Palynostratigraphy and vegetation history of the Triassic–Jurassic transition in East Greenland

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Abstract: We present a palynological study of a terrestrial Triassic–Jurassic (Tr–J; c. 200 Ma) boundary section at Astartekløft, East Greenland. We have generated a new palynostratigraphic scheme and vegetation history for this locality, and have integrated these with existing carbon isotope records. Samples for palynological analysis were collected from precisely the same stratigraphic horizons as plant macrofossils and samples used for geochemical analyses. Our results highlight four local sporomorph assemblage zones that are compositionally distinct from each other at Astartekløft. The extremely low abundance of Classopollis pollen in all samples, and the pronounced decline of Ricciisporites tuberculatus during the Late Rhaetian are notable features of the sporomorph record of Tr–J vegetation at Astartekløft. Correlation of Astartekløft and a marine Tr–J boundary section at St Audrie’s Bay, UK, provides no support for the idea that extinction and diversity loss in terrestrial ecosystems preceded biotic change in marine ecosystems at the Tr–J. Instead, the available data support suggestions that the onset of the Tr–J biotic crisis was synchronous in terrestrial and marine environments. Peak extinction among plants at Astartekløft occurred relatively late in the sequence of events across the Tr–J, and may represent a response to long-term cumulative effects of volcanism at this time.

Supplementary material: Plates of selected sporomorphs recovered from Astartekløft and a full pollen diagram are available at www.geolsoc.org.uk/SUP18553.

During the transition from the Triassic to the Jurassic period (Tr–J; 201.31 ± 0.43 Ma; Schoene et al. 2010) the Earth’s biota underwent a major reorganization that culminated in the extinction of 23% of marine families and 22% of terrestrial families (Benton 1995). It is generally thought that the effects of flood basalt eruption in the Central Atlantic Magmatic Province, such as rising CO2 and global warming (e.g. McElwain et al. 1999; Bonis et al. 2010a; Schaller et al. 2011; Steinthorsdottir et al. 2011), were the cause of Tr–J biotic change (e.g. Deenen et al. 2010; Whiteside et al. 2010). In East Greenland, plant macrofossils (mostly leaves) preserve a c. 17% genus-level extinction and an abrupt decline in terrestrial plant diversity (McElwain et al. 2007, 2009). Sporomorph (pollen and spore) assemblages from this region are 10–12% less taxonomically diverse in the Tr–J boundary interval than in the Late Triassic, and there is evidence that emigration and/or extirpation of plants led to compositional change in the source vegetation (Mander et al. 2010).

However, owing to the lack of a robust correlation between the exact horizons containing plant macrofossils in East Greenland (the ‘plant beds’ of McElwain et al. 2007) and Tr–J boundary sections in well-studied areas such as Europe, it is difficult to fit the results of palaeoecological investigations in East Greenland (e.g. McElwain et al. 2007, 2009; Mander et al. 2010) into the wider picture of Tr–J biotic change (e.g. Deenen et al. 2010; Whiteside et al. 2010). Additionally, since the earlier palynological work in East Greenland (Pedersen & Lund 1980; Koppelhus 1996) there has been a surge in palynological studies of Tr–J boundary sections (e.g. Kuerschner et al. 2007; Bonis et al. 2009, 2010b; Götz et al. 2009, 2011; Larsson 2009; Ruckwied & Götz 2009; van de Schootbrugge et al. 2009; Bonis & Kürschner 2012), but the exact nature of Tr–J vegetation change as recorded by sporomorphs from the plant beds in East Greenland is also unclear, and this hampers regional comparison of Tr–J vegetation change.

To address these issues, we have undertaken a palynological study of a Tr–J boundary section at Astartekløft, East Greenland. We have generated a new palynostratigraphic scheme and vegetation history for this locality and have integrated these with existing carbon isotope records. Samples for palynological analysis were collected from precisely the same stratigraphic horizons as plant macrofossils and samples used for geochemical analyses. This allows the results of palaeoecological analyses based on macrofossils at this locality to be directly compared with palaeoecological analyses of other fossil organisms in other regions.

Building on the work of Mander et al. (2010), the aims of this paper are as follows: (1) to develop a palynostratigraphic scheme for the plant beds at Astartekløft; (2) to correlate the plant beds at Astartekløft with a marine Tr–J boundary section at St Audrie’s Bay (Fig. 1) and integrate the palynostratigraphic schemes and carbon isotope records at these localities; (3) to compare the pattern of extinction among plants at Astartekløft with the pattern of extinction among marine bivalves at St Audrie’s Bay; (4) to reconstruct Tr–J vegetation history at Astartekløft using sporomorphs and compare the results with palynological investigations of other Tr–J boundary sections.

Materials and methods

Geological setting
The rock succession at Astartekløft comprises the fluviolacustrine Kap Stewart Group, which was deposited on the margins of the Kap Stewart lake, situated in the south of the East Greenland
rift basin (Dam & Surlyk 1992). The plant beds at Astartekløft are a series of muddy and silty horizons within the Primulaelv Formation, which was deposited in a delta plain setting (Dam & Surlyk 1992; Surlyk 2003; McElwain et al. 2007). The absence of marine palynomorphs from Astartekløft indicates that environments of depositional sites were exclusively terrestrial (Pedersen & Lund 1980; Koppelhus 1996). 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 channel (McElwain et al. 2007; Table 1). Plant bed 6 consists of coaly mudstones and all other plant beds consist of dark grey mudstones and siltstones.

