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

20 *Ricciisporites tuberculatus* Lundblad is a prominently sculptured palynomorph that is
21 dispersed at maturity as tetrads. It has a wide geographic distribution and reaches a
22 stratigraphically important acme in the Norian and Rhaetian of Europe. As it has not
23 yet been found in situ in a fossilized reproductive structure its botanical affinity is
24 poorly understood. Recent work on the morphology and ultrastructure of *R.*
25 *tuberculatus* has shown that individual grains within the *R. tuberculatus* tetrad have a
26 single distal colpus, and that the sporoderm consists of a granular inner sexine, and an
27 electron-dense laminated nexine. These characters are typical of gymnosperms.
28 However, in their previous palynological studies, Kürschner and co-workers assigned
29 *R. tuberculatus* to the spore plants, in line with older interpretations of the botanical
30 affinity of *R. tuberculatus*. In the present contribution, we re-evaluate Triassic–
31 Jurassic (Tr-J) palynological records and discuss the consequences of a gymnosperm
32 affinity for *R. tuberculatus* for Late Triassic vegetation reconstruction, as well as
33 inferred palaeoecological interpretations. At a Tr-J boundary locality in East
34 Greenland, the relative abundance of *R. tuberculatus* through time is similar to the
35 bennettites *Anomozamites* and *Pterophyllum*. We suggest that *R. tuberculatus* may
36 have been produced by a gymnosperm characterized by an herbaceous ruderal life
37 habit. The poor preservation potential of the vegetative structures of such a plant may
38 explain why *R. tuberculatus* has not yet been found *in situ* in a fossil reproductive
39 structure. We suggest that the parent plants of *R. tuberculatus* and *Classopollis* (the
40 Cherirolepidiaceae) may have had different ecological preferences.

41

42 **Keywords:** Late Triassic, palynology, *in situ* pollen and spores, herbaceous
43 gymnosperm, *Classopollis*.

44

45 **Introduction**

46 The fossil palynomorph *Ricciisporites tuberculatus* Lundblad is a conspicuous
47 component of palynological assemblages from the Norian to the Hettangian
48 (Kürschner and Herngreen 2010 and literature cited herein). *Ricciisporites*
49 *tuberculatus* is permanently united in tetrahedral tetrads (Lundblad 1959) and
50 measures 80–110µm in maximum dimension (Fig. 1; Mander et al. 2012). Each
51 member of the tetrad is prominently sculptured with clavae and gemmae, and the
52 distal face of each member is equipped with a single elongated furrow (Fig. 1;
53 Lundblad 1959; Mander et al. 2012). *R. tuberculatus* has a fairly thick exine, and as
54 result is usually dark brown in colour when viewed using transmitted light
55 microscopy.

56 *Ricciisporites tuberculatus* appears to be restricted to the northern hemisphere,
57 and although it is not presently known to occur in the classic Triassic–Jurassic (Tr-J)
58 successions of North America (e.g. Cornet and Traverse 1975), it is found in
59 sediments from arctic Canada (Suneby and Hills 1988) to China (Yong et al. 2003).
60 *Ricciisporites tuberculatus* is stratigraphically valuable in sediments of Upper Triassic
61 age, and reaches an acme in the Rhaetian of northwest Europe (Pedersen and Lund
62 1980; Bonis et al. 2010a; Pienkowski et al. 2012). This acme forms part of the
63 stratigraphic framework that has been used to correlate terrestrial and marine
64 sediments of Upper Triassic age, which is particularly useful in the context of debates
65 about the relative timing of biotic events during the late Triassic mass extinction
66 (~200Ma; Hesselbo et al. 2007) (e.g. Kürschner et al. 2007; Mander et al. 2013), and
67 has also been used to provide a latest Rhaetian age for theropod dinosaur footprints in
68 Sweden (Vajda et al. 2013).

69 In addition to its value as a biostratigraphic marker, the abundance of *R.*

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.

