a parent plant known at the family level (median 56%), between 61% and 84% of sporomorph taxa were produced by a parent plant known at the order level (median 71%), and between 79% and 96% of sporomorph taxa were produced by a parent plant known at the class level (median 87%) (Table 3; Fig. 3). A Kruskal–Wallis test indicates that there is a statistically significant difference in the median of each group (family, order and class) ($KW = 103.1_{40, 40, 40}$ $p < 0.0001$), and this is confirmed by pairwise Mann–Whitney tests (Table 4).

The proportion of sporomorphs that have a known botanical affinity remains fairly constant through time at Astartekløft and no single plant bed stands out as having a markedly lower, or higher, proportion of such sporomorphs (Fig. 4). There is no statistically significant difference in the proportion of sporomorphs with known botanical affinities at the family or order level between plant beds (family: $KW = 12.29_{6, 1, 4, 7, 6, 9, 3, 4}$ $p = 0.0915$; order: $KW = 9.196_{6, 1, 4, 7, 6, 9, 3, 4}$ $p = 0.2389$). However, plant bed 6 has a higher proportion of sporomorphs with a known botanical affinity at the class level (Fig. 4), and this difference is statistically significant using a Kruskal–Wallis test ($KW = 17.72_{6, 1, 4, 7, 6, 9, 3, 4}$ $p = 0.0133$).

Multiple botanical affinities

Of those sporomorphs that have a known botanical affinity at Astartekløft, 36% have affinities to more than one parent plant family, 28% have affinities to more than one parent plant order, and 23% have affinities to more than one parent class (Table 3).

There is also considerable variation in the proportion of sporomorphs with affinities to more than one parent plant between individual samples at Astartekløft. Some samples have a smaller proportion of multi-affinity sporomorphs and some samples have a larger proportion of multi-affinity sporomorphs than might be expected based on the total pooled sample set. Within individual samples from Astartekløft, between 10% and 50% of sporomorphs with a known botanical affinity at the family level have affinities to more than one parent plant family (median 39%). Between 0% and 40% of sporomorphs with a known botanical affinity at the order level have affinities to more than one parent plant order (median 30%). Between 7.7% and 39% of sporomorphs with a known botanical affinity at the class level have affinities to more than one parent plant class (median

Spore taxon	Family	Order	Class	Reference
<i>Baculatisporites comanensis</i>	Osmundaceae	Filicales	Filicopsida	van Konijnenburg-van Cittert (2000)
<i>Baculatisporites wellmanii</i>	Osmundaceae	Filicales	Filicopsida	van Konijnenburg-van Cittert (2000)
<i>Calamospora tener</i>	Equisetaceae	Equisetales	Sphenopsida	Kelber & van Konijnenburg-van Cittert (1998)
<i>Cingulizonates rhaeticus</i>	—	—	Lycopsida	Bonis (2010)
<i>Conbaculatisporites mesozoicus</i>	Dipteridaceae	Filicales	Filicopsida	Pedersen & Lund (1980)
<i>Concavisporites A</i>	Dipteridaceae; Matoniaceae	Filicales	Filicopsida	Van Konijnenburg-van Cittert (1993); Guignard <i>et al.</i> (2009)
<i>Concavisporites</i> sp.	Dipteridaceae; Matoniaceae	Filicales	Filicopsida	Van Konijnenburg-van Cittert (1993); Guignard <i>et al.</i> (2009)
<i>Conitignisporites problematicus</i>	—	—	—	—
<i>Deltoidospora toralis</i>	Cyathaceae; Dicksoniaceae; Dipteridaceae; Matoniaceae	Filicales	Filicopsida	van Konijnenburg-van Cittert (1993); Balme (1995); Guignard <i>et al.</i> (2009)
<i>Heliosporites almarkensis</i>	—	—	Lycopsida	Bonis (2010)
<i>Laevigatosporites</i> sp.	Marattiaceae	Marattiales	Filicopsida	Balme (1995); Wang <i>et al.</i> (2001)
<i>Limbosporites lundbladii</i>	—	—	Lycopsida	Balme (1995)
<i>Lycopodiacidites rugulatus</i>	—	—	Filicopsida	Balme (1995)
<i>Lycopodiumsporites austroclavitidites</i>	—	—	Lycopsida	—
<i>Lycopodiumsporites seminuris</i>	—	—	Lycopsida	—
<i>Neochomotriletes triangularis</i>	—	—	—	—
<i>Nevesisporites limatulus</i>	—	—	—	—
<i>Polypodiisporites polymicroforatus</i>	Schizaceae	Filicales	Filicopsida	van de Schootbrugge <i>et al.</i> (2009)
<i>Polypodiisporites</i> sp.	Schizaceae	Filicales	Filicopsida	van de Schootbrugge <i>et al.</i> (2009)
<i>Punctatisporites globosus</i>	Marattiaceae; Osmundaceae	Filicales; Marattiales	Filicopsida	Balme (1995); Wang <i>et al.</i> (2001)
<i>Stereisporites cicatricosus</i>	Sphagnaceae	Sphagnales	Sphagnopsida	Askin (1990)
<i>Stereisporites seebergensis</i>	Sphagnaceae	Sphagnales	Sphagnopsida	Askin (1990)
<i>Stereisporites stereoides</i>	Sphagnaceae	Sphagnales	Sphagnopsida	Askin (1990)
<i>Trachysporites asper</i>	—	—	Filicopsida	Bonis (2010)
<i>Trachysporites cf. sparsus</i>	—	—	Filicopsida	Bonis (2010)
<i>Trachysporites fuscus</i>	—	—	Filicopsida	Bonis (2010)
<i>Triancoraesporites ancorae</i>	—	—	Lycopsida	Bonis (2010)
<i>Uvaeisporites reisingerii</i>	Selaginellaceae	Selaginellales	Lycopsida	Balme (1995); Looy <i>et al.</i> (2005)

Order- and class-level affinities from Mander *et al.* (2010). ‘—’ indicates an unknown botanical affinity, or that no published information on the botanical affinity of a particular sporomorph was available.