**Palynology**

Forty rock samples from plant beds 1–7 at Astartekløft were productive for sporomorphs (Table 1). Samples from sediments between each plant bed were barren for sporomorphs. Between 15 and 20 g of each rock sample was washed and crushed, then dried for 24 h at 60 °C. Each sample was treated twice alternately with cold HCl (30%) to remove carbonate minerals. The residue from each sample was washed with water until pH neutral, then sieved with 250 μm and 15 μm 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 are available on request. At least 350 sporomorphs were counted per slide, but where one morphotype dominated the sporomorph assemblage, counts were increased until at least 150 sporomorphs of the non-dominant type were recorded. A total of 14579 single sporomorphs and 56 sporomorph taxa were recorded from the 40 productive samples. Sporomorph identification was based on Morbey (1975), Lund (1977) and Pedersen & Lund (1980). The computer program Tilia (Grimm 1991–2001) has been used to display changes in the proportion of each sporomorph taxon through time at Astartekløft. Statigraphically constrained cluster analysis (CONISS; Grimm 1977) has been used to define local sporomorph assemblage zones at Astartekløft so as to develop a palynostratigraphy of this locality.

**Palynostratigraphy and correlation of Astartekløft**

**Definition of sporomorph assemblage zones**

There are marked changes in the relative abundance of sporomorph taxa through time at Astartekløft and four local sporomorph assemblage zones can be recognized (Fig. 2). These are as follows.

**Zone A1.** This zone comprises plant beds 1, 1.5 and 2. It is characterized by abundant Ricciisporites tuberculatus, which regularly constitutes 40–50% of the total sporomorph assemblages, and the frequent occurrence of Ovalipollis ovalis and Rhaetipollis germanicus. Limbosporites lunbladii and Lunatisporites sp. are also present in this zone.

**Zone A2.** This zone comprises plant beds 3 and 4. The base of this zone is marked by a local acme of L. lunbladii, which reaches 51% of the total sporomorph assemblage in one sample from plant bed 3, and an increase in the relative abundance of Uvaeasporites reissingeri. An increase in the relative abundance of Deltoidospora toralis is characteristic of Zone A2 and R. tuberculatus remains an important component of sporomorph assemblages in this zone. R. germanicus remains frequent in this zone and Lunatisporites sp. is also present. O. ovalis disappears in the upper part of this zone (single occurrences of this species in samples from stratigraphically higher plant beds are probably reworked).

**Zone A3.** This zone comprises plant bed 5, and represents the ‘Transition Zone’ of Harris (1937). It is characterized by the co-dominance of U. reissingeri and Baculatisporites comaumensis, and also records local acmes of Calamospora tener and Peripolenenites elatoides. L. lunbladii is scarce and this zone perhaps records the local disappearance of this species (a single occurrence some 23 m higher in the section may be reworked). R. tuberculatus declines in importance and constitutes less than 20% of the sporomorph assemblages, before disappearing at the top of this zone. Lunatisporites sp. also disappears in the upper part of this zone and R. germanicus disappears in this zone at 46.98 m in the section (single occurrences of these species in samples from stratigraphically higher plant beds are probably reworked). This zone records the lowest occurrence of Cerebropollenites thiergartii at 46.68 m in the section.

**Zone A4.** This zone comprises plant beds 6 and 7. The base of this zone is marked by local acmes of D. toralis (55%) and Punctatisporites globosus (25%). This zone records the lowest occurrence of Heliosporites altmarkensis and is characterized by an increase in the relative abundance of Trachysporites fuscus. The stratigraphic position of the top of this zone is unknown, but the highest samples in this study (plant bed 7) are characterized by an increase in the relative abundance of B. comaumensis (c. 50%) and the more frequent occurrence of C. thiergartii. No specimens of Cerebropollenites macroverrucosus were found in this study.
**Table 1. Details of rock samples collected from Astartekløft and prepared for palynological analysis**

