We thank the two reviewers for providing comments on our manuscript. The reviewers' original comments are shown in black with our responses in red. Also in the manuscript attached, changes made to the earlier version are given in red.

In response to comments by reviewer #2, we calculated variability in process length within each specimen, and found these in general to be small (a table was added to the supplementary file to show the variability and the frequency with which it occurs). We also clarified better the methodology and discussed other options for process length variability. We also added a figure to the supplementary file showing the individual measurements per acritarch and the averages for each interval (Fig. S1).

Anonymous Reviewer #1

This paper documents nicely the potential of the process length of acritarchs as a palaeo-proxy for salinity.
After a first version of this manuscript, submitted to another journal, where the main problem was an over-interpretation of the results, the present version clearly points out the potential of morphology studies of organic-walled microphytoplankton for tracking ancient salinity of temperature changes.
This is still very much hypothetical, but the study is been carried out with precision, and the results show a clear trend. It is made clear that the interpretations have to take with caution. This study should be published; these results will surely stimulate further investigations!

We like to thank the reviewer for the positive feedback. Feedback on the previous version of this manuscript, mentioned by the reviewer has been very helpful and improved the manuscript a great deal. We hope that this study will indeed stimulate further research on acritarch morphology.

Anonymous Reviewer #2

We like to thank the reviewer for the constructive comments. Below each comment we provide a response.

Comment:

1) To study the changes in processes length across the section the authors measured three processes per specimen (Lines 140 – 141). The specimens selected for these study include "only those with a spherical central body and many (>10) simple processes with closed tips" belonging to the Micrhystridium breve Group (lines 137 – 138). Why did the author measure only 3 processes per specimen? How did they select the three processes to measure? In Fig. 3 it seems that the processes of M. breve Group acritarchs vary in length within a single specimen. What is the process length variability in one specimen? How could the selection of only 3 out of 10 processes bias the analysis? These methodological issues must be assessed, discussed and taken into account for the interpretation of the data. I strongly recommend the authors to expand the discussion on the methodological aspect, which I believe is the most important theme of this study.

Reply:

1

The selection of the processes on the acritarchs was limited by the fact that the acritarchs are compressed into a two dimensional shape and, as a consequence, some of the processes are not visible. We therefore chose a focal plane that showed the most, and best preserved processes. From these we measured the three longest, following the methodology by Mertens et al., (2012). We will clarify this in the methodology.

We agree with the reviewer that the length of the processes varies within a single specimen. In about 50% of the measured acritarchs this variation within one specimen is smaller than 1 μm, in 28% the variation within one specimen was between 1-2μm, in 15% between 2-3 μm, and only in 7% larger than 3 μm. In addition, we measured 20-30 specimens per sample in order to minimize noise and decrease the standard error within one sample. The overall trend over the studied section is a shortening of process length of 3-5 μm. The variability of the process length within one specimen therefore is smaller than the general trend. We expanded the method section to explain better the selection of the processes, and in the results section we now describe the degree of variability within individual acritarchs.

2) The observed changes in acritarch average processes length are interpreted as the evidence of changing salinity in the water column. This conclusion seems to be based on the assumption that the Micrhystridium acritarchs considered for this study belong to one species. According to the authors, this assumption is suggested by the unimodal distribution of body size and processes length (Fig. 5). However, considering data through time (Fig. 6), there is indeed a difference (lines 192 – 194) in processes length and in body size between the acritarchs extracted from laminated rocks (after the extinction; Wordie Creek Formation) and those from bioturbated rocks (before the extinction; Schuchert Dal Formation). This is actually the main conclusion of the study. So, could these facies-dependant differences in both processes length and body size just mean that different species (with a different body size and length of the processes) are found in the different formations? Do the acritarchs' morphological differences represent a salinity-related mutation in one species through time or do these morphological characters show different Micrhystridium species? Acritarch con centrations at Fiskegrav, before and after the extinction, also suggest a change in the community structure, and in fact a change in the marine palynomorphs' assemblage is detected (see below, point 3). Similarly and as an example, van de Schootbrugge fet al. (2007; P3, 244, 126–141) found an increase in actritarch abundance and diversity at the Triassic – Jurassic boundary.

Reply:

Although several different Micrhystridium-species have been described for the late Permian (e.g. Lei et al., 2013b), it has also been noted by several authors that the different species are difficult to distinguish (Lei et al., 2013a; Sarjeant and Stancliffe, 1994). We follow the simple classification proposed by Lei et al., (2013) in which all spherical specimens belonging to the Micrhystridium/Veryhachium complex are grouped together in a Micrhystridium breve-group (independent of the process length or body size). The purpose of our study is to find out if some of the observed variability in morphology of the late Permian Micrhystridium-group might be explained by environmental conditions rather than different species. Thus, we indeed assume that the acritarchs of the Micrhystridium breve-group, found in our section, belong to one species. This assumption is tested by the frequency analysis of all body size and process length. The unimodal distribution (uniform morphology) of the studied acritarch population does not support the presence of 2 or more different species.