Table 1. Botanical affinities of spores recovered from the plant beds at Astartekløft.

Pollen taxon	Family	Order	Class	Reference
<i>Alisporites diaphanus</i>	Corystospermaceae	Coniferales; Corystospermales	Coniferopsida; Pteridospermopsida	Osborn & Taylor (1993); Balme (1995); Traverse (2007); <i>Masculostrobus</i> unknown Family (Alvin <i>et al.</i> , 1994)
<i>Alisporites radialis</i>	Corystospermaceae	Coniferales; Corystospermales	Coniferopsida; Pteridospermopsida	Osborn & Taylor (1993); Balme (1995); Traverse (2007); <i>Masculostrobus</i> unknown Family (Alvin <i>et al.</i> , 1994)
<i>Alisporites robustus</i>	Corystospermaceae	Coniferales; Corystospermales	Coniferopsida; Pteridospermopsida	Osborn & Taylor (1993); Balme (1995); Traverse (2007); <i>Masculostrobus</i> unknown Family (Alvin <i>et al.</i> , 1994)
<i>Alisporites</i> sp.	Corystospermaceae	Coniferales; Corystospermales	Coniferopsida; Pteridospermopsida	Osborn & Taylor (1993); Balme (1995); Traverse (2007); <i>Masculostrobus</i> unknown Family (Alvin <i>et al.</i> , 1994)
<i>Araucariacites australis</i>	Araucariaceae	Coniferales	Coniferopsida	Balme (1995)
<i>Cerebropollenites thiergartii</i>	—	Coniferales	Coniferopsida	van Konijnenburg-van Cittert & van der Burgh (1989)
<i>Chasmatosporites elegans</i>	—	Cycadales; Ginkgoales	Cycadopsida; Ginkgopsida	Batten & Dutta (1997)
<i>Chasmatosporites hians</i>	—	Cycadales; Ginkgoales	Cycadopsida; Ginkgopsida	Batten & Dutta (1997)
<i>Classopollis ?zwoinskai</i>	Cheirolepidiaceae	Coniferales	Coniferopsida	Harris (1979); Balme (1995)
<i>Classopollis meyeriana</i>	Cheirolepidiaceae	Coniferales	Coniferopsida	Harris (1979); Balme (1995)
<i>Classopollis torosus</i>	Cheirolepidiaceae	Coniferales	Coniferopsida	Harris (1979); Balme (1995)
<i>Cycadopites</i> sp.	Cycadaceae; Ginkgoaceae; Peltaspermales; Bennettiales	Cycadales; Ginkgoales; Peltaspermales; Bennettiales	Cycadopsida; Ginkgopsida; Pteridospermopsida; Bennettitopsida	Townrow (1960); Balme (1995)
<i>Eucommiidites troedssonii</i>	Erdtmanitheaceae	Erdtmanithecales	—	Friis & Pedersen (1996)
<i>Lunatisporites rhaeticus</i>	Corystospermaceae	Coniferales; Corystospermales	Coniferopsida; Pteridospermopsida	Balme (1995); Traverse (2007); <i>Masculostrobus</i> unknown Family (Alvin <i>et al.</i> , 1994)
<i>Monosulcites minimus</i>	—	Bennettiales	Bennettitopsida	Pedersen <i>et al.</i> (1989)
<i>Ovalipollis breviformis</i>	—	—	—	—
<i>Ovalipollis ovalis</i>	—	—	—	—
<i>Perinopollenites cf. elatoides</i>	Taxodeaceae	Coniferales	Coniferopsida	van Konijnenburg-van Cittert & van der Burgh (1989)
<i>Perinopollenites elatoides</i>	Taxodeaceae	Coniferales	Coniferopsida	van Konijnenburg-van Cittert & van der Burgh (1989)
<i>Pinuspollenites</i> cf. <i>pinoides</i>	—	—	Coniferopsida; Pteridospermopsida	Traverse (2007); Leslie (2008)
<i>Pinuspollenites minimus</i>	—	—	Coniferopsida; Pteridospermopsida	Traverse (2007); Leslie (2008)
<i>Protahaploxyipinus hercynicus</i>	—	Coniferales; Glossopteridales	Coniferopsida; Pteridospermopsida	Traverse (2007)
<i>Quadraeculina anaeallaeformis</i>	—	Coniferales	Pteridospermopsida	Bonis (2010)
<i>Ricciisporites tuberculatus</i>	—	—	—	—
<i>Rhaetipollis germanicus</i>	—	—	—	—
<i>Vesicaspora fuscus</i>	—	—	—	—
<i>Vitreisporites bjuvensis</i>	—	Caytonales	Pteridospermopsida	Balme (1995); Traverse (2007)
<i>Vitreisporites pallidus</i>	—	Caytonales	Pteridospermopsida	Balme (1995); Traverse (2007)

Order- and class-level affinities from Mander *et al.* (2010). '—' indicates an unknown botanical affinity, or that no published information on the botanical affinity of a particular sporomorph was available. Pollen referable to *Monosulcites minimus* has been found *in situ* within the Triassic seed cone *Vardekloefia* (Pedersen *et al.*, 1989) but *Vardekloefia* has not yet been assigned to a family (Pedersen *et al.*, 1989; see Stockey & Rothwell, 2003).