| Hand specimen label (2002 field season) | Sample height (cm) | Sample number (Mander et al. 2010) | Vial and microscope slide label | FMNH accession number |
|----------------------------------------|-------------------|-----------------------------------|-------------------------------|----------------------|
| Abandoned channel, plant bed 7*        |                   |                                   |                               |                      |
| AST 01 - marker                        | 7269              | 7,7269                            | UT SS A21                      | PP55348              |
| AST 02 - 10                            | 7259              | 7,7259                            | UT SS A22                      | PP55349              |
| AST 03 - 20                            | 7249              | 7,7249                            | LM PB7.1                      | PP55350              |
| AST 04 - 30                            | 7239              | 7,7239                            | LM PB7.2                      | PP55351              |
| Coal swamp, plant bed 6                |                   |                                   |                               |                      |
| AST 05                                 | 6106              | 6,6106                            | UT SS A20                      | PP55352              |
| AST 03                                 | 6086              | 6,6086                            | UT SS A19                      | PP55353              |
| AST 02                                 | 6076              | 6,6076                            | LM PB6.2                      | PP55354              |
| Crevasse splay, plant bed 5            |                   |                                   |                               |                      |
| AST 01                                 | 4718              | 5,4718                            | UT SS A11                      | PP55355              |
| AST 02                                 | 4708              | 5,4708                            | UT SS A12                      | PP55356              |
| AST 03                                 | 4698              | 5,4698                            | UT SS A13                      | PP55357              |
| AST 04                                 | 4688              | 5,4688                            | UT SS A14                      | PP55358              |
| AST 05                                 | 4678              | 5,4678                            | UT SS A15                      | PP55359              |
| AST 06                                 | 4668              | 5,4668                            | UT SS A16                      | PP55360              |
| AST 07                                 | 4658              | 5,4658                            | UT SS A17                      | PP55361              |
| AST 08                                 | 4648              | 5,4648                            | UT SS A18                      | PP55362              |
| AST 09                                 | 4638              | 5,4638                            | UT SS A18.5                    | PP55363              |
| Crevasse splay, plant bed 4            |                   |                                   |                               |                      |
| AST 06                                 | 4107              | 4,4107                            | UT SS A10                      | PP55364              |
| AST 05                                 | 4097              | 4,4097                            | LM PB4.5                      | PP55365              |
| AST 04                                 | 4087              | 4,4087                            | LM PB4.4                      | PP55366              |
| AST 03                                 | 4077              | 4,4077                            | UT SS A9                      | PP55367              |
| AST 02                                 | 4067              | 4,4067                            | LM PB4.3                      | PP55368              |
| AST 01                                 | 4057              | 4,4057                            | LM PB4.2                      | PP55369              |
| Crevasse splay, plant bed 3            |                   |                                   |                               |                      |
| AST 04                                 | 3771              | 3,3771                            | UT SS A8                      | PP55370              |
| AST 03                                 | 3761              | 3,3761                            | LM PB3.2                      | PP55371              |
| AST 02                                 | 3751              | 3,3751                            | UT SS A7                      | PP55372              |
| AST 01                                 | 3715              | 3,3715                            | LM PB3.1                      | PP55373              |
| Crevasse splay, plant bed 2            |                   |                                   |                               |                      |
| AST 08                                 | 3413              | 2,3413                            | LM PB2.7                      | PP55374              |
| AST 07                                 | 3403              | 2,3403                            | LM PB2.6                      | PP55375              |
| AST 06                                 | 3393              | 2,3393                            | LM PB2.5                      | PP55376              |
| AST 04                                 | 3373              | 2,3373                            | LM PB2.3                      | PP55377              |
| AST 03                                 | 3363              | 2,3363                            | LM PB2.2                      | PP55378              |
| AST 02                                 | 3353              | 2,3353                            | UT SS A6                      | PP55379              |
| AST 01                                 | 3343              | 2,3343                            | LM PB2.1                      | PP55380              |
| Crevasse splay, plant bed 1.5          |                   |                                   |                               |                      |
| AST 20 above                           | 2321              | 1.5,2321                          | UT SS A3.5                    | PP55381              |
| Crevasse splay, plant bed 1            |                   |                                   |                               |                      |
| AST 50 above                           | 1388              | 1,1388                            | LM PB1.5                      | PP55382              |
| AST 40 above                           | 1378              | 1,1378                            | LM PB1.4                      | PP55383              |
| AST 30 above                           | 1368              | 1,1368                            | LM PB1.3                      | PP55384              |
| AST 20 above                           | 1358              | 1,1358                            | LM PB1.2                      | PP55385              |
| AST 10 above                           | 1348              | 1,1348                            | UT SS A2                      | PP55386              |
| AST 0 - marker                         | 1338              | 1,1338                            | UT SS A1                      | PP55387              |

*Depositional environment is from McElwain et al. (2007). Microscope slides used in this study have been deposited at the Field Museum of Natural History, Chicago (FMNH).

**Age of the plant beds at Astartekløft**

Zones A1 and A2 (plant beds 1–4) represent Zone 1 of Pedersen & Lund (1980) and the Rhaetipollis–Limbosporites Zone of Lund (1977) (Fig. 3). Zone A1 represents the Lower Subzone and Zone A2 represents Zone 2 of Pedersen & Lund (1980) and the Pinuspollenites–Trachysporites Zone of Lund (1977) (Fig. 3). We are unable to correlate Zone A3 (plant bed 5), which represents the Transition Zone of Harris (1937) at Astartekløft, with previously published sporomorph zones of this locality (Pedersen & Lund 1980). Samples from plant bed 5 contain sporomorph assemblages of a Latest Rhaetian aspect that have not been reported in previous work on the Astartekløft section (Pedersen & Lund 1980; Koppelhus 1996). In particular, the complete absence of Ovalipollis and presence of C. thiergartii (Fig. 2) indicate that a Middle Rhaetian age for samples from plant bed 5 is untenable. There is no sedimentological evidence for a major break in stratigraphy within plant bed 5, and samples from this horizon cluster together in compositional space and are more similar in composition to samples from plant beds 6 and 7 than samples from beds 1–4 (CONISS, Fig. 2). This indicates that samples from plant bed 5 should be treated as a single zone, rather than split into two separate zones. Zone A3 overlaps the Upper Subzone in Zone 1 of Pedersen & Lund (1980), and is overlain by Zone 2 of Pedersen & Lund (1980) (Fig. 3). We suggest that Zone A3 may be a local equivalent of samples containing a mixture of sporomorphs with Rhaetian and Hettangian affinities that were referred to the “Topmost Upper Rhaetic” in the Danish borehole Rodby 1 by Lund (1977, p. 31) (latest Late Rhaetian in Fig. 3). The oldest age of the samples from Astartekløft investigated here is Middle Rhaetian based on the first occurrence of L. lundbladii (Kürschner & Herngreen 2010).