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95 To do this we re-investigate Tr-J palynological data undertaken by Bonis et al. (2009,
96 2010a) and Bonis et al. (2012), who interpreted *R. tuberculatus* as a liverwort in line
97 with Balme (1995), rather than as gymnosperm. We also undertake multivariate
98 ordination of Tr-J palynological data from East Greenland and Germany.

99

100 **Materials and methods**

101 Comparison of macrofossil and sporomorph records

102 We build on previous work comparing the macrofossil and sporomorph records of Tr-
103 J vegetation at a boundary section at Astartekløft in Jameson Land, East Greenland
104 (Mander et al. 2010). The rock succession at this locality comprises the fluvial–
105 lacustrine Kap Stewart Group and is rich in plant macrofossils, which are restricted to
106 a series of discrete fossiliferous intervals known as “plant beds” (Harris 1937;
107 McElwain et al. 2007). Plant beds 1–4 are of Upper Triassic (Rhaetian) age, plant
108 beds 6 and 7 are of Lower Jurassic (Hettangian) age, and plant bed 5 contains the
109 Triassic/Jurassic boundary, which is approximated at Astartekløft by the first
110 appearance of the pollen morphospecies *Cerebropollenites thiergartii* (Mander et al.
111 2013). Plant beds 1–5 represent overbank crevasse-splay deposits, plant bed 6
112 represents a poorly developed coal swamp, and plant bed 7 represents an abandoned
113 channel (McElwain et al. 2007).

114 In this paper, we analyze a group of plants that is abundant in the macrofossil
115 record at Astartekløft, but is thought to be a minor component of the sporomorph
116 record at this locality. This group of plants consists of the classes Cycadopsida,
117 Ginkgoopsida, Bennettitopsida and the order Peltaspermales, which are all thought to
118 have produced “boat-shaped” monocolpate pollen grains of the
119 *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 Astartekløft (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) Astartekløft, 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 Astartekløft 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 Astartekløft 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 Astartekløft, 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 Astartekløft (Mander et al. 2010) (Table 2). This disagreement between the macrofossil and sporomorph records of Tr-J vegetation at Astartekløft 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 Astartekløft that are similar to that of *R. tuberculatus* at this locality include the bennettites *Anomozamites* and *Pterophyllum* (Fig. 3). Macrofossil “Monocolpate Producers” which show the opposite pattern at Astartekløft include *Czekanowskia* and *Sphenobaiera* (Fig. 3).

Ordination of Tr-J palynological data

The distribution of pollen and spores in the Astartekløft, Wüstenwelsberg, St. Audries

170 bay and Hochalplgraben sections are shown as the species scores on the first and the
171 second axis of the PCA ordination diagrams (Figs 4-7). We interpret the distribution
172 of sporomorph taxa within these PCA plots as the net result of interplay between the
173 ecology and environmental preferences of the pollen producing mother plants and
174 taphonomical factors.

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

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

193 Figure 6 shows the distribution of sporomorph taxa from the St. Audries Bay
194 section in the PCA ordination diagram. The first axis explains 45% of the total

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 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

220 macrofossil and sporomorph records of the “Monocolpate Producers” group of plants
221 in East Greenland, which highlights that a plant producing monocolpate pollen, albeit
222 permanently united in tetrads, was comparable in abundance to macrofossils of the
223 classes Cycadopsida, Ginkgoopsida, Bennettitopsida and the order Peltaspermales in
224 this region (Fig. 2; Table 2).