Table 2. Botanical affinities of pollen recovered from the plant beds at Astartekløft.

Depositional environment	Plant bed	Total number of samples from Astartekløft	Total number of sporomorph taxa at Astartekløft	Sporomorphs with known affinity						Sporomorphs with multiple affinities					
				Family			Order			Class			Family		
				n	%	n	n	%	n	n	%	n	n	%	n
		40	56	28	50.0	36	64.3	48	85.7	10	35.7	10	27.8	11	22.9
		Sample number (Mander <i>et al.</i> , 2010)	Total number of sporomorph taxa in sample												
Abandoned channel	7	7_7269 7_7259 7_7249 7_7239 6_6106 6_6086 6_6076 5_4718 5_4708 5_4698 5_4688 5_4678 5_4668 5_4658 5_4648 5_4638 4_4107 4_4097 4_4087 4_4077 4_4067 4_4057 3_3771 3_3761 3_3751 3_3715 2_3413 2_3403 2_3393 2_3373 2_3363 2_3353 2_3343 15_2321 1_1388 1_1378 1_1368 1_1358 1_1348 1_1338	40 23 35 33 18 26 24 33 25 28 28 20 26 25 25 15 29 29 30 24 32 31 25 33 30 31 29 30 31 28 34 31 30 29 30 31 28 34 30 33 33 27 32 28	21 13 19 20 11 16 13 19 17 15 16 13 16 16 13 10 15 15 17 13 18 17 12 18 16 15 15 16 19 14 19 17 18 20 14 17 15 16 14 15 16 19 14 13 16 16	52.5 56.5 54.3 60.6 61.1 61.5 54.2 57.6 68.0 53.6 57.1 65.0 61.5 64.0 52.0 66.7 51.7 51.7 56.7 54.2 56.3 54.8 48.0 53.3 54.5 57.1 48.4 51.7 53.3 61.3 50.0 55.9 54.8 60.0 60.6 56.0 51.5 51.9 56.3 57.1	28 17 25 26 11 21 17 25 21 21 21 15 20 18 17 10 22 22 20 15 22 22 16 23 20 21 21 22 22 22 22 22 26 22 22 24 18 23 19 22 20	70.0 73.9 71.4 78.8 61.1 80.8 70.8 75.8 84.0 75.0 75.0 75.0 76.9 72.0 68.0 66.7 72.4 75.9 66.7 62.5 68.8 71.0 64.0 66.7 69.7 71.4 67.7 70.0 71.0 65.5 67.5 71.0 73.3 72.0 69.7 70.4 68.8 71.4	34 22 32 30 17 25 30 23 25 25 18 24 22 21 13 26 26 25 20 28 22 27 20 28 28 25 25 25 25 26 28 28 27 27 26 27 29 23 27 25	85.0 95.7 91.4 90.9 94.4 96.2 91.7 90.9 92.0 89.3 89.2 90.0 92.3 88.0 84.0 86.7 86.2 89.7 83.3 83.3 87.5 87.1 80.0 84.8 90.7 90.7 80.6 82.8 83.3 83.9 78.6 91.2 90.3 86.7 81.8 80.0 87.9 85.2 89.3	7 5 8 8 4 6 8 8 8 4 5 4 6 5 4 1 6 7 7 6 6 9 6 3 9 7 5 7 5 5 6 8 6 6 5 8 6 7 6 6 6 7 6 6	33.3 38.5 42.1 40.0 36.4 37.5 46.2 42.1 47.1 26.7 31.3 30.8 37.5 31.3 30.8 10.0 40.0 46.7 35.3 46.2 50.0 35.3 25.0 50.0 43.8 41.7 46.7 40.0 31.3 36.8 35.7 42.1 35.3 38.9 40.0 42.9 41.2 42.9 38.9 37.5	7 5 9 9 1 5 6 9 8 6 5 5 6 5 0 23 8 8 4 6 4 6 3 9 6 4 5 7 4 5 6 7 10 7 7 6 6 8 6 7 6 6 6 6 6 6 6 6	25.0 29.4 36.0 34.6 9.1 23.8 35.3 36.0 38.1 28.6 23.8 26.7 30.0 27.8 29.4 0.0 23.8 36.4 20.0 40.0 36.4 22.7 18.8 39.1 30.0 26.7 33.3 26.3 28.6 31.8 31.6 38.5 31.8 31.8 29.2 33.3 34.8 31.6 31.8 30.0	8 6 10 10 2 5 6 10 9 7 6 5 7 6 1 5 9 9 4 5 7 5 4 4 10 7 8 5 7 11 8 7 8 6 9 7 8 7 7 7 7	23.5 27.3 31.3 33.3 11.8 20.0 27.3 33.3 39.1 28.0 24.0 27.8 29.2 27.3 28.6 7.7 20.0 34.6 20.0 35.0 32.1 18.5 20.0 35.7 28.0 26.3 32.0 20.8 28.0 30.8 31.8 35.5 28.6 26.9 29.6 30.0 31.0 30.4 29.6 28.0

Environments of deposition from McElwain *et al.* (2007). Sample number as follows: [plant bed number]_[stratigraphic height in centimetres]. Stratigraphic height from the sedimentary log of Hesselbo *et al.* (2002).

