A gymnosperm affinity for Ricciisporites tuberculatus Lundblad: implications for vegetation and environmental reconstructions in the Late Triassic

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A gymnosperm affinity for *Ricciisporites tuberculatus* Lundblad: implications for vegetation and environmental reconstructions in the Late Triassic

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Abstract

Ricciisporites tuberculatus Lundblad is a prominently sculptured palynomorph that is dispersed at maturity as tetrads. It has a wide geographic distribution and reaches a stratigraphically important acme in the Norian and Rhaetian of Europe. As it has not yet been found in situ in a fossilized reproductive structure its botanical affinity is poorly understood. Recent work on the morphology and ultrastructure of R. tuberculatus has shown that individual grains within the R. tuberculatus tetrad have a single distal colpus, and that the sporoderm consists of a granular inner sexine, and an electron-dense laminated nexine. These characters are typical of gymnosperms.

However, in their previous palynological studies, Kürschner and co-workers assigned R. tuberculatus to the spore plants, in line with older interpretations of the botanical affinity of R. tuberculatus. In the present contribution, we re-evaluate Triassic–Jurassic (Tr-J) palynological records and discuss the consequences of a gymnosperm affinity for R. tuberculatus for Late Triassic vegetation reconstruction, as well as inferred palaeoecological interpretations. At a Tr-J boundary locality in East Greenland, the relative abundance of R. tuberculatus through time is similar to the bennettites Anomozamites and Pterophyllum. We suggest that R. tuberculatus may have been produced by a gymnosperm characterized by an herbaceous ruderal life habit. The poor preservation potential of the vegetative structures of such a plant may explain why R. tuberculatus has not yet been found in situ in a fossil reproductive structure. We suggest that the parent plants of R. tuberculatus and Classopollis (the Cheriolepidiaceae) may have had different ecological preferences.

Keywords: Late Triassic, palynology, in situ pollen and spores, herbaceous gymnosperm, Classopollis.
Introduction
The fossil palynomorph *Ricciisporites tuberculatus* Lundblad is a conspicuous component of palynological assemblages from the Norian to the Hettangian (Kürschner and Herngreen 2010 and literature cited herein). *Ricciisporites* *tuberculatus* is permanently united in tetrahedral tetrads (Lundblad 1959) and measures 80–110µm in maximum dimension (Fig. 1; Mander et al. 2012). Each member of the tetrad is prominently sculptured with clavae and gemmae, and the distal face of each member is equipped with a single elongated furrow (Fig. 1; Lundblad 1959; Mander et al. 2012). *R. tuberculatus* has a fairly thick exine, and as a result is usually dark brown in colour when viewed using transmitted light microscopy.

*Ricciisporites tuberculatus* appears to be restricted to the northern hemisphere, and although it is not presently known to occur in the classic Triassic–Jurassic (Tr-J) successions of North America (e.g. Cornet and Traverse 1975), it is found in sediments from arctic Canada (Suneby and Hills 1988) to China (Yong et al. 2003). *Ricciisporites tuberculatus* is stratigraphically valuable in sediments of Upper Triassic age, and reaches an acme in the Rhaetian of northwest Europe (Pedersen and Lund 1980; Bonis et al. 2010a; Pienkowski et al. 2012). This acme forms part of the stratigraphic framework that has been used to correlate terrestrial and marine sediments of Upper Triassic age, which is particularly useful in the context of debates about the relative timing of biotic events during the late Triassic mass extinction (~200Ma; Hesselbo et al. 2007) (e.g. Kuerschner et al. 2007; Mander et al. 2013), and has also been used to provide a latest Rhaetian age for theropod dinosaur footprints in Sweden (Vajda et al. 2013).