**Comparison of palynostratigraphic zonation scheme with a palaeoecological zonation based on macrofossils**

The sporomorph assemblage zones delineated here (Figs 2 and 3) correspond well to a palaeoecological zonation scheme at Astartekløft based on macrofossils proposed by McElwain et al. (2007) (Fig. 4). The tight match between the sporomorph assemblage zones and macrofossil palaeoecological phases (Fig. 4) is interesting, as each scheme was created independently using different methods. The sporomorph zonation scheme (Figs 2 and 3) was generated using a combination of CONISS stratigraphically constrained cluster analysis (Grimm 1987) and occurrences of stratigraphically important sporomorph taxa. In contrast, the palaeoecological zonation based on macrofossils was constructed by grouping plant beds together on the basis of a combination of diversity, proportional extinction, origination, proportion of singletons (those taxa occurring in only one plant bed) and composition (McElwain et al. 2007). That the two fossil groups and approaches agree on the relative timing of changes in the vegetation at Astartekløft perhaps lends a degree of support to the results of each analysis, and suggests that the recorded changes are probably representative of the whole flora, rather than the part of the flora sampled by each fossil group.

**Correlation of Astartekløft and St Audrie’s Bay and integration of the carbon isotope records at these localities**

Using the local sporomorph assemblage zones described here, we have developed a correlation between the plant beds at Astartekløft with a dominantly marine Tr–J boundary section at
St Audrie’s Bay, UK. Plant beds 1–4 represent the *Rhaetipollis–Limbosporites* Zone of Lund (1977), which coincides with the *Rhaetipollis* Zone of Orbell (1973) (see Fig. 3). Therefore, plant beds 1–4 represent strata up to and including the lower Cotham Member (Fig. 5). Samples from the Transition Zone (plant bed 5) are apparently younger than suggested by Pedersen & Lund (1980) (Fig. 3) and using the first appearance of *C. thiergartii* as a stratigraphic marker (e.g. Kuerschner et al. 2007) our results suggest that plant bed 5 correlates approximately to the onset of the ‘main’ negative carbon isotope excursion, in the upper ‘Pre-Planorbis Beds’ at c. 17.5 m at St Audrie’s Bay (see fig. 2 of Hesselbo et al. 2002; Fig. 5).

This correlation implies that the negative carbon isotope excursion recorded at Astartekloft (e.g. Hesselbo et al. 2002; McElwain et al. 2007; Bacon et al. 2011) represents the ‘main’ carbon isotope excursion as defined at St Audrie’s Bay by Hesselbo et al. (2002), and that the ‘initial’ carbon isotope excursion has not yet been recorded at Astartekloft (Fig. 5). This correlation suggests that the ‘initial’ carbon isotope excursion, if it is present at all, should be located between plant beds 4 and 5 of McElwain et al. (2007). This interval is likely to be condensed (Fig. 5), highlighted by the formation of ironstone, which requires the constant presence of a redox front that may hamper the deposition of sediment (see fig. 3 of Hesselbo et al. 2002). The presence of rootlets attests to the formation of soil horizons, which also suggests periods of non-deposition (see fig. 3 of Hesselbo et al. 2002). To place this correlation in a wider stratigraphic framework, we have provided a summary correlation of Tr–J boundary sections at Astartekloft, St Audrie’s Bay and Hochalplgraben (Fig. 6). Correlations that place the ‘initial’ carbon isotope excursion near plant bed 1 (Bartolini et al. 2012) or plant bed 3 (Whiteside et al. 2010) at Astartekloft are incompatible with our data.

It has been suggested that carbon isotope excursions at the Tr–J reflect changing proportions of organic components of varied isotopic composition (e.g. van de Schootbrugge et al. 2008). However, pronounced carbon isotope excursions have been recognized in geographically widespread Tr–J boundary sections that record different sea level and thermal subsidence histories (e.g. Hesselbo et al. 2007). Additionally, a recent study has shown that the negative carbon isotope excursion at Astartekloft is expressed in the cuticles of both Ginkgoales and Bennettitales (Bacon et al. 2011), which are thought to have had different life habits and ecological roles at the Tr–J in East Greenland (McElwain et al. 2007; Bacon et al. 2011). These observations strongly suggest that changes in the carbon isotope value of organic matter at the Tr–J represent a real disturbance to the global carbon cycle (e.g. Ruhl et al. 2010; Bacon et al. 2011).