We agree with the reviewer, that there is indeed, on average, a difference in process length between acritarchs from the laminated and form the bioturbated intervals. However, while the changes in facies are abrupt, the change in process length is gradual, and starts before the facies change. Also in body size there is no consistent off-set throughout the whole record. So, both the changes observed in process length and body size are not directly related to facies.

3) The authors say that "studies of acritarch process length and palaeoenvironment show that species and individuals with longer processes are generally found in more offshore locations, while in inshore settings acritarchs with shorter processes are more abundant" (lines 293 – 295). These differences have been tentatively attributed to salinity differences between off-shore and nearshore environments (Servais et al., 2004; Palaeontology, 47, 395–414). So, could the change in average process length found in the studied section just be an effect of transport of acritarchs living in different environments? Is it possible that inshore species of Micrhystridium acritarchs with shorter process length, were transported to the more distal setting? The processes length change is coupled to a change in the assemblage from "Veryhachium/Micrhystridium to Micrhystridium/leiosphere dominance" (lines 275 – 276). Leiosphere are common in fluvial-deltaic environments (e.g. Zavattieri & Pramparo 2006; Palaeontology, 49, 1185–1209), and indeed in the Fiskegrav section the reduction of average process length is coupled to an increase in leiosphere abundance (Fig. 6). The authors indeed acknowledge that "during the extinction event the acritarch assemblage changes to a more typical near-shore assemblage, despite the ongoing sea-level rise" (lines 286 – 287), but they do not discuss the possible effect of transport. This is a crucial point that must be discussed to understand whether the observed changes in acritarch morphology reflect actual changes in salinity of the water column or just transport of nearshore species towards more distal environments after the extinction interval.

Reply: Transport is rejected as an explanation of changing process length for two reasons: First, the preservation is very good throughout, and especially in the laminated rocks the Micrhystridium are of good quality, which argues against large-scale transport of the acritarchs. Second, and most importantly, if there was transport of acritarchs with short processes into a deeper water environment, this would result in a mixture of acritarchs with long and short processes in those samples. This is not the case. Although there is certainly variability within each sample in process length, the samples do not show such a bimodal distribution. A figure showing process length and body size for each specimen, and average values per sample, will be added to the supplementary file.

4) Local vs global signal. Data collected in this study come from one stratigraphic section that has been deposited in a narrow basin. The observed changes in acritarch assemblage, body size, and process length thus represent a very local signal. What is the significance of this local change in a global perspective?

Reply: The data are indeed local, but the inferred changes in rainfall suggest changes in the hydrological cycle and support climate models for the later Permian. Future research on acritarch process length from other locations will provide further insight into climate and oceanographic changes in the later Permian, and will allow predictions made from global climate models to be tested.

5) I think the title of the manuscript does not satisfactorily mirror its content.

Reply: We kindly disagree with the reviewer and think the title describes the content well.

Other minor comments

Line 67: Servais et al. (2004) talk about Cambrian – Ordovician acritarchs. Given the fact that acritarchs are a group of uncertain affinity, is there any more appropriate citation supporting the statement that "many acritarchs are, however, found exclusively in marine rocks"? In other words, is this true also for the Permian – Triassic?

Reply: We change the sentence to "considered to be phytoplankton" and add a citation of Lei et al., 2013 for a review of late Permian acritarchs found in marine successions.

Lines 72 – 75: The reference provided (Martens et al., 2009) discusses the effect of salinity in one modern dinocyst morphology. Is it possible to provide any reference about the effects of salinity on acritarchs?

Reply: We added a reference to Servais et al., 2004, Palaeontology, Vol. 47, Part 2. In which the possible effects of salinity changes on acritarch morphology of Cambrian-Ordovician acritarchs is discussed.

Lines 192 – 194: The numbers, e.g. average body size, average processes length, errors, etc. . ., to support these statements should be presented. This would help the reader. A simple reference to the figure is not sufficient. Is it possible to introduce in the results the changes in acritarch assemblage later discussed in 286 – 287 and following lines? How could this change affect the measurement and interpretation of acritarch processes length?

Reply: Following the advice of the reviewer, we added values to the last paragraph in results section 4.2 aquatic palynomorphs. The text now introduces better the discussion part of section 5.2. The values are also given in a table in the supplementary files. As discussed above, changes in assemblage do not affect the measurement and interpretation of acritarch process length.