In addition to its value as a biostratigraphic marker, the abundance of *R.
*Ricciisporites* tuberculatus in Upper Triassic palynological assemblages indicates that the parent plant of this palynomorph is likely to have been abundant in Upper Triassic terrestrial ecosystems, and may have played an important ecological role before and during the late Triassic mass extinction (Mander et al. 2013; Vajda et al. 2013). *Ricciisporites* tuberculatus has not yet been found *in situ* in a fossilized reproductive structure, and consequently the identity of its parent plant is unknown (Lundblad 1954, 1959; Jovet-Ast 1967; Balme 1995; Mander et al. 2012). However, recent work on the morphology of *R. tuberculatus* has shown that the furrow on the distal face of each member of the tetrad is likely to be a colpus (Mander et al. 2012), and ultrastructural data have shown that the sporoderm of *R. tuberculatus* consists of a granular inner sexine, and an electron-dense laminated nexine (Mander et al. 2012). These characters are typical of gymnosperm pollen, and the sporoderm of *R. tuberculatus* bears the closest ultrastructural resemblance to pollen of the bennettite *Cycadeoidea dacotensis* (Mander et al. 2012). This provide a first-order botanical affinity for *R. tuberculatus*, and argues against earlier suggestions that *R. tuberculatus* was produced by a liverwort comparable to extant *Riccia* (Marchantiales) (e.g. Lundblad 1954; Balme 1995).

The first objective of this paper is to examine the implications of *R. tuberculatus* as a gymnosperm for Late Triassic vegetation reconstructions. To do this, we re-examine a comparison of the macrofossil (mostly leaves) and sporomorph (pollen and spore) records of Tr-J vegetation at a locality in East Greenland undertaken by Mander et al. (2010), who did not include *R. tuberculatus* in their analysis because of its dubious botanical affinity. The second objective of this paper is to investigate the implications of *R. tuberculatus* as a gymnosperm for the inference of Tr-J palaeoecological and palaeoclimatological conditions from palynological data.
To do this we re-investigate Tr-J palynological data undertaken by Bonis et al. (2009, 2010a) and Bonis et al. (2012), who interpreted R. tuberculatus as a liverwort in line with Balme (1995), rather than as gymnosperm. We also undertake multivariate ordination of Tr-J palynological data from East Greenland and Germany.

Materials and methods

Comparison of macrofossil and sporomorph records

We build on previous work comparing the macrofossil and sporomorph records of Tr-J vegetation at a boundary section at Astartekløft in Jameson Land, East Greenland (Mander et al. 2010). The rock succession at this locality comprises the fluvial–lacustrine Kap Stewart Group and is rich in plant macrofossils, which are restricted to a series of discrete fossiliferous intervals known as “plant beds” (Harris 1937; McElwain et al. 2007). Plant beds 1–4 are of Upper Triassic (Rhaetian) age, plant beds 6 and 7 are of Lower Jurassic (Hettangian) age, and plant bed 5 contains the Triassic/Jurassic boundary, which is approximated at Astartekløft by the first appearance of the pollen morphospecies Cerebropollenites thiergartii (Mander et al. 2013). Plant beds 1–5 represent overbank crevasse-splay deposits, plant bed 6 represents a poorly developed coal swamp, and plant bed 7 represents an abandoned channel (McElwain et al. 2007).

In this paper, we analyze a group of plants that is abundant in the macrofossil record at Astartekløft, but is thought to be a minor component of the sporomorph record at this locality. This group of plants consists of the classes Cycadopsida, Ginkgoopsida, Bennettitopsida and the order Peltaspermales, which are all thought to have produced “boat-shaped” monocolpate pollen grains of the Monosulcites/Cycadopites and Chasmatosporites morphotypes (Mander et al. 2010;
Mander 2011) (Table 1). We group these plants together under the heading “Monocolpate Producers”. We use scatter diagrams firstly to compare the relative representation of this group of plants in the macrofossil record and sporomorph record at Astarteklöft (following Mander et al. (2010), and secondly to illustrate the importance of the parent plant of *R. tuberculatus* in the vegetation at this locality.