**Comparison of terrestrial and marine extinction records at Astartekloft and St Audrie’s Bay**

To examine the relative timing of extinction and palaeoecological change among terrestrial plants and marine organisms at the Tr–J, the stratigraphic ranges of plant macrofossil genera at Astartekloft have been compared with the stratigraphic ranges of shelly marine invertebrates at St Audrie’s Bay (Fig. 5). Plant bed 5 contains the local last occurrences of four macrofossil genera *Podozamites, Pseudoctenis, Stachyotaxus* and *Taeniopteris* (Fig. 5), preserves a c. 80% plant species turnover among macrofossils (e.g. Harris 1937; McElwain et al. 2007, 2009), and also records diversity decline and compositional change among sporomorph assemblages (Mander et al. 2010). This indicates that peak extinction recorded in East Greenland considerably post-dates the main interval of extinction and palaeoecological change among marine invertebrates at
St Audrie’s Bay (e.g. Mander et al. 2008; Fig. 5), and occurred at a time when benthic marine ecosystems were in a recovery phase disrupted by anoxic or euxinic conditions (Barras & Twitchett, 2007; Mander & Twitchett 2008; Mander et al. 2008). This contrasts with the situation in Stenlille (Denmark), where there is no evidence for vegetation change during this Hettangian recovery phase (Lindström et al. 2012).

Owing to the absence of strata and plant macrofossils coeval with the ‘initial’ carbon isotope excursion and the immediate aftermath of the main extinction phase at St Audrie’s Bay (Fig. 5), assessing the relative timing of the onset of the Tr–J biotic crisis in terrestrial and marine ecosystems is difficult. Nevertheless, the cluster of range truncations of marine invertebrates in the stratigraphic interval spanning the upper Westbury Formation to the lower Cotham Member occurs prior to the ‘initial’ carbon isotope excursion at St Audrie’s Bay (Mander & Twitchett 2008; Mander et al. 2008) and therefore coincides with an abrupt loss of plant generic diversity and onset of palaeoecological change in plant beds 3 and 4 that has been inferred from relative abundance distributions at Astartekløft (McElwain et al. 2009; Fig. 5). The cluster of range truncations of marine invertebrates in the Langport Member (Fig. 5) cannot be directly correlated to the Astartekløft section because this interval of stratigraphy is barren of plant macrofossils and may be condensed at Astartekløft (Fig. 5). However, these data argue strongly against the idea that extinction and diversity loss in terrestrial ecosystems preceded biotic change in marine ecosystems.

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ecosystems at the Tr–J (e.g. Pálfy et al. 2000), and instead support the views of Kuerschner et al. (2007) and Götz et al. (2009), who suggested that the onset of the Tr–J biotic crisis was synchronous in terrestrial and marine environments.

Relationship of Tr–J vegetation change at Astartekloft to Central Atlantic Magmatic Province volcanism

Can the correlation presented here allow the patterns of vegetation change at Astartekloft to be temporally linked to any specific phases of Central Atlantic Magmatic Province volcanism? Four major pulses of Central Atlantic Magmatic Province volcanism occurred in the Late Rhaetian: the Lower and Intermediate Units in Morocco, the Orange Mountain Basalt in North America (Deenen et al. 2010) and the North Mountain Basalt in Canada (Schoene et al. 2010). These volcanic units have been correlated to St Audrie’s Bay using palaeomagnetic data, cyclostratigraphy and geochemistry (Deenen et al. 2010). The Lower Unit and the North Mountain Basalt were emplaced around the same time as the ‘initial’ carbon isotope excursion in the Cotham Member (Deenen et al. 2010; Schoene et al. 2010), whereas the Intermediate Unit and the Orange Mountain Basalt are considered to be coeval and were emplaced prior to the onset of the ‘main’ carbon isotope excursion in the Langport Member (Deenen et al. 2010).

Fig. 5. Correlation of Tr–J boundary sections at Astartekloft and St Audrie’s Bay and a comparison of the stratigraphic ranges of macrofossil leaves and marine bivalves at these two localities. Correlation is based on sporomorph assemblage zones and the first appearance of the pollen morphospecies Cerebropollenites thiergartii (Kuerschner et al. 2007). Carbon isotope data and stratigraphic schemes at Astartekloft and St Audrie’s Bay are from Hesselbo et al. (2002). Position of ‘Precursor’ carbon isotope excursion is from Ruhl & Kürschner (2011). Sporomorph zones at St Audrie’s Bay are from Orbell (1973) and Bonis et al. (2010b). Abbreviations of stratigraphic units at St Audrie’s Bay: PPB, ‘Pre-planorbis beds’; Lil. Fm., Lilstock Formation; CM, Cotham Member; LM, Langport Member. Central Atlantic Magmatic Province volcanic rocks: L. u., Lower unit; I. u., Intermediate Unit. Correlation line ‘A’ indicates the first appearance of C. thiergartii (first appearance of C. thiergartii at St Audrie’s Bay (18.50 m) from Bonis et al. (2010b)). Correlation line ‘B’ connects the top of Sporomorph Assemblage Zone A2 at Astartekloft to the top of the Rheiptopollis Zone at St Audrie’s Bay (Orbell 1973; SAB 1 & 2 of Bonis et al. 2010b). Macrofossil leaves at Astartekloft from McElwain et al. (2007) and Mander et al. (2010): 1, Hausmannia; 2, Baiiera; 3, Lepidopteris; 4, Podozamites; 5, Dictyophyllum; 6, Equisetites; 7, Pterophyllum; 8, Anomozamites; 9, Czekanowskia; 10, Nilssonia; 11, Ginkgo; 12, Elatocladus; 13, Pseudococcos; 14, Stachyotaxus; 15, Cladophlebis; 16, Clathropteris; 17, Rhaetipollis; 18, Phlebopteris; 19, Doratophyllum; 20, Tenuipteris; 21, Sphenobaiera; 22, Anthrophyopsis; 23, Ctenis; 24, Macrotaeniopteris; 25, Marattia; 26, Pagiophyllum; 27, Ptilozamites; 28, Sagenopteris; 29, Thaumatopteris. Marine bivalves at St Audrie’s Bay from Mander et al. (2008): 1, Permophorus elongatus; 2, Pteromya crowcombia; 3, Thalassina elegans; 4, Pecten sp.; 5, Chlamys sp.; 6, Isocyprina sp.; 7, Oxytoma sp.; 8, Plagiostoma giganteum; 9, Pseudomytiloides dubius; 10, Rollieria bronni; 11, Palaemonula navis.
that the onset of plant diversity loss in plant beds 3 and 4 at Astartekløft (McElwain et al. 2009; Fig. 4) predates the emplacement of the Lower Unit in Morocco and the North Mountain Basalt in Canada (Fig. 5). The floral turnover preserved in plant bed 5 at Astartekløft (e.g. McElwain et al. 2007, 2009; Mander et al. 2010) apparently post-dates the emplacement of the Intermediate unit, as well as the minor Upper Unit in Morocco, which directly overlies the Intermediate Unit (Fig. 5; Deenen et al. 2010).