Salinity changes and anoxia resulting from enhanced runoff during the late Permian global warming and mass extinction event

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Abstract. The Late Permian biotic crisis had a major impact on marine and terrestrial environments. Rising CO_2 levels following Siberian Trap volcanic activity were likely responsible for expanding marine anoxia and elevated water temperatures. This study focusses on one of the stratigraphically most expanded Permian-Triassic records known, from Jameson land, east Greenland. High resolution sampling allows for a detailed reconstruction of the changing environmental conditions during the extinction event and the development of anoxic water conditions. Since very little is known about how salinity was affected during the extinction event, we especially focus on the aquatic palynomorphs and infer changes in salinity from changes in the assemblage and morphology. The start of the extinction event, here defined by a peak in spore/pollen, indicating disturbance and vegetation destruction in the terrestrial environment, postdates a negative excursion in the total organic carbon, but predates the development of anoxia in the basin. Based on the newest estimations for sedimentation rates, the marine and terrestrial ecosystem collapse took between 1.6 to 8 kyrs, a much shorter interval than previously estimated. The palynofacies and palynomorph records show that the environmental changes can be explained by enhanced runoff, increased primary productivity and water column stratification. A lowering in salinity is supported by changes in the acritarch morphology. The length of the processes of the acritarchs becomes shorter during the extinction event and we propose that these changes are evidence for a reduction in salinity in the shallow marine setting of the study site. This inference is supported by changes in acritarch distribution, which suggest a change in palaeoenvironment from open marine conditions before the start of the extinction event to more near-shore conditions during and after the crisis. In a period of sea-level rise, such a reduction in salinity can only be explained by increased runoff. High amounts of both terrestrial and marine organic fragments in the first anoxic layers suggest that high runoff, increased nutrient availability, possibly in combination with soil erosion, are responsible for the development of anoxia in the basin. Enhanced runoff could result from changes in the hydrological cycle during the late Permian extinction event, which is a likely consequence of global warming. In addition, vegetation destruction and soil erosion may also have resulted in enhanced runoff. Salinity stratification could potentially explain the development of anoxia in other shallow marine sites. The input of fresh water and related changes in coastal salinity could also have implications for the interpretation of oxygen isotope records and seawater temperature reconstructions in some sites.

1. Introduction

The late Permian extinction event was the most severe global crisis of the Phanerozoic in terms of both taxonomic loss and ecological impact (e.g. McGhee et al., 2012). The current consensus is that the extinction was likely due to global warming and associated environmental changes caused by CO_2 emissions from Siberian Trap volcanic activity, because of the close timing between the volcanic activity and the extinction event (e.g., Burgess et al., 2017; Burgess and Bowring, 2015). Most studies on the late Permian extinction have inferred that expanding marine anoxia (e.g. Wignall and Hallam, 1992) is a key biotic factor causing marine extinction and ecosystem collapse. There are different theories to explain the spreading of anoxia, which affected both deep and shallow sites (e.g. Bond and Wignall, 2010; Isozaki, 1997; Wignall and Twitchett, 1996). A weakened temperature gradient between equator and pole would have slowed ocean circulation and may have facilitated expansion of the oxygen minimum zone (Hotinski et al., 2001). Increased weathering and detrital input (Algeo and Twitchett, 2010), and soil erosion (Sephton et al., 2005) led to enhanced terrestrial matter input in marine sections, and may also have contributed to eutrophication and in stratified waters led to hypoxia or anoxia (Sephton et al., 2005). Other factors that are thought to play important roles in the extinction are elevated water temperatures (e.g. Sun et al., 2012), and ocean acidification (Clapham and Payne, 2011). One important environmental parameter that has received relatively little attention is salinity, even though low salinity ocean conditions were once considered to be a leading cause of the marine extinction (Fischer, 1964; Stevens, 1977). Furthermore, potential impacts of changes in salinity, which might be expected from enhanced discharge of freshwater into shelf seas (Winguth and Winguth, 2012), have been largely ignored.