Table 3. Summary of data reported in this study.

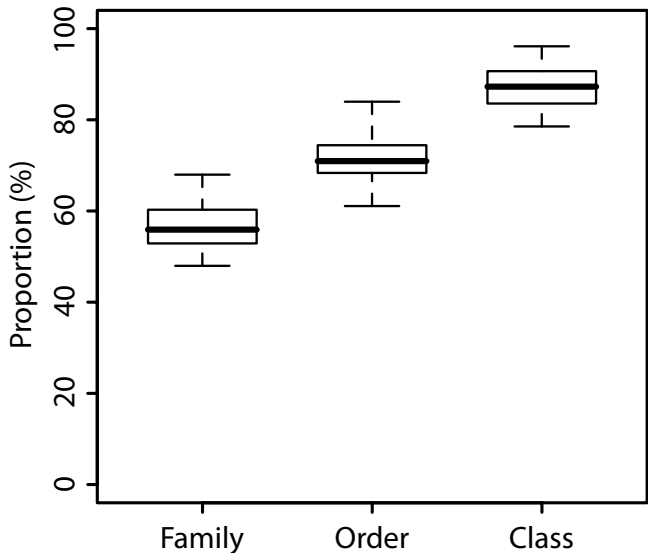


Fig. 3. Box and whisker plot showing the percentage of sporomorphs with a known botanical affinity at the family, order and class levels in individual samples from Astartekløft. Boxes show median and inter-quartile range, whiskers represent maximum and minimum values.

28%) (Table 3; Fig. 5). A Kruskal–Wallis test indicates that there is a statistically significant difference in the median of each group (family, order and class) ($KW = 42.94_{40, 40, 40}$ $p < 0.0001$). Pairwise Mann–Whitney tests show that the median proportion of sporomorphs with multiple botanical affinities at the family level is significantly higher than the median proportion of multi-affinity sporomorphs at both the order and class level (Table 4). However, there is no statistically significant difference in the median proportion of multi-affinity sporomorphs between the order and class levels (Table 4).

There is a qualitative increase in the range of percentage values from plant bed 1 to plant bed 5 at Astartekløft, such that the difference between the maximum and minimum proportions of multi-affinity sporomorphs is greatest in plant bed 5 (Fig. 6). Indeed, a single sample from plant bed 5 (labelled 5_4638 in Table 3) has a considerably lower proportion of multi-affinity sporomorphs at all taxonomic levels than other samples (Table 3; Fig. 6). However, there are no statistically significant differences in the median proportion of sporomorphs with multiple botanical affinities between plant beds at Astartekløft (family: $KW = 7.446_{6, 1, 4, 7, 6, 9, 3, 4}$ $p = 0.384$; order: $KW = 3.165_{6, 1, 4, 7, 6, 9, 3, 4}$ $p = 0.8693$; class: $KW = 6.690_{6, 1, 4, 7, 6, 9, 3, 4}$ $p = 0.4618$).

DISCUSSION

With how much taxonomic precision do sporomorphs record the source vegetation across the Tr–J at Astartekløft?

The data presented here provide a clear picture about the taxonomic precision with which sporomorphs record the source vegetation at Astartekløft. Something is known of the botanical affinity of almost all sporomorphs across the Tr–J at Astartekløft at the class level (e.g. Table 3; Fig. 3), and this strongly supports the idea that ‘at least the broad botanical relationship is known for practically all Mesophytic sporomorphs’ (Traverse, 2007, p. 312). However, just 50% of sporomorph taxa at Astartekløft have a known botanical affinity at the family level (e.g. Table 3), and this highlights that reconstructions of Tr–J vegetation based on sporomorphs at Astartekløft (e.g. Pedersen & Lund, 1980) are hampered by considerable taxonomic imprecision because the parent plants of many sporomorphs are unknown at the family level.

Additionally, although something is known of the botanical affinity of most sporomorphs at Astartekløft (e.g. Fig. 3), a considerable number of these sporomorphs have affinities to more than one parent plant. For example, ~23% of all sporomorph taxa at Astartekløft have affinities to more than one parent plant class, and ~36% of all sporomorph taxa at Astartekløft have affinities to more than one parent plant family (e.g. Table 3), and this compounds the taxonomic imprecision of sporomorph assemblages at Astartekløft. Three groups of sporomorphs stand out as ‘problem taxa’ that are morphologically invariant among certain parent plant classes, orders and/or families: smooth trilete spores, smooth or scabrate ‘boat-shaped’ monosulcate pollen grains, and bisaccate pollen grains. Among smooth trilete spores, *Deltoidospora toralis* has affinities to four parent families and *Concavisporites* spp. has affinities to two parent plant families (Table 1). Among bisaccate pollen grains, *Alisporites*, *Pinuspollenites*, *Lunatisporites* and *Protohaploxypinus* have affinities to two parent classes and orders (Table 2). Among ‘boat-shaped’ monosulcate pollen grains, *Cycadopites* has affinities to four parent classes, orders and families, while *Chasmatosporites* has affinities to two classes and orders (Table 2).