The correlation presented here places the patterns of Tr–J plant diversity loss and extinction from the plant beds of Astartekløft into a clear stratigraphic framework. The abrupt loss of plant generic diversity and onset of palaeoecological change in plant beds 3 and 4 at Astartekløft (McElwain et al. 2009) is temporally linked to the earliest phase of Central Atlantic Magmatic Province activity (Fig. 5). This is thought to have consisted of extensive Late Triassic dyke and sill intrusions, which led to the release of carbon from subsurface organic-rich sediments, and is represented by a ‘Precursor’ carbon isotope excursion in the middle Westbury Formation (Ruhl & Kürschner 2011; Fig. 5). Peak extinction in plant bed 5 occurs relatively late in the sequence of events across the Tr–J (Fig. 5) and, as such, it is perhaps best explained either as a response to the long-term cumulative effects of Central Atlantic Magmatic Province volcanism, including those responsible for the ‘initial’ carbon isotope excursion (see Lindström et al. 2012), or as a biological tipping point. The effects of volcanic activity in the Central Atlantic Magmatic Province are thought to include direct effects such as aerosol release (van de Schootbrugge et al. 2009), and indirect effects such as release of thermogenic methane (Ruhl et al. 2011) or other gases generated by the continued intrusion of Central Atlantic Magmatic Province volcanic rocks (Hesselbo et al. 2007; McElwain et al. 2009).

Tr–J vegetation history at Astartekløft

Vegetation history: spore plants

Spores are common in samples from the plant beds at Astartekløft (Fig. 2). This supports previous palynological studies at Astartekløft (Pedersen & Lund 1980; Koppelhus 1996), and is in contrast to macrofossil assemblages at Astartekløft, which are dominated by gymnosperms (e.g. Harris 1937; McElwain et al. 2007). Mosses make up <5% of the total sporomorph assemblage at Astartekløft, and the appearance of Stereisporites cicatricosus in plant bed 6 may be the local expression of the Early Jurassic evolution of the...
Horsetails are represented by Calamospora tener, which is a persistent but minor (<5%) component of the sporomorph assemblages, although it reaches c. 15% in plant bed 5 (Fig. 2). Lycopsids are represented by seven sporomorph taxa, but only U. reissingeri and L. lundbladii represent >5% of the total sporomorph assemblage (Fig. 2). U. reissingeri rises in importance from <20% in plant beds 1–2 to 30–40% in plant bed 5, and lycopsids are almost absent in plant beds 6 and 7 (Fig. 2). Sharp rises in both U. reissingeri and L. lundbladii provide evidence of a sharp increase in the relative abundance of lycopsids in plant bed 3 (Fig. 2). Ferns are the dominant spor plant group at Astartekloft and there is an overall rise in the relative abundance of this plant group from plant bed 1 to plant bed 7 (Fig. 2). The trilette spores D. toralis and Baculatisporites spp. are particularly abundant, as highlighted by Pedersen & Lund (1980). The Osmundaceae, represented by Baculatisporites spp. and Punctatisporites globosus, increase in importance in plant beds 5–7 (Fig. 2).