**Ordination of Tr-J palynological data**

Principal component analysis (PCA) is a multivariate statistical technique that uses orthogonal transformation to identify patterns in data (e.g. Abdi and Williams, 2010). In the present study, PCA was applied to pollen count data sets in order to summarize pollen and spore relative abundances from 4 locations: 1) Hochalplgraben in the Northern Calcareous Alps in Austria, 2) Wüstenwelsberg located in the German Triassic Basin, southern Germany; 3) St. Audries bay in the British Keuper basin, UK; and 4) Astarteklöft, east Greenland. The palynological data from Hochalplgraben were previously published in Bonis (2009), those from St. Audries bay in Bonis et al. (2010a), those from Wüstenwelsberg in Bonis et al. (2010b) and those from Astarteklöft in Mander et al. (2013). These four locations represent a North–South transect from the boreal region (Greenland) to the western Tethys realm (Hochalplgraben). All PCA’s were calculated in C2 (Juggins, 2007) with a square-root transformation of the species % data. The data were centered by variables (taxa). PCA of the palynological assemblages from Hochalplgraben and St. Audries bay were previously performed in Bonis & Kürschner (2012) while the PCA for the Astarteklöft and Wüstenwelsberg are performed in the present study.

**Results**
Comparison of macrofossil and sporomorph records

The “Monocolpate Producers” group of plants is a major component of plant macrofossil assemblages at Astartekloft, and often constitutes between ~55% and ~95% of the total number of macrofossil assemblages (McElwain et al. 2007) (Table 2). There are certain horizons where this group of plants constitutes less than ~12% of the total macrofossil assemblage, such plant beds 3, 5 and 6 (McElwain et al. 2007) (Table 2). In contrast, this group of plants does not account for more than ~4% of the total sporomorph assemblage in any plant bed at Astartekloft (Mander et al. 2010) (Table 2). This disagreement between the macrofossil and sporomorph records of Tr-J vegetation at Astartekloft is shown in Figure 2A. Interpreting R. tuberculatus as monocolpate gymnosperm pollen (Mander et al. 2012) and adding it to the “Monocolpate Producers” sum inevitably improves the agreement between the macrofossil and sporomorph records of this plant group at this locality (Fig. 2B), and this highlights the importance of the parent plant of R. tuberculatus in the vegetation at this locality. Ricciisporites tuberculatus is an abundant component of sporomorph assemblages in plant beds 1–4, is rare in plant bed 5, and is absent from younger plant beds except for a singleton occurrence in plant bed 7 that may represent reworking (Fig. 3; Table 2) (Mander et al. 2013). Macrofossil “Monocolpate Producers” which show patterns of relative abundance through time at Astartekloft that are similar to that of R. tuberculatus at this locality include the bennettites Anomozaamites and Pterophyllum (Fig. 3). Macrofossil “Monocolpate Producers” which show the opposite pattern at Astartekloft include Czekanowskia and Sphenobaiera (Fig. 3).

Ordination of Tr-J palynological data

The distribution of pollen and spores in the Astartekloft, Wüstenwelsberg, St. Audries
bay and Hochalplgraben sections are shown as the species scores on the first and the second axis of the PCA ordination diagrams (Figs 4-7). We interpret the distribution of sporomorph taxa within these PCA plots as the net result of interplay between the ecology and environmental preferences of the pollen producing mother plants and taphonomical factors.

Figure 4 shows the distribution of sporomorph taxa from the Astartekløft section in the PCA ordination diagram. The first axis explains 22% of the total variance within the data set and the second axis explains 34%. Most striking is the high score of *R. tuberculatus* on the negative side of the first axis. The pollen taxa *Vitreisporites* (*V. bjuvensis* and *V. pallidus*) and *Araucariacites australis*, as well as *Ovalippolis ovalis*, also plot on the negative side of the first axis but with lower scores. Except for *Baculatisporites comaumensis*, there are no sporomorphs with high scores on the positive side of the first axis. On the second axis, spores such as *Deltoidospora* spp. and *Punctatisporites* sp. have high positive values, while *Uvaesporites reissingeri* and *B. comaumensis* are characterized by very negative values.