Microfossils of marine algae are excellent recorders of environmental change in the water column. Of these, the organic-walled cysts of dinoflagellates have proven especially useful in palaeo-environmental studies (e.g. Ellegaard, 2000; Mertens et al., 2009, 2012, Mudie et al., 2001, 2002; Sluijs and Brinkhuis, 2009; Vernal et al., 2000). While dinocysts are absent or sparse in Palaeozoic deposits, acritarchs are commonly recorded (e.g. Tappan and Loeblich, 1973), even during the late Permian when acritarch diversity was declining (Lei et al., 2013b). Acritarchs are a group of microfossils of organic composition and unknown affinity (Evitt, 1963). Many acritarchs are, however, considered to be phytoplankton, and some are thought to be precursors of modern dinoflagellate cysts (e.g. Lei et al., 2013b; Servais et al., 2004). Several studies in East Greenland have reported fluctuating abundances of acritarchs during the Late Permian and Early Triassic (e.g. Balme, 1979; Piasecki, 1984; Stemmerik et al., 2001), but very few late Permian studies have documented the relative abundance of the different genera of aquatic palynomorphs (for example, Shen et al., 2013). Similar to dinocysts, acritarch morphology has been linked to environmental conditions, and acritarchs with longer processes are generally more abundant in more open marine settings (Lei et al., 2012; Stricanne et al., 2004). Both dinocyst and acritarch studies show that salinity might be an important factor that influences cyst morphology (Servais et al., 2004). It is thought that the longer processes in higher salinities stimulate clustering with other cysts or particles in the water column, and thus enhance sinking to the seafloor (Mertens et al., 2009).

The rock record of Jameson Land, East Greenland, has provided key insights into marine environmental changes during the late Permian extinction event. Previous work on this section by Twitchett et al. (2001) showed that collapse of marine and terrestrial ecosystems was synchronous and took between 10 to 60 kyr. Palynological work by Looy et al. (2001) showed that the terrestrial ecosystem collapse is characterized by a

| 78 | distinct rise in spores, indicative of the loss of woodland and increase in disturbance taxa. The onset of anoxic |

distinct rise in spores, indicative of the loss of woodland and increase in disturbance taxa. The onset of anoxic conditions is not as abrupt at this location as seen in some other sections, but instead Wignall and Twitchett, (2002) found unusual alternating patterns of bioturbated and laminated siltstones in the top of the Schuchert Dal Formation and lowest of the Wordie Creek Formation (Fig. 1). In a recent study, Mettam et al., (2017) showed that rapidly fluctuating redox conditions occurred during the late Permian extinction, while sedimentological observations imply that sea level was rising in this period. Estimations of sedimentation rates indicate that each bioturbated/laminated rock interval, which are between 2-10 cm thick, have been deposited in a period of 50-1000 years (Mettam et al., 2017). To study the environmental conditions associated with the deposition of these sediments we look in detail at a short (9 m) interval covering the late Permian extinction and the Formation boundary between the Schuchert Dal and Wordie Creek Formation. Palaeoenvironment is studied by looking at variations in the palynofacies (organic particles) and the acritarch assemblage. In addition we present a record of morphological changes within the acritarch *Micrhystridium*. Runoff and erosion, salinity, sea-level fluctuations and temperature rise are discussed as possible reasons for the changing environmental conditions.

2. Geological setting and stratigraphy

Samples were collected at the Fiskegrav location of Stemmerik et al. (2001), an outcrop in East Greenland (N71°32'01.6", W024°20'03.0"), in a small stream section on the east side of Schuchert Dal (Fig. 1). The section was deposited within a relatively narrow, north-south oriented basin (Stemmerik et al., 2001; Wignall and Twitchett, 2002). Active rifting and rapid subsidence has resulted in the deposition of one of the most expanded P-Tr sections. At the Fiskegrav location there are no obvious breaks in sedimentation, even though large erosive channels exist in P-Tr sections in more northern locations (Twitchett et al., 2001; Wignall and Twitchett, 2002).

The Fiskegrav section shows a transition from the Schuchert Dal Formation into the Wordie Creek Formation. The Permian/Triassic boundary, defined by the first occurrence of the conodont *Hindeodus parvus* (Yin, 1996), is located at 23.5 m above the base of the Wordie Creek Formation (Twitchett et al., 2001). This study focusses on a ca. 9 m section interval including the late Permian extinction and the formation boundary (Fig. 1). The upper part of the Schuchert Dal Formation consists of blocky (bioturbated), micaceous, greenish mudstones (muddy siltstones), whereas the lower Wordie Creek Formation consists mainly of laminated, dark grey mudstones (clay-siltstones) that often contain framboidal pyrite (Twitchett et al., 2001; Wignall and Twitchett, 2002). The extinction event occurs in the upper metres of the Schuchert Dal Formation, and the start of the biotic crisis is synchronous in marine and terrestrial ecosystems (Looy et al., 2001; Twitchett et al., 2001). For more details on biostratigraphy see Mettam et al., (2017); Stemmerik et al., (2001) and Twitchett et al., (2001).