Vegetation history: seed plants

Sporomorphs that can be unambiguously related to seed-ferns, such as Vitreisporites spp., account for <5% of the total sporomorph assemblage at Astartekloft (Fig. 2). Sporomorphs that can be unambiguously related to conifers are also a fairly minor component of the sporomorph assemblage, and Araucariacites australis declines from c. 10% at the base of the section to <5% at the top of the section. Perinopollenites elatoides, which was probably produced by conifers of the Taxodiaceae family (van Konijnenburg-van Cittert & van der Burgh 1989), sharply increases in abundance in plant bed 5, reaching c. 25% in one sample (Fig. 2). The frequency of Classopolis spp. (produced by conifers of the Cheirolepidae family) is low in all horizons (Fig. 2), in agreement with previous palynological work on the Tr–J transition in East Greenland (Pedersen & Lund 1980; Koppelhus 1996). Sporomorphs of the Alisporites and Pinuspollenites morphotypes and the taeniate bisaccates Lunatisporites and Protohaploxipinus were probably produced by both seed-ferns and conifers (e.g. Balme 1995). Of these, P. minimus is the most abundant in the section, and a striking feature of the record of this pollen grain is the lack of change in its relative abundance through time (Fig. 2). The morphology of P. minimus is similar to modern Pinus pollen and is thus likely to have had good dispersal properties (e.g. Prentice 1988). In Quaternary pollen spectra, such a monotonic record of well-dispersed pollen is characteristic of regional pollen rain from the hinterland (e.g. Prentice 1988), and this perhaps reflects waterborne transport of sporomorphs from the Jameson Land region to Astartekloft (e.g. Muller 1959; Farley 1990; Hoffman 2002). Riciisporites tuberculatus declines from c. 70% in the lowermost sample in the section, before disappearing at the top of plant bed 5 (Fig. 2). Plants that produced ‘boat-shaped’ smooth or scabrate monosulcate pollen grains (cycads, Bennettites, ginkgos and the seed-fern Lepidopteris) make up <5% of the total sporomorph assemblage. Consequently, the sporomorph record preserves no major changes in the relative abundance of these plants across the Tr–J at Astartekloft, in contrast to the macrofossil record (e.g. Harris 1937; McElwain et al. 2007; Mander et al. 2010).

Comparison of Tr–J vegetation history at Astartekloft with other Tr–J boundary sections

The extremely low abundance of Classopolis pollen in sporomorph assemblages from Astartekloft (Fig. 2) matches previous palynological work in East Greenland (Pedersen & Lund 1980; Koppelhus 1996), and highlights clear floral provincialism at the Tr–J. Changes in the relative abundance of Classopolis are a major feature of Tr–J sporomorph assemblages in most other Tr–J boundary sections, including those in North America (e.g. Fowell & Olsen 1993), Nova Scotia (Fowell & Traverse 1995) and the wider European region (e.g. Warrington 1974; Morbey 1975; Lund 1977; Schuurman 1979; Kuerschner et al. 2007; Bonis et al. 2009; van de Schootbrugge et al. 2009). Classopolis pollen has been shown to increase in abundance with decreasing palaeolatitude (Vakhrameev 1981, 1991) and the more northerly palaeolatitude of Astartekloft (40.9°N; Kent & Tauxe 2005) compared with sections in Europe such as St Audrie’s Bay (palaeolatitude 25.8°N; Kent & Tauxe 2005), is a possible explanation for the low frequency of Classopolis in East Greenland (Pedersen & Lund 1980). The frequency of Classopolis pollen is also low in samples from Arctic Canada (e.g. Sunely & Hills 1988) and this highlights that the Cheirolepidae were probably restricted to lower latitudes at the Tr–J. This study also suggests regional differences in climate at this time. A possible switch to wetter conditions across the Tr–J in East Greenland is suggested by an increase in the relative abundance of ferns in plant beds 5–7 (Fig. 2) and the deposition of poorly developed coal in bed 6 (McElwain et al. 2007). This matches a similar gradual switch to wetter conditions in Slovakia (Ruckwied & Götz 2009), Hungary (Götz et al. 2011) and Austria, where the abundance of ferns and other spor plants increases in the Hettangian (Kuerschner et al. 2007; Bonis 2010). However, this pattern is strikingly different from patterns in North America (Fowell & Olsen 1993), Germany and Sweden (van de Schootbrugge et al. 2009) and St Audrie’s Bay (Bonis 2010) where Hettangian sporomorph assemblages are dominated by Classopolis pollen, perhaps indicating a change to drier and/or warmer environments.

The pronounced decline in R. tuberculosis from plant bed 1 to plant bed 5 is a particularly striking feature of the sporomorph record of Tr–J vegetation at Astartekloft (Fig. 2). A decline in the abundance of this sporomorph is characteristic of the Tr–J boundary interval in many sections in the wider European region such as Germany and Sweden (Larsson 2009; van de Schootbrugge et al. 2009), the UK (Bonis 2010), Hungary (Götz et al. 2009) and Slovakia (Ruckwied & Götz 2009). However, in certain sections such as Holchlapgraben and the GSSP at Kuhjoch in Austria, R. tuberculosis appears to increase in abundance from c. 5% to c. 20% across the Tr–J (Bonis et al. 2009). R. tuberculosis is absent from North American Tr–J boundary sections such as those in the Newark Basin (e.g. Fowell & Olsen 1993). A recent ultrastructural study indicates that R. tuberculosis was produced by a gymnosperm, and there are some ultrastructural similarities between R. tuberculosis and pollen produced by the Bennettite Cycadeoida dactylosis (Mander et al. 2012). R. tuberculosis is permanently united in large tetrads that measure 80–110 μm in maximum dimension, and single members of the tetrad are prominently sculptured with clavae and gemmae (Lundblad 1959; Mander et al. 2012). These morphological features may reflect adaptation for animal rather than wind pollination (Mander et al. 2012), and it is interesting that the decline in R. tuberculosis at Astartekloft (Fig. 2) mirrors the decline in macrofossils of plants that were probably insect pollinated at this locality (e.g. McElwain et al. 2007). If the suggestion that R. tuberculosis was produced by an animal pollinated plant (Mander et al. 2012) is correct, then fluctuations in the abundance of this pollen grain in Tr–J boundary sections worldwide may represent fluctuations in the abundance of a reproducitively specialized plant at the Tr–J. This is important because reproducitively specialized plants that are common in the macrofossil record at Astartekloft such as cycads, Bennettites and peltasperm seed-ferns (McElwain et al. 2007) are under-represented in Tr–J sporomorph assemblages at this locality (Mander et al. 2010), and the
low taxonomic resolution of Tr–J sporomorph records masks the extinction of plants such as the Peltaspermaeae (Mander et al. 2010; Mander 2011).