Figure 5 shows the distribution of sporomorph taxa from the Wüstenwelsberg section in the PCA ordination diagram. The first axis explains 71% of the total variance within the dataset, the second axis explains 15%. Similar to the Greenland PCA plot, *R. tuberculatus* show a very high score on the negative side of the first axis. Pollen, such as *V. bjuvensis + pallidus* and *O. ovalis* plot also on the negative side of the first axis but with lower scores. In contrast to Greenland, pollen taxa such as *Classopollis* spp. and *A. australis* as well as spores such as *Deltoidospora* spp. show a high score on the positive side of the first PCA axis.

Figure 6 shows the distribution of sporomorph taxa from the St. Audries Bay section in the PCA ordination diagram. The first axis explains 45% of the total variance.
variance within the dataset, and the second axis explains 18%. *Classopollis meyeriana* shows the highest score on the negative side of the first axis while *C. torosus, O. ovalis, Rhaetipollis germanicus, R. tuberculatus* and *Vitreisporites* score high on the positive side of the first axis. On the second axis, various spore taxa such as *Heliosporites reissingeri, Deltoidospora* spp., *Conbaculatisporites* spp., *Trachysporites* spp., and *Todisporites* spp. have a positive score while various pollen taxa such as *C. meyeriana, C. torosus, O. ovalis* and *R. germanicus* have a high negative score.

Figure 7 shows the distribution of sporomorph taxa from the Hochalplgraben section in the PCA ordination diagram. The first axis explains 44% of the total variance within the data set, and the second axis explains 20%. Various pollen taxa, such as *C. meyeriana, C. torosus, Vitreisporites* spp., and *O. ovalis* have high positive scores on the first axis. Spores such as *Trachysporites fuscus* and *H. reissingeri*, but also *R. tuberculatus* have high negative values on the first axis. On the positive side of the second axis *C. meyeriana* has the highest scores, while on the negative side pollen such as *Vitreisporites* spp. and *R. tuberculatus* as well as *C. torosus* have very negative values, together with some spore taxa such as *Polypodiisporites* and *Deltoidospora* spp.

**Discussion**

Comparison of macrofossil and sporomorph records

The suggestion that *R. tuberculatus* was a produced by a gymnosperm (Mander et al. 2012) clearly implies that gymnosperms were a more important component of Tr-J terrestrial ecosystems than was previously thought based on palynological data (e.g. Bonis et al. 2010; Bonis et al. 2012). This is illustrated by the comparison of the
macrofossil and sporomorph records of the “Monocolpate Producers” group of plants in East Greenland, which highlights that a plant producing monocolpate pollen, albeit permanently united in tetrads, was comparable in abundance to macrofossils of the classes Cycadopsida, Ginkgoopsida, Bennettitopsida and the order Peltaspermales in this region (Fig. 2; Table 2).

The palaeoclimatic and ecological preferences of the parent plant of R. 
*tuberculatus* relative to other Tr-J plants are suggested by patterns in the global occurrence and local abundance of this palynomorph. In particular, *R. tuberculatus* appears to be restricted to the northern hemisphere (Mander et al. 2012), and is particularly abundant in more northerly Tr-J boundary sections in East Greenland (Mander et al. 2013). In contrast, the abundance of *Classopollis* pollen declines with increasing palaeolatitude (Pedersen and Lund 1980; Koppelhus 1997; Bonis et al. 2012; Mander et al. 2013). Additionally, pollen diagrams of sediments spanning the Tr-J in Austria (Bonis et al. 2009; 2012) and the UK (Bonis et al. 2010a) show that where *Classopollis* and *R. tuberculatus* are important components of the palynoflora (>20%) they alternate in abundance so that where *Classopollis* is common, *R. tuberculatus* is rare and *vice versa*. A possible exception to this pattern is data from Tr-J boundary sections in Germany and Sweden (van de Schootbrugge et al. 2009). But the global biogeographic pattern of *R. tuberculatus* and *Classopollis* occurrences, the relationship between these two pollen grains in several pollen diagrams spanning the Tr-J, and the opposite direction of *R. tuberculatus* and *Classopollis* vectors in the PCA plots of the present study (Figs 4–7), together raise the possibility that the parent plants of *Classopollis* and *R. tuberculatus* were ecologically reciprocal in status (Chaloner pers. comm. January 2013).
The prominent clavate–gemmate ornamentation that characterizes the surface of *R. tuberculatus* is suggestive of animal rather than wind pollination (Mander et al. 2012), and it is intriguing that the decline in the abundance of *R. tuberculatus* at Astartekloft matches the decline in the abundance of macrofossils of plants that were likely to have been animal pollinated at this locality such as bennettites (McElwain et al. 2007) (Fig. 3). However, the reproductive structures that are present in Tr-J sediments in East Greenland (Table 1) are only associated with pollen grains referable to the genus *Monosulcites* (see Pedersen et al. (1989) for *Vardekloeftia*, and Osborne and Taylor (1995) for *Weltrichia* and *Wielandiella*), and the *in situ* record provides no evidence for a botanical relationship between any plant macrofossil and *R. tuberculatus*. This is surprising given the history of intensive palaeobotanical work in this region that has recovered many well-preserved reproductive structures (e.g. Harris 1937; McElwain et al. 2007), and highlights that further investigations of macrofossils in the field and museum collections are needed.