3. Material and Method

3.1 Material

114 A total of 36 samples were collected from the top 4.5m of the Schuchert Dal Formation and the lower 4.2m of

115 the Wordie Creek Formation. Sample resolution is highest (10cm intervals) in the 2.5m interval covering the

116 formation boundary and the extinction event. Depths are given in m, relative to the formation boundary between

117 Schuchert Dal and Wordie Creek Fm. Some of the samples used in this study were also analysed by Mettam et

118 al. (2017) during their study of changes in redox conditions at the formation boundary.

119

120 **3.2 palynofacies and palynological analysis**

121 Samples (of ca.5 g) were crushed, and a tablet with a known amount of lycopodium spores was added

122 to allow quantification of organic particles and palynomorphs. Samples were then treated with hydrochloric acid

123 and hydrofluoric acid to remove carbonates and silicates, and subsequently sieved through 7 µm sieves. Heavy

124 liquid separation was used to remove heavy minerals like pyrite. The residue, containing palynomorphs and

125 other organic particles, was mounted onto microscope slides. Material was counted using a Leitz Diaplan

126 microscope and an AxioCam ERc 5s camera attached to a computer with Zen microscope software (Zen 2 lite,

127 2011). A minimum of 300 particles per sample were counted for palynofacies analyses. Aquatic palynomorphs

128 were counted to reach 100 specimens when abundant and at least 30 specimens when abundance was low. Still,

129 due to low abundances during the biotic crisis, in some samples counts were below 30 (these 6 samples are

130 indicated in Fig. 4).

131

132 **3.3 Acritarch measurements**

133 The genus *Micrhystridium* includes many species, of which ca. 20 are known from the Permian-

134 Triassic interval, which differ in their body size, number of processes and process length (Lei et al., 2013b;

135 Sarjeant, 1970). Only those with a spherical central body and many (>10) simple processes with closed tips

136 were included in this study (i.e. the *M. breve* Group, according to Lei et al., 2013b). Thus, amongst others, *M.*

137 *pentagonale* was excluded. Specimens were excluded if they were too damaged (folded or broken) to allow

138 measurements. To counteract the effects of compression (which can make the body look longer), body size was

139 calculated from the average of two linear measurements perpendicular to each other. The choice of processes

140 was limited due to compaction of the acritarchs. If more than 3 processes were available for measurement, a

141 focal plane was chosen that showed most, and best preserved processes, from which we measured the three

142 longest, following the methodology by Mertens et al., (2012). The aim was to measure 20-30 specimens per

143 sample, but acritarch concentrations were low during the biotic crisis interval, and therefore 5 samples had

144 lower counts (indicated in Fig. 6).

145

146 **4. Results**

147 **4.1 Palynofacies**

148   The most abundant organic particles are phytoclasts and amorphous organic matter (AOM) which together
149   comprise 45 to 90% of the palynofacies (Fig. 2). Phytoclasts are dominant in the bioturbated samples in the
150   lower part of the section, while AOM dominates the palynofacies in the laminated intervals. Other terrestrially
151   derived organic (wood fragments and charcoal) particles make up a small portion (<20%) of the palynofacies
152   and are not influenced by the alternating anoxic/oxic depositional conditions (Fig. 2). Palynomorphs were
153   divided into three groups: pollen, spores and aquatic palynomorphs. Pollen abundance relative to other
154   palynofacies is higher in the upper 0.5 m of the Schuchert Dal Formation and lowest metre of the Wordie Creek
155   Formation (5-20%), which is mainly caused by the high number of pollen fragments (sacci) during and
156   following the extinction event (Fig. 2). Spores have highest abundance in the upper metre of the Schuchert Dal
157   Formation (up to 35%), where also the spore/pollen ratio is highest. Aquatic palynomorphs (acritarchs and other
158   algal remains like *Tasmanites* and *Cymatiosphaera*) make up a very small fraction of the palynofacies in the
159   Schuchert Dal Formation (<2%), but become relatively more abundant in the Wordie Creek Formation (up to
160   14%).

161

162   4.2 Aquatic palynomorphs

163   Although Permian acritarch diversity is considered to be low, an overview of Permian phytoplankton by Lei et
164   al. (2013b) showed a richness of about 20-30 genera during most of the Permian, with acritarchs belonging to
165   the genera *Micrhystridium* and *Veryhachium* being the most common (Lei et al., 2013b, 2013a; Sarjeant and
166   Stancliffe, 1994). Since cysts are generally small in size it is difficult to study them under light microscope and
167   identification at species level can be difficult (Sarjeant, 1970). Several revisions and simplifications have been
168   proposed for the genera (Lei et al., 2013a; Sarjeant and Stancliffe, 1994). We follow the simple classification
169   scheme proposed by Lei et al. (2013a), in which different species of acritarchs are grouped together, based on
170   geometrical shape of the acritarchs. Photos of selected aquatic palynomorphs are shown in the plate of Fig. 3.