Several authors have commented on these ‘problem taxa’. Balme (1995) noted that smooth or scabrate ‘boat-shaped’ monosulcate pollen grains are almost identical when viewed under light microscopy despite being produced by several plant orders (e.g. Frederiksen, 1980) and Mesozoic bisaccate pollen is similarly difficult to cope with systematically (e.g. Traverse, 2007). The bisaccate morphogenus *Alisporites* has strong affinities to both conifers and corystosperms (a clade of

<i>p</i> -values for Mann–Whitney tests of differences in median							
	Known affinity				Multiple affinities		
	Family	Order	Class		Family	Order	Class
Family	—	—	—	Family	—	—	—
Order	<0.0001	—	—	Order	<0.0001	—	—
Class	<0.0001	<0.0001	—	Class	<0.0001	0.1223	—

Table 4. Pairwise Mann–Whitney significance tests of differences in the median proportion of sporomorphs with known botanical affinities and multiple botanical affinities, at the family order and class level at Astartekløft.

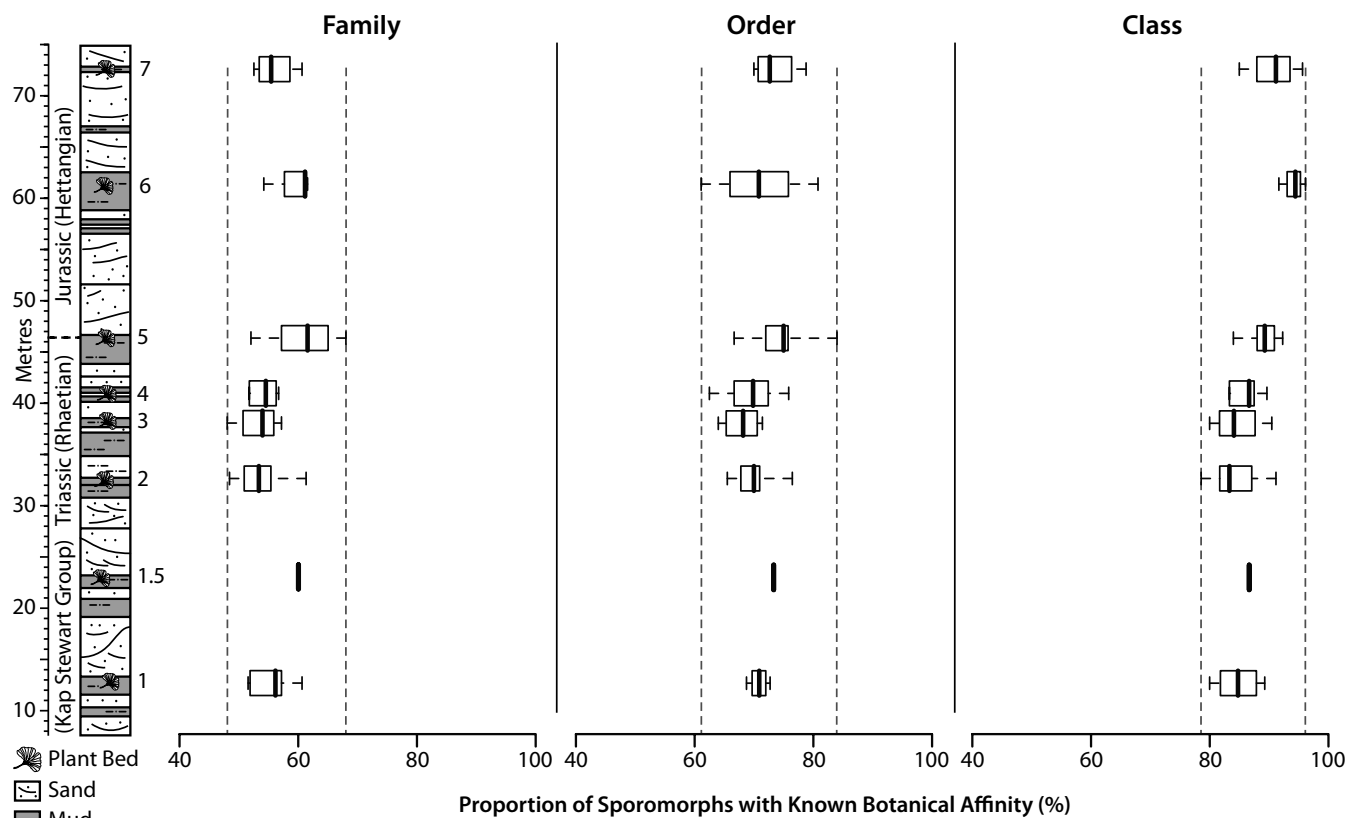


Fig. 4. Box and whisker plots showing the percentage of sporomorphs with a known botanical affinity at the family, order and class levels within each plant bed at Astartekløft. Boxes show median and interquartile range, whiskers represent maximum and minimum values. Vertical grey dashed lines represent minimum and maximum percentages recorded in the entire section, which correspond to the maximum and minimum percentages shown in Figure 3 (see also Table 3).

seed-ferns) (Table 2) and is a classic case of morphological invariance of a sporomorph at a high taxonomic level.