One possibility that could explain the discrepancy between the high abundance of *R. tuberculatus* in the dispersed sporomorph record (Fig. 3) and the apparent absence of its parent plant from sediments that are generally favourable for the preservation of plant macrofossils (e.g. McElwain et al. 2007), is that the parent plant of *R. tuberculatus* was characterized by an herbaceous life habit. Herbaceous plants have considerably lower preservation potential compared to woody plants (e.g. Spicer 1989; Gastaldo 2001), and macrofossil assemblages at Astartekloft are weighted towards woody taxa whereas sporomorph assemblages are weighted towards more delicate ferns and lycopods (Mander et al. 2010). This is a contentious suggestion because the herbaceous life habit has evolved several times among angiosperms, but the remainder of seed plant diversity is essentially composed of woody perennial
plants (Boyce and Leslie 2012; Rowe and Paul-Victor 2012). However, the case of
Aethophyllum, a Triassic gymnosperm that produced such a small amount of
secondary xylem before cone senescence that it is thought to have had an herbaceous
life habit (Rothwell et al. 2000), demonstrates that R. tuberculatus would not be
unique as an herbaceous gymnosperm in the context of the fossil record.

Viewed in this light, the stratigraphic distribution of R. tuberculatus at
Astartekloft provokes further speculation. In particular, it is interesting that R.
tuberculatus is common in plant beds 1–5, which are thought to represent overbank
crevasse splay deposits (McElwain et al. 2007), and essentially absent in plant beds 6
& 7, which represent a poorly developed coal swamp and an abandoned channel,
respectively (McElwain et al. 2007). The abundance of R. tuberculatus appears to
track disturbance regimes in the local environment at Astartekloft, being abundant in
active disturbed settings such as overbank crevasse splays, and absent from more
stable habitats. By analogy with the interpretation of Aethophyllum as an herbaceous
ruderal plant (Rothwell et al. 2000), the abundance of R. tuberculatus at Astartekloft
appears consistent with a ruderal plant characterized by rapid opportunistic growth
colonizing disturbed habitats. In this context, it is perhaps notable that R. tuberculatus
is also rare in Tr-J mire habitats in Sweden and Denmark, where it does not constitute
more than 4% of the total sporomorph assemblage in coals and coaly beds in this
region (Petersen and Lindström 2012). If the notion of R. tuberculatus as an
herbaceous ruderal gymnosperm is correct, then R. tuberculatus presents a challenge
to the idea that ephemeral herbs did not exist before angiosperm evolution (Boyce and
Leslie 2012), and may question the suggestion that the parent plant of R. tuberculatus
had a mid-canopy habit (Petersen and Lindström 2012; Petersen et al. 2013).
Ordination of Tr-J palynological data