171   Concentrations of aquatic palynomorphs were on average ca.4 times higher in the laminated rocks
172   compared to the bioturbated rocks (Fig. 4). Acritarch abundance also declines during the extinction event. The
173   majority (25 - 100%) of the acritarchs belong to the *Micrhystridium breve* Group (Fig. 4). This group includes
174   all acritarchs with a spherical central body and numerous processes. The *Veryhachium laidii* Group (acritarchs
175   with a rectangular central body shape), the *V. trispinosum* Group (triangular shape), *V. cylindricum* Group
176   (ellipsoidal shape) and *M. pentagonale* Group (pentagonal or hexagonal shape) were mostly found in
177   bioturbated intervals of the upper part of the Schuchert Dal Formation, especially just before and during the
178   extinction interval (Fig. 4). The leiospheres include all aquatic palynomorphs with a spherical shape and either a
179   smooth surface or with small ornamentation, but no processes. The highest abundances (up to 70%) of
180   leiospheres are found in the laminated sediments of the Wordie Creek Formation (Fig. 4). *Cymatiosphaera* are
181   rare in the record and found in both the oxidized siltstones of the Schuchert Dal Formation, but also in some
182   intervals in the laminated siltstones. *Tasmanites* were found only in one sample, also during the marine
183   extinction phase. The apparent relatively higher abundance of *Cymatiosphaera* and *Tasmanites* in the top of the
184   Schuchert Dal Formation is a consequence low total count of the aquatic palynomorphs during the extinction

185   event. The most diverse samples were found in the bioturbated rocks of the upper metre of the Schuchert Dal

186   Formation, an interval that partly overlaps with the extinction interval.

187   The *Micrhystridium* Group has a diverse morphology, and shows variation in vesicle size and number

188   of processes. Most of the measured specimens are very similar to the species *M. breve* as described by Jansonius

189   (1962) in both the number and shape of the processes. However, the size of the central body and the length of

190   the processes of many of the measured acritarchs fall outside of the defined size-range of *M. breve*. Variability

191   in process length within one specimen was generally small (in almost 80% of the specimen measured <2μm)

192   and in only 7% of the cases >3μm) (see also table S4). The distributions of both body size and process length

193   are unimodal (Fig. 5), which suggests that the measured specimens all belong to a single species of

194   *Micrhystridium*. Body size is variable, with a decrease around -150cm from 16.5 to 13.5μm, followed by a

195   gradual increase throughout the extinction event up to 19μm at 75cm, followed by an abrupt decrease to 14μm,

196   after which body size stabilizes between 14.5 and 16μm. In the two-metre interval spanning the formation

197   boundary, acritarchs in the laminated rocks are on average larger compared to those in the bioturbated rocks,

198   however, this is not consistently true further up or down the section (Fig. 6). The average process length first

199   increases before the start of the extinction from an average 7.7 at -450cm to 11.5 μm at -250cm, after which

200   processes gradually become shorter down to a minimum of around 5μm during the extinction event. Processes

201   then remain shorter through to the top of the studied section. Process length not only changes in absolute terms,

202   but also relatively to the size of the body.

203

204   **5. Discussion**

205   **5.1 The extinction event and onset of anoxia**

206   Consistent with the results of Looy et al. (2001), we find a strong increase in spores, relative to pollen,

207   in the upper Schuchert Dal Formation (Fig. 2). Since this peak in spores coincides with the interval of marine

208   ecosystem collapse defined by Twitchett et al. (2001), we define the period with highest spore/pollen ratios as

209   the extinction interval. Twitchett et al. (2001) found large changes in marine plankton abundance in their study

210   of the Fiskegrav section, with a bloom just before the disappearance of trace fossils, followed by almost

211   complete absence of acritarchs immediately after the collapse of the marine ecosystem. This phytoplankton

212   bloom is not obvious in our higher resolution data, and may simply be an artefact of the relatively low-

213   resolution sampling of Twitchett et al., (2001), but the number of acritarchs is indeed greatly reduced during the

214   biotic crisis (Fig. 4). The peak in spore/pollen and decrease in acritarch abundance occurs in an interval of ca.

215   0.8m, which is comparable to the interval found by Twitchett et al., (2001) for marine and terrestrial ecosystem

216   collapse. Twitchett et al., (2001) estimated the collapse to have taken between 10 and 60 kyrs, however, recently

217   improved estimations of sedimentation rates in the Fiskegrav section (Mettam et al 2017) now give an estimated

218   duration of between 1.6 to 8 kyrs for the marine and terrestrial ecosystem collapse.