225 The palaeoclimatic and ecological preferences of the parent plant of *R.*
226 *tuberculatus* relative to other Tr-J plants are suggested by patterns in the global
227 occurrence and local abundance of this palynomorph. In particular, *R. tuberculatus*
228 appears to be restricted to the northern hemisphere (Mander et al. 2012), and is
229 particularly abundant in more northerly Tr-J boundary sections in East Greenland
230 (Mander et al. 2013). In contrast, the abundance of *Classopollis* pollen declines with
231 increasing palaeolatitude (Pedersen and Lund 1980; Koppelhus 1997; Bonis et al.
232 2012; Mander et al. 2013). Additionally, pollen diagrams of sediments spanning the
233 Tr-J in Austria (Bonis et al. 2009; 2012) and the UK (Bonis et al. 2010a) show that
234 where *Classopollis* and *R. tuberculatus* are important components of the palynoflora
235 (>20%) they alternate in abundance so that where *Classopollis* is common, *R.*
236 *tuberculatus* is rare and *vice versa*. A possible exception to this pattern is data from
237 Tr-J boundary sections in Germany and Sweden (van de Schootbrugge et al. 2009).
238 But the global biogeographic pattern of *R. tuberculatus* and *Classopollis* occurrences,
239 the relationship between these two pollen grains in several pollen diagrams spanning
240 the Tr-J, and the opposite direction of *R. tuberculatus* and *Classopollis* vectors in the
241 PCA plots of the present study (Figs 4–7), together raise the possibility that the parent
242 plants of *Classopollis* and *R. tuberculatus* were ecologically reciprocal in status
243 (Chaloner pers. comm. January 2013).

244 The prominent clavate–gemmate ornamentation that characterizes the surface
 245 of *R. tuberculatus* is suggestive of animal rather than wind pollination (Mander et al.
 246 2012), and it is intriguing that the decline in the abundance of *R. tuberculatus* at
 247 Astartekløft matches the decline in the abundance of macrofossils of plants that were
 248 likely to have been animal pollinated at this locality such as bennettites (McElwain et
 249 al. 2007) (Fig. 3). However, the reproductive structures that are present in Tr-J
 250 sediments in East Greenland (Table 1) are only associated with pollen grains referable
 251 to the genus *Monosulcites* (see Pedersen et al. (1989) for *Vardekloeftia*, and Osborne
 252 and Taylor (1995) for *Weltrichia* and *Wielandiella*), and the *in situ* record provides no
 253 evidence for a botanical relationship between any plant macrofossil and *R.*
 254 *tuberculatus*. This is surprising given the history of intensive palaeobotanical work in
 255 this region that has recovered many well-preserved reproductive structures (e.g.
 256 Harris 1937; McElwain et al. 2007), and highlights that further investigations of
 257 macrofossils in the field and museum collections are needed.

258 One possibility that could explain the discrepancy between the high abundance
 259 of *R. tuberculatus* in the dispersed sporomorph record (Fig. 3) and the apparent
 260 absence of its parent plant from sediments that are generally favourable for the
 261 preservation of plant macrofossils (e.g. McElwain et al. 2007), is that the parent plant
 262 of *R. tuberculatus* was characterized by an herbaceous life habit. Herbaceous plants
 263 have considerably lower preservation potential compared to woody plants (e.g. Spicer
 264 1989; Gastaldo 2001), and macrofossil assemblages at Astartekløft are weighted
 265 towards woody taxa whereas sporomorph assemblages are weighted towards more
 266 delicate ferns and lycopods (Mander et al. 2010). This is a contentious suggestion
 267 because the herbaceous life habit has evolved several times among angiosperms, but
 268 the remainder of seed plant diversity is essentially composed of woody perennial

269 plants (Boyce and Leslie 2012; Rowe and Paul-Victor 2012). However, the case of
 270 *Aethophyllum*, a Triassic gymnosperm that produced such a small amount of
 271 secondary xylem before cone senescence that it is thought to have had an herbaceous
 272 life habit (Rothwell et al. 2000), demonstrates that *R. tuberculatus* would not be
 273 unique as an herbaceous gymnosperm in the context of the fossil record.
 Viewed in this light, the stratigraphic distribution of *R. tuberculatus* at
 Astartekløft 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 Astartekløft, 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 Astartekløft
 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).

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

310 Moreover, PCA plots of Astartekløft and Wüstenwelsberg are similar with
 311 respect to the maximum score of *R. tuberculatus* on the first axis, which reflects its
 312 predominance in the palynomorph assemblages in these two localities. In both
 313 sections, *R. tuberculatus* plots together with pollen such as *Vitreisporites* and
 314 *Ovalipollis* on the positive side of the first axes but the latter with lower values. The
 315 parent plant of *Ovalipollis* is unknown, but *Vitreisporites* was produced by the
 316 Caytoniales, a clade of seed ferns (e.g. van Konijnenburg – van Cittert, 2008). The
 317 covariance of *R. tuberculatus* and *Vitreisporites* may hint that the parent plants of
 318 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 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 Cherirolepidiaceae) 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).