The PCA plots from Astartekløft, Wüstenwelsberg, St. Audries bay and Hochalplgraben show a complex pattern of pollen and spore distribution that reflect differences in the environment and climate, vegetation history and sedimentary setting of the four different sections. Nevertheless, certain similarities can be found and used for the interpretation of the ecology of the parent plant of *R. tuberculatus*. Most striking is distribution of the *R. tuberculatus* and *Classopollis*, in particular *C. meyeriana*, vectors in opposite directions of PCA plots of St. Audries bay and Wüstenwelsberg on the first axis, and in the Hochalplgraben PCA plot on the second axis. This distribution strongly suggests that the parent plants were characterized by contrasting ecologies. This observation, combined with the palaeoenvironmental interpretation of PCA diagrams in Bonis and Kürschner (2012) and the global biogeographic distribution of *R. tuberculatus*, suggest that the parent plant of *R. tuberculatus* may have preferred a relative cooler, temperate climate in comparison to the *Classopollis* producing Cheirolepidiaceae, which preferred semi-arid hot (subtropical) climates (Vakharmeev, 1981, 1987, 1991).

Moreover, PCA plots of Astartekløft and Wüstenwelsberg are similar with respect to the maximum score of *R. tuberculatus* on the first axis, which reflects its predominance in the palynomorph assemblages in these two localities. In both sections, *R. tuberculatus* plots together with pollen such as *Vitreisporites* and *Ovalipollis* on the positive side of the first axes but the latter with lower values. The parent plant of *Ovalipollis* is unknown, but *Vitreisporites* was produced by the Caytoniales, a clade of seed ferns (e.g. van Konijnenburg – van Cittert, 2008). The covariance of *R. tuberculatus* and *Vitreisporites* may hint that the parent plants of these two taxa occupied similar ecological niches. Considering the large differences in
morphology and the differences in physical properties (buoyancy) between the two palynomorphs that would result, we suggest that taphonomical factors such as selective transport and deposition are unlikely to have caused this co-variance.

Conclusions

(1) The suggestion that R. tuberculatus was a produced by a gymnosperm (Mander et al. 2012) implies that gymnosperms were a more important component of Tr-J ecosystems than was previously thought based on palynological data (e.g. Bonis et al. 2010; Bonis et al. 2012). At Astartekløft, R. tuberculatus was comparable in abundance to macrofossils of the classes Cycadopsida, Ginkgoopsida, Bennettitopsida and the order Peltaspermales (Fig. 2).

(2) By analogy with the interpretation of Aethophyllum (Rothwell et al. 2000), we suggest that the parent plant of R. tuberculatus may have been a ruderal herbaceous plant that colonized disturbed habitats. This suggestion is consistent with the likely disturbance regimes at Astartekløft, East Greenland, and may explain the apparent lack of a fossil reproductive structure with R. tuberculatus in situ.

(3) The parent plants of R. tuberculatus and Classopollis (the Cheriolepidiaceae) may have had different ecological preferences. This is suggested by the apparent restriction of R. tuberculatus to the northern hemisphere, the pattern of R. tuberculatus and Classopollis relative abundances in pollen diagrams spanning the Tr-J, and the opposite direction of R. tuberculatus and Classopollis vectors in the PCA plots of the present study (Figs 4–7).
Acknowledgements

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*Palaeogeography, Palaeoclimatology, Palaeoecology*, 156, 139–145.


Figure legends

Figure 1. Ricciisporites tuberculatus imaged using brightfield microscopy. Note prominent surface sculpture and colour.

Figure 2. A Scatter diagram comparing the macrofossil and sporomorph records of plants that produced monocolpate pollen grains at Astartekløft, East Greenland (adapted from Mander et al. 2010). B Scatter diagram comparing the macrofossil and sporomorph records of monocolpate producing plants with Ricciisporites tuberculatus included in the ‘Monocolpate Producers’ sum. Each plant bed is represented by a single data point (n=8). Closed black circles=plant beds 1–5 (overbank deposits), open circle=plant bed 6 (poorly developed coal swamp) and closed grey circle=plant bed 7 (abandoned channel) (McElwain et al. 2007). Dashed diagonal line bisecting each scatter diagram represents line of equality.