219   During the start of the biotic crisis rocks remain bioturbated but within the upper 0.5 m of the

220   Schuchert Dal Formation there are intervals with laminated rocks (Fig. 2), indicative for anoxia (Twitchett et al.,

221   2001). AOM, which is structureless organic matter, is dominant in the laminated rocks. AOM can derive from

222   degraded macrophyte, phytoplankton or higher plant tissue, or it may also be bacterially derived (Tyson, 1995).

223   Anoxic conditions can stimulate the production of marine AOM (Pacton et al., 2011), but also result in better

224   preservation after sedimentation (Tyson, 1995). The relative proportions of AOM versus phytoclasts thus

225   indicate the amount of oxygenation of the depositional environment (Tyson, 1995). A recent, high-resolution

226   study of the $\delta^{13}C$ of total organic carbon (TOC) by Mettam et al., (2017) shows a negative shift of 5-6‰ that

227   begins 1.80m below the top of the Schuchert Dal Formation at Fiskegrav, (Fig. 2). The onset of this negative

228   excursion coincides closely with the last occurrence of Permian macroinvertebrate fossils (Mettam et al., 2017),

229   but pre-dates the collapse of marine and terrestrial ecosystems defined by disappearance of bioturbation.

230   Mettam et al. (2017) record a small, but consistent, offset in $\delta^{13}C$ values between the laminated/bioturbated

231   intervals (Fig. 2). This offset can be explained by the differences in organic matter source, which is mostly

232   phytoclasts (terrestrial) in the bioturbated intervals while AOM (marine and terrestrial) dominates in the

233   laminated intervals. However, the main shift is not associated with major changes in the palynofacies, and

234   occurs in a part of the section where the palynofacies mainly consist of terrestrially derived organic matter (Fig.

235   2). This negative shift in carbon isotopes associated with the late Permian extinction event is recognized

236   worldwide (e.g. Korte and Kozur, 2010) and usually precedes, the extinction event (e.g. Burgess and Bowring,

237   2015; Korte and Kozur, 2010). It has been interpreted as resulting from atmospheric changes in $\delta^{13}C$ values,

238   which can be directly, or indirectly, related to Siberian trap volcanism (e.g. Cui and Kump, 2015; Svensen et al.,

239   2009).

240   Mettam et al. (2017) studied redox conditions in the same section and showed that conditions became

241   potentially anoxic, and ferruginous (Fe^{2+}- rich) in the laminated intervals near the formation boundary. Within

242   the lowermost Wordie Creek Formation, from 0.6-0.7 m above the formation boundary, anoxic conditions are

243   confirmed by Fe speciation (Mettam et al., 2017). Since the extinction started before conditions became

244   ferruginous, spreading anoxia cannot be the main cause for the marine biotic crisis in the Fiskegrav section.

245   Grasby et al. (2015) distinguished three phases of extinction in the shallow marine sequence of Festningen

246   (Svalbard): first is the loss of carbonate macrofauna, followed by loss of siliceous sponges, and finally a loss of

247   all trace fossils. Thus, similar to what is observed in East Greenland, the first laminated sediments do not

248   represent the start of the biotic crisis. This is unsurprising as expanding marine hypoxia is a predicted

249   consequence of global warming, which was probably caused by elevated CO_2 flux from Siberian Trap

250   volcanism (Benton and Twitchett, 2003; Grard et al., 2005). Therefore, extinctions that occurred prior to the

251   appearance of widespread anoxia were more likely due to the direct, short-term effects of volcanic activity (e.g.

252   metal toxicity), or the more immediate effects of CO_2 rise or temperature increase. The laminated rocks are

253   associated with higher amount of pollen fragments (Fig. 2), which could be an indication for elevated terrestrial

254   organic matter input (e.g. soil erosion), while the higher amount of AOM can be partly explained by terrestrial

255   organic matter input, and partly by increased marine productivity and better preservation of organic matter due

256   to low oxygen conditions. Increased weathering and run-off are expected consequences of atmospheric and

257   hydrological changes associated with global warming. Algeo and Twitchett, (2010) demonstrated that sediment

258   accumulation rates greatly increased in shallow shelf seas in the latest Permian and earliest Triassic, consistent

259   with enhanced weathering and run-off, and Sephton et al. (2005) found evidence for large-scale soil erosion.