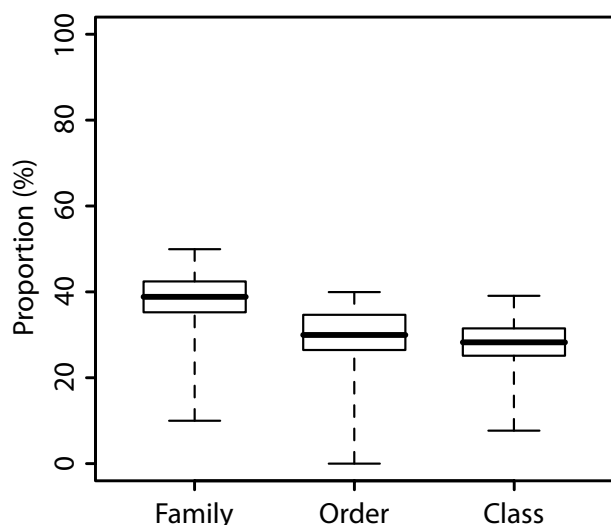


Fig. 5. Box and whisker plot showing the percentage of sporomorphs with multiple botanical affinities at the family, order and class levels in individual samples from Astartekløft. Boxes show median and interquartile range, whiskers represent maximum and minimum values.

Traverse (2007, p. 317) commented, ‘It seems likely that the conifer and corytosperm bisaccate pollen referred to this morphogenus will eventually be separated’, but splitting sporomorphs into biologically meaningful morphotypes is not straightforward. Scanning electron microscopy (SEM) can be used to separate different sporomorph morphotypes but characters visible under SEM, such as very fine surface sculpture, are not always visible under light microscopy (e.g. Liu *et al.*, 2007) because the diffraction limit of light limits the resolution of most high numerical aperture objectives to 250–300 nm (Weiss, 2000). Just as one sporomorph morphotype can have affinities to more than one parent plant, one plant can produce a number of different sporomorph morphotypes. For example, Lindström *et al.* (1997) demonstrated that Late Permian glossopterid sporangia contained saccate pollen grains referable to at least two separate bisaccate morphogenera (*Protohaploxypinus* and *Striatopodocarpidites*), together with sporadic monosaccate and trisaccate grains that could be assigned to several other morphotaxa. Such intraspecific and/or ontogenetic variation in sporomorph morphology highlights that separation of dispersed sporomorphs into as many morphotypes as possible is not an appropriate way to improve the taxonomic resolution of the sporomorph record, and reinvestigation of *in situ* material, together with focused ultrastructural studies, is essential.