Figure 3. Bar charts comparing the relative abundance of Ricciisporites tuberculatus and the most abundant macrofossils from the “Monocolpate Producers” group at Astartekløft, East Greenland (see Table 3). Relative abundance shown as a percentage of the total sporomorph sum in the case of R. tuberculatus, and as a percentage of the total macrofossil sum in the case of macrofossils. Numbers along the x-axis of the Sphenobaiera bar chart denote plant bed number. R. tuberculatus shown in dark grey, and plant macrofossils shown in pale grey.

Figure 4. PCA diagram of pollen and spore taxa from Astartekløft, East Greenland.

Figure 5. PCA diagram of pollen and spore taxa from Wüstenwelsberg, Germany.
Figure 6. PCA diagram of pollen and spore taxa from St Audrie’s Bay, UK.

Figure 7. PCA diagram of pollen and spore taxa from Hochalplgraben, Austria.

Table legends

Table 1. Details of the “Monocolpate Producers” group of plants analyzed in this study. Classification of macrofossils and botanical affinities of sporomorphs at Astartekløft from Mander et al. (2010) and Mander (2011). *Vardekloeftia*, Weltrichia and *Wielandiella* are fossil reproductive structures, all other genera are fossil leaves (McElwain et al. 2007). Broad botanical affinity of *Ricciisporites tuberculatus* from Mander et al. (2012).

Table 2. Abundance and percentage of the “Monocolpate Producers” group of plants at Astartekløft. “Monocolpate Pollen” refers to the “boat-shaped” monocolpate pollen grains of the *Monosulcites/Cycadopites* and *Chasmatosporites* morphotypes. Data from Mander et al. (2010).

Table 3. Relative abundance (reported as a percentage) of macrofossil genera referable to the classes Cycadopsida, Ginkgoopsida, Bennettitopsida and the order Peltaspermales, which are thought to have produced “boat-shaped” monocolpate pollen grains of the *Monosulcites/Cycadopites* and *Chasmatosporites* morphotypes (Mander et al. 2010; Mander 2011).
Figure 2

(A) Monocolpate Producers

(B) Monocolpate Producers with *Ricciisporites tuberculatus*
Figure 4

Astartekloft

PCA axis 1, 34% explained

PCA axis 2, 22% explained

Deltoidospora toralis

Punctatisporites globosus

Vitreisporites bjuvensis, pallidus

Ovalipollis ovalis

Cerebropollenites thiergartii

Araucariacites australis

Uvaesporites reissingeri

Baculatisporites comaumensis

Ovalipollis ovalis

Punctatisporites globosus

Vitreisporites bjuvensis, pallidus

Cerebropollenites thiergartii

Araucariacites australis

Uvaesporites reissingeri

Baculatisporites comaumensis

Astartekloft
Wuestenwelsberg, Germany

PCA axis 1, 71% explained

PCA axis 2, 15% explained

Classopollis spp
Araucariacites australis
Cycadopites spp#
Ovalipollis pseudoalatus
Perinopollenites elatoides
Pinuspollenites minimus
Vitreisporites bjuvensis
Concavisporites spp#
Deltoidospora spp#
Todisporites spp#
Cycadopites spp#
Ricciisporites tuberculatus
Ovalipollis pseudoalatus
Vitreisporites bjuvensis
Trachysporites fuscus
Pinuspollenites minimus
Araucariacites australis
Classopollis spp

Figure 5
St. Audrie’s Bay

Figure 6

PCA axis 1, 46.5% explained

PCA axis 2, 17.8% explained

Classopollis meyeriana
Trachysporites fuscus
Conbaculatisporites spp.
Heliosporites reissingeri
Acanthotriletes varius
Todisporites minor + major
Deltoidospora spp.
Polypodiisporites polymicroforatus
Calamospora tener
Ricciisporites tuberculatus
Rhaetipollis germanicus
Ovalipollis pseudoalatus
Classopollis torosus
Granuloperticulatipollis rudis
Vitreisporites bjuvensis
Classopollis torosus
Hochalplgraben

Figure 7
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<th>Macrofossils</th>
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<th>Sporomorph taxon</th>
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