344

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457 **Figure legends**

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

460

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

470

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

478

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

480

481 **Figure 5.** PCA diagram of pollen and spore taxa from Wüstenwelsberg, Germany.

482

483 **Figure 6.** PCA diagram of pollen and spore taxa from St Audrie’s Bay, UK.

484

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

486

487 **Table legends**

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

494

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

499

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

(A) Figure 2
Monocolpate Producers

(B) Monocolpate Producers with
Ricciisporites tuberculatus

Figure 4

Figure 5

Wuestenwelsberg, Germany

Figure 6

St. Audrie's Bay

Figure 7

Hochalplgraben

Table 1

Macrofossils		Sporomorphs	
Genus	Class	Sporomorph taxon	Botanical Affinity
Anomozamites	Bennettitopsida	Chasmatosporites elegans	Cycadopsida; Ginkgoopsida
Baiera	Ginkgoopsida	Chasmatosporites hians	Cycadopsida; Ginkgoopsida
Ctenis	Cycadopsida	Cycadopites sp.	Cycadopsida; Ginkopsida; Pteridospermopsida; Bennettitopsida
Cycadolepis	Bennettitopsida	Monosulcites minimus	Bennettitopsida
Czekanowskia	Ginkgoopsida	Ricciisporites tuberculatus	Gymnosperm
Doratomyllum	Cycadopsida		
Ginkgo	Ginkgoopsida		
Lepidopteris	Pteridospermopsida		
Nilssonia	Cycadopsida		
Pseudocstenis	Cycadopsida		
Pterophyllum	Bennettitopsida		
Sphenobaiera	Ginkgoopsida		
Vardekloeftia	Bennettitopsida		
Weltrichia	Bennettitopsida		
Wielandiella	Bennettitopsida		

Table 2

Plant Bed	Macrofossils		Sporomorphs			
	Monocolpate Producers		Monocolpate Pollen		<i>Ricciisporites tuberculatus</i>	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
7	797	96.37	53	3.76	1	0.07
6	5	3.97	4	0.37	0	0.00
5	39	10.43	41	1.28	239	7.45
4	477	86.73	26	1.22	801	37.45
3	62	11.13	27	1.83	220	14.92
2	169	68.15	50	1.98	865	34.22
1.5	34	56.67	5	1.39	118	32.69
1	116	74.36	48	2.02	1189	49.98

Table 3

Genus	Plant Bed							
	1	1.5	2	3	4	5	6	7
<i>Anomozamites</i>	21.79	28.33	9.27	0.18	26.73	0.27	0	0.48
<i>Baiera</i>	9.62	0	0	1.26	0	0	0	0
<i>Ctenis</i>	0	0	0	0	0	0.53	0	0
<i>Cycadolepis</i>	0	0	1.61	0	7.45	0.53	0	0.12
<i>Czekanowskia</i>	3.21	0	0	0	0	0	0	50.67
<i>Doratophyllum</i>	0	0	0	7.54	0	0	0	0
<i>Ginkgo</i>	8.33	0	34.68	0	0	1.34	0	24.55
<i>Lepidopteris</i>	0.64	3.33	4.84	0	1.82	0	0	0
<i>Nilssonia</i>	4.49	15.00	0	0.72	0	0	0	0.12
<i>Pseudoctenis</i>	0	5.00	0	0	0	8.56	0	0
<i>Pterophyllum</i>	26.28	5.00	17.74	1.08	49.27	0.27	3.97	0
<i>Sphenobaiera</i>	0	0	0	0.36	0	0	0	20.44
<i>Vardekloeftia</i>	0	0	0	0	0	0.27	0	0
<i>Weltrichia</i>	0	0	0	0	0.36	0	0	0
<i>Wielandiella</i>	0	0	0	0	1.09	0	0	0