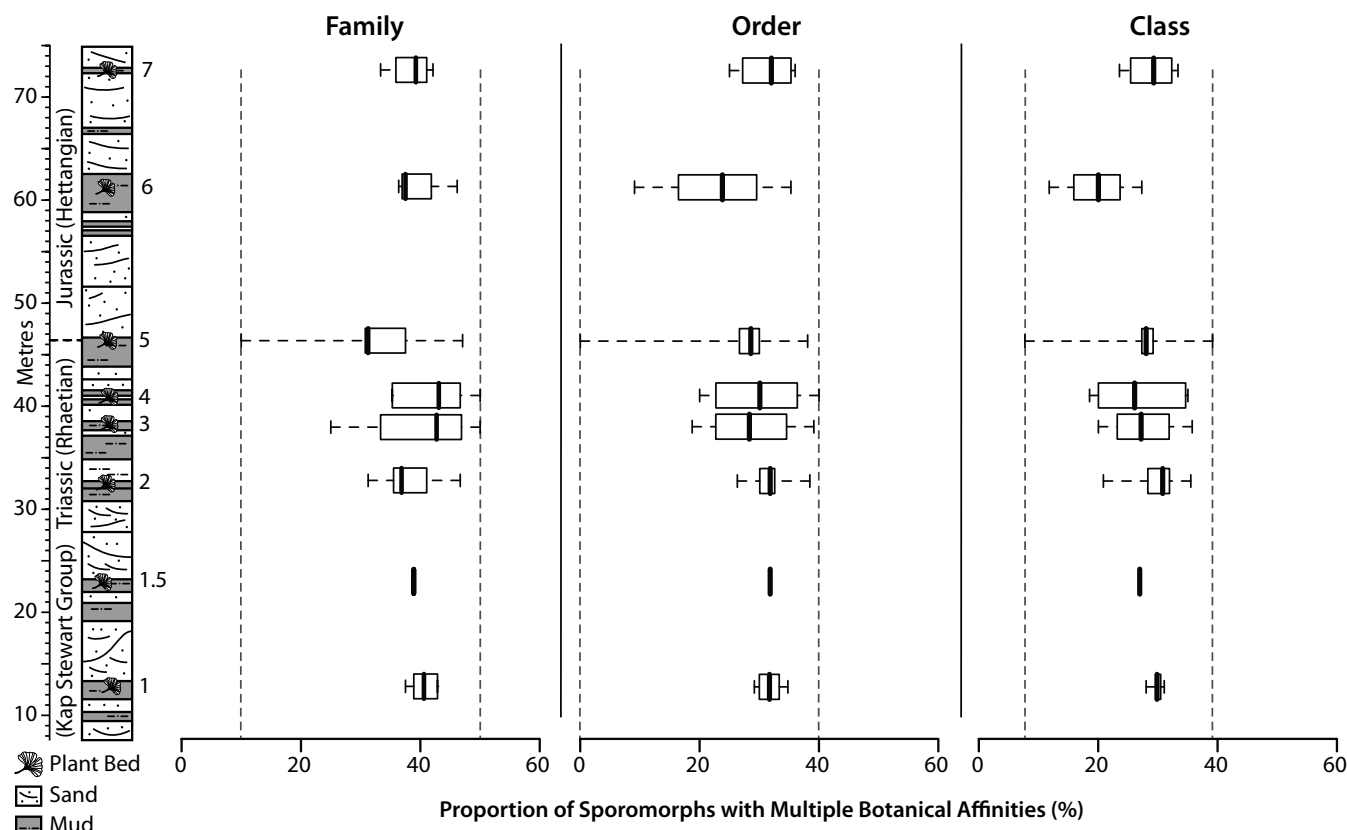


Fig. 6. Box and whisker plots showing the percentage of sporomorphs with multiple botanical affinities at the family, order and class levels within each plant bed at Astartekløft. Boxes show median and interquartile range, whiskers represent maximum and minimum values. Vertical grey dashed lines represent minimum and maximum percentages recorded in the entire section, which correspond to the maximum and minimum percentages shown in Figure 5 (see also Table 3).

Vegetation composition and diversity at Astartekløft

The taxonomic resolution of the sporomorph record at Astartekløft does not change appreciably through time (Figs 4, 6). This implies that reconstructions of vegetation based on sporomorphs will be taxonomically smoothed to a very similar degree in the eight plant beds and three different depositional environments at Astartekløft that have been analysed here (see Fig. 2). It has been shown previously that there is a significant and likely permanent change in the composition of sporomorph assemblages across the Tr–J at Astartekløft (Mander *et al.*, 2010). This compositional change begins in the topmost upper Rhaetian (plant bed 5; see Fig. 2) and is sustained into the Hettangian (plant beds 6 and 7; see Fig. 2) (Mander *et al.*, 2010). Given that the proportion of sporomorphs with a known botanical affinity at the class level is highest in plant bed 6 and that certain samples in plant bed 5 contain the lowest proportion of multi-affinity sporomorphs (Figs 4, 6), this compositional change did not result in a loss of taxonomic precision among Tr–J sporomorph assemblages at Astartekløft.

The results presented here also strongly support the idea that sporomorphs underestimate the number of plant taxa in the source vegetation at Astartekløft (Mander *et al.*, 2010). For example, the pollen grain *Cycadopites* was produced by at least four different plant families at the Tr–J (Table 2). Under the assumption that each of these families is monospecific, then this taxon masks at least three additional species. By repeating this

for each sporomorph taxon at Astartekløft (see Tables 1, 2), the total number of sporomorph taxa rises from 56 to 75. This suggests that sporomorphs underestimate the diversity of the source vegetation at Astartekløft by at least ~25%. Such underestimation of diversity is expected based on comparisons of floristic and sporomorph diversity in the modern world. For example, as reviewed by Odgaard (1999), 2990 species were reported in the flora of vascular plants in the British Isles by Stace (1991), but just 390 sporomorph taxa were included in the list of pollen and spore types of vascular plants in the British Isles by Bennett (1996). Changes in sporomorph diversity across the Tr–J in East Greenland (Mander *et al.*, 2010) and in central Europe (e.g. Bonis *et al.*, 2009) are, therefore, likely to underestimate the magnitude of diversity changes in the source vegetation, as has been suggested for the sporomorph record of vegetation change during the Paleocene–Eocene Thermal Maximum in North America (Harrington & Jaramillo, 2007).

Taxonomic imprecision of Tr–J sporomorph assemblages at Astartekløft: macrofossils and implications

Macrofossil assemblages at Astartekløft contain a high proportion of woody plants, such as cycads, bennettites, ginkgos and conifers, whereas sporomorph assemblages contain a high proportion of spore-producing plants, such as ferns (Table 5; Mander *et al.*, 2010). This highlights that macrofossils and sporomorphs provide different and complementary pictures of

Plant group	Macrofossils vs. sporomorphs	Mean difference (%)
Ferns	Generally a greater component of sporomorph record	-22
Conifers and corytosperms	Far greater component of macrofossil record where <i>Podozamites</i> and <i>Stachyotaxus</i> dominate	12
Monosulcate producers	Almost entirely absent from sporomorph record	49

The plant group 'Monosulcate producers' comprises cycads, bennettites, ginkgos and the seed-fern *Lepidopteris*. 'Mean difference' refers to the average discrepancy between the macrofossil and sporomorph records of each plant group at Astartekløft (from Mander *et al.*, 2010).

Table 5. Comparison of macrofossil and sporomorph records of the source vegetation at Astartekløft.

the source vegetation at Astartekløft. Certain aspects of Tr–J vegetation change at Astartekløft are not recorded in the sporomorph record but are clearly expressed in the macrofossil record. For example, the extinction of the Peltaspermaeae at the Tr–J boundary is clear in the macrofossil record and is marked by the disappearance of the leaf genus *Lepidopteris* (e.g. McElwain *et al.*, 2007), but this extinction is masked in the sporomorph record because of the morphological invariance of the pollen grain *Cycadopites* among the Cycadales, Ginkgoales, Bennettitales and Peltaspermales (Table 2; Mander *et al.*, 2010). This provides support for the view that macrofossils can offer a more taxonomically precise view of the source vegetation than sporomorphs (e.g. Jackson & Booth, 2007), and highlights that in certain situations macrofossils can be usefully incorporated into studies of Tr–J vegetation change.