These data also highlight that Tr–J vegetation change varies widely from region to region. Rather than a globally uniform scenario, there is a complex pattern of regional vegetation changes and plant extinctions that are the result of local and regional environmental and climate changes, most probably associated with Central Atlantic Magmatic Province volcanism (Bonis & Kürschner 2012). Some regions, such as East Greenland where plant extinction and diversity loss is most apparent, may have been affected more acutely by environmental changes associated with Central Atlantic Magmatic Province volcanism (e.g. Bonis & Kürschner 2012).

Conclusions

(1) Four local sporomorph assemblage zones are recognized at Astartekløft (Fig. 2): Zone A1 comprises plant beds 1, 1.5 and 2; Zone A2 comprises plant beds 3 and 4; Zone A3 comprises plant bed 5 and represents the ‘Transition Zone’ of Harris (1937); Zone A4 comprises plant beds 6 and 7. Zones A1 and A2 are of Mid- to Late Rhaetian age and Zone A4 is of Hettangian age (Fig. 3). Zone A3 may be a local equivalent of samples containing a mixture of sporomorphs with Rhetaetian and Hettangian affinities that were referred to the ‘Topmost Upper Rhaetic’ in the Danish Borehole Rodby 1 by Lund (1977, p. 31) (latest Late Rhaetian in Fig. 3).

(2) Correlation of Astartekløft and St Audrie’s Bay using this palynostratigraphic scheme suggests that plant beds 1–4 represent strata up to and including the lower Cotham Member at St Audrie’s Bay, and that plant bed 5 correlates approximately to the onset of the ‘main’ negative carbon isotope excursion, in the upper ‘Pre-Planorbis Beds’ at this locality (Fig. 5). This indicates that the negative carbon isotope excursion recorded at Astartekløft (e.g. Hesselbo et al. 2002; McElwain et al. 2007; Bacon et al. 2011) represents the ‘main’ carbon isotope excursion as defined at St Audrie’s Bay by Hesselbo et al. (2002), and that the ‘initial’ carbon isotope excursion has not yet been recorded at Astartekløft (Fig. 5). This correlation suggests that the ‘initial’ carbon isotope excursion should be located between plant beds 4 and 5 of McElwain et al. (2007), an interval that may be condensed.

(3) There is no evidence to support the idea that extinction and diversity loss in terrestrial ecosystems preceded biotic change in marine ecosystems at the Tr–J (e.g. Pálfy et al. 2000). Instead, the available data support the views of Kürschner et al. (2007) and Götz et al. (2009), who suggested that the onset of the Tr–J biotic crisis was synchronous in terrestrial and marine environments. The correlation presented here also highlights that peak extinction and vegetation change in plant bed 5 at Astartekløft post-dates the main interval of extinction and palaeoecological change among marine invertebrates at St Audrie’s Bay (e.g. Mander et al. 2008; Fig. 5), and occurred at a time when benthic marine ecosystems were in a recovery phase disrupted by anoxia (Barras & Twitchett 2007; Mander & Twitchett 2008; Mander et al. 2008).

(4) The abrupt loss of plant generic diversity and onset of palaeoecological change in plant beds 3 and 4 at Astartekløft (McElwain et al. 2009; Fig. 4) predates the emplacement of the Lower Unit in Morocco and the North Mountain Basalt in Canada (Fig. 5) and is therefore temporally linked to the very earliest phases of Central Atlantic Magmatic Province volcanism (Fig. 5). Peak extinction in plant bed 5 post-dates the emplacement of the Intermediate Unit, as well as the minor Upper Unit in Morocco, which directly overlies the Intermediate Unit (Fig. 5; Deenen et al. 2010). This distinctive aspect of Tr–J vegetation change in East Greenland therefore occurs relatively late in the sequence of events across the Tr–J (Fig. 5), and as such is perhaps best explained as a response to the long-term cumulative effects of Central Atlantic Magmatic Province volcanism, including those responsible for the ‘initial’ carbon isotope excursion (see Lindström et al. 2012).

(5) Spores are generally a more important component of sporomorph assemblages at Astartekløft than pollen (Fig. 2). Ferns are the dominant sporangium plant group in samples from Astartekløft, and lycopods are also important components of sporomorph assemblages in plant beds 1–5 (Fig. 2). A pronounced decline in R. tuberculatus (a gymnosperm pollen grain; Mander et al. 2012) from plant bed 1 to plant bed 5 is a particularly striking feature of the sporomorph record of Tr–J vegetation change at Astartekløft, and Classopolis pollen is notably rare (Fig. 2; see also Pedersen & Lund 1980; Koppelhus 1996). A possible switch to wetter conditions across the Tr–J in East Greenland is suggested by an increase in the relative abundance of ferns in plant beds 5–7 (Fig. 2) and the deposition of poorly developed coal in plant bed 6 (McElwain et al. 2007).

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