There are other cases, however, that urge caution in the use of macrofossils to study vegetation change across the Tr–J. For example, 10 species of *Pterophyllum* have been reported from the Jameson Land region in East Greenland (Harris, 1937), but a recent comprehensive macromorphological and cuticular study of bennettitaleans from Sweden has reduced the number of mid-Mesozoic bennettite species within *Pterophyllum* to just five (Pott & McLoughlin, 2009). Such taxonomic over-splitting means that the ~85% decline in standing species richness in the Jameson Land region at the Tr–J (Harris, 1937; McElwain *et al.*, 2007) is probably too high and full taxonomic revision of the macrofossils in this region is necessary. This highlights that for some groups it is unclear to what extent current fossil leaf taxonomy reflects true plant diversity in the source vegetation. Palaeoecological studies undertaken at the generic level (e.g. McElwain *et al.*, 2007, 2009) are more robust to such problems because they are more taxonomically conservative.

Sporomorphs provide an excellent record of ancient vegetation because they have high fossilization potential, are widely dispersed and thus representative of regional vegetation (e.g. Farley, 1990), and can be sampled at very high stratigraphic resolution. This study has provided an example of one key limitation of sporomorphs: they record the source vegetation at low taxonomic resolution (e.g. Figs 4, 6). There are some situations in which such taxonomic imprecision may be less problematic, such as in large-scale analyses of sporomorph diversity over long time periods where the number of morphospecies (rather than their systematic affinity) is the primary consideration (e.g. Jaramillo *et al.*, 2006). There are other situations, however, where such taxonomic imprecision is wholly undesirable. For example, when interpreting diagrams of the percentages of sporomorph taxa across the Tr–J (e.g. Pedersen & Lund, 1980; Kuerschner *et al.*, 2007; Bonis *et al.*, 2009; van de

Schootbrugge *et al.*, 2009), it should be borne in mind that smooth trilete spores (such as *Deltoidospora*), smooth or scabrate 'boat-shaped' monosulcate pollen grains (such as *Cycadopites*) and bisaccate pollen grains (such as *Alisporites*) are 'problem taxa' that have affinities to several parent plant groups (e.g. Tables 1, 2).

CONCLUDING REMARKS

1. Reconstructions of Tr–J vegetation based on sporomorphs at Astartekløft (e.g. Pedersen & Lund, 1980) are hampered by considerable taxonomic imprecision. Something is known of the botanical affinity of almost all sporomorphs at Astartekløft at the class level (e.g. Table 3; Fig. 3), but just 50% of sporomorph taxa at Astartekløft have a known botanical affinity at the family level (e.g. Table 3). Additionally, ~23% of all sporomorph taxa at Astartekløft have affinities to more than one parent plant class, and ~36% of all sporomorph taxa at Astartekløft have affinities to more than one parent plant family (e.g. Table 3). This taxonomic imprecision should be taken into account when interpreting diagrams of the percentages of sporomorph taxa across the Tr–J in East Greenland (e.g. Pedersen & Lund, 1980) and elsewhere in Europe (e.g. Kuerschner *et al.*, 2007; Bonis *et al.*, 2009; van de Schootbrugge *et al.*, 2009).
2. The taxonomic resolution of the sporomorph record remains fairly constant across the Tr–J at Astartekløft. No single plant bed or depositional environment stands out as having a markedly lower or higher proportion of sporomorphs with a known botanical affinity (Fig. 4), or a markedly lower or higher proportion of sporomorphs with affinities to more than one parent plant (Fig. 6).
3. Three groups of sporomorphs stand out as 'problem taxa' that are morphologically invariant among certain parent plant classes, orders and/or families. These are: (a) the smooth trilete spores *Deltoidospora toralis* (four parent families) and *Concavisporites* spp. (two parent plant families) (Table 1); (b) the bisaccate pollen grains *Alisporites*, *Pinuspollenites*, *Lunatisporites* and *Protohaploxylinus* (two parent classes and orders) (Table 2); (c) the 'boat-shaped' monosulcate pollen grains *Cycadopites* (four parent classes, orders and families) and *Chasmatosporites* (two parent classes and orders) (Table 2). Detailed investigation of reproductive structures to find sporomorphs *in situ*, re-investigation of existing *in situ* material, and ultrastructural studies of problematic sporomorphs should improve the taxonomic resolution of the Tr–J sporomorph record.

4. Sporomorphs probably underestimate the diversity of the source vegetation at Astartekløft by at least ~25%, and changes in sporomorph diversity across the Tr–J (e.g. Bonis *et al.*, 2009; Mander *et al.*, 2010) are likely to underestimate the magnitude of diversity changes in the source vegetation. If data from the plant fossil record are to be brought to bear on issues such as the present-day climate and biodiversity crises (e.g. McElwain & Punyasena, 2007), it is essential that the relationship between dispersed sporomorph diversity and the diversity of plants in the source vegetation is well understood.

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