260

5.2 Sea-level and salinity changes

If the laminated rocks are indeed a consequence of enhanced runoff, this is expected to affect also marine environmental conditions, such as a decrease in (surface) salinity. At the same time, sea-level fluctuations at and near the boundary need to be considered, since these would also affect marine environmental conditions and could potentially affect salinity. The Fiskegrav section has well preserved aquatic palynomorphs, and their diversity, distribution and morphology can provide valuable information on marine environmental changes. Palaeozoic studies have shown that acritarch diversity is generally higher in deeper, more distal settings (e.g. Lei et al., 2012; Stricanne et al., 2004). In addition, different studies have shown that *Veryhachium* favoured more open marine settings, while *Micrhystridium* favoured near-shore environments (e.g. Wall 1965, Lei et al., 2012). It is possible that some of the leiospheres in the Fiskegrav section belong to the genus *Leiosphaeridia,* as the dimensions are comparable to *L. microgranifera* and *L. minutissima* that were found in Chinese Permian-Triassic sections (Lei et al., 2012), but the small ornamentations on both of those species is different (Fig. 3). In these Chinese Permian sections the *Leiosphaeridia* are associated with deeper/more open marine waters (Lei et al., 2012). On the other hand, studies of early Palaeozoic acritarchs show that, in general, leiospheres, or sphaeromorphs, are most frequent in proximal environments (Li et al., 2004; Stricanne et al., 2004). The leiosphere-group might be polyphyletic and some species might have prasinophyte affinities (Colbath and Grenfell, 1995), which complicates their use for environmental reconstructions. Whatever the biological origin of the leiosphere is, in this study site they apparently favoured the palaeoenvironmental conditions associated with the deposition of the laminated rocks, starting during the extinction event.

In the Fiskegrav section, the decline in diversity from the upper Schuchert Dal Formation to the Wordie Creek formation, together with the change in assemblage from *Veryhachium/Micrhystridium* to *Micrhystridium/*leiosphere dominance could thus be interpreted as a change from a distal to a more proximal setting, which would suggest a marine regression. Although this was once considered as a possible cause of the late Permian extinction event (Hallam and Cohen, 1989), the current consensus is that eustatic sea-level fall occurred prior to collapse of marine ecosystems and the extinction, and the subsequent transition from the Permian to the Triassic happened during sea-level rise (Wignall and Hallam, 1992). In some East Greenland locations, apparently missing biozones and local erosive conglomeratic channels have been proposed as evidence for sea-level fall near the boundary between the Schuchert Dal and Wordie Creek formations (Surlyk et al., 1984), but Wignall and Twitchett (2002) demonstrated that in central Jameson Land the sedimentological changes are consistent with sea-level rise, and that the erosive, conglomeratic channels occur at multiple stratigraphic levels and postdate the extinction and Permian/Triassic boundary.

Thus, during the extinction event the acritarch assemblage changes to a more typical near-shore assemblage, despite the ongoing sea-level rise. Instead of a marine regression, the observed shift in acritarch assemblages could be explained by an increase in runoff which affects the near-shore environment by lowering surface water salinity and delivering nutrients, both of which are found to affect the distribution of modern phytoplankton (e.g. Bouimetarhan et al., 2009; Devillers and de Vernal, 2000; Pospelova et al., 2004; Zonneveld et al., 2013). Dinocyst morphology has also been linked to environmental conditions (e.g., Mertens et al., 2009, 2011), with salinity identified as an important factor influencing process length (Ellegaard et al., 2002; Mertens et al., 2011). Similarly, studies of acritarch process length and palaeoenvironment show that species and individuals with longer processes are generally found in more offshore locations, while in inshore settings

acritarchs with shorter processes are more abundant (Lei et al., 2013a; Servais et al., 2004; Stricanne et al., 2004). The average process length of specimens belonging to the *Micrhystridium breve* -group, show a decreasing trend during the extinction interval, with higher values before the extinction event, and lower values after the event (Fig. 6). The overall trend shows a shortening of on average 3-5 μm, which is substantially larger than the variability within one specimen. The trend is also gradual, in contrast to the facies changes, which are abrupt, and the shorter processes are thus not directly linked with stratification. Instead, the shortening of the processes could be interpreted as a lowering in salinity during the extinction event. Within the 2m interval including the extinction interval (-1 – +1m) there is also a small, offset in body size between samples from bioturbated and laminated rocks, however, this is difference is not consistent when considering the full record. The body size of some dinocysts has been found to vary with temperature and salinity (e.g. Ellegaard et al., 2002; Mertens et al., 2012), however, the relation has not been well studied. Possibly low oxygen or salinity conditions or increased nutrient availability influenced acritarch body size in this interval. Runoff, lower salinity, and salinity stratification together can explain the observed changes in palynofacies and acritarch records. In addition, transport of acritarchs with shorter processes from near shore environment into deeper marine environment could also result in on average shorter processes. However, this would result in a bimodal distribution of process length within one interval (near shore specimens with shorter processes, and deep-water specimens with longer processes). Instead process length, although variable within each interval, changes gradually (see also Fig. S1). The changed environmental conditions continued through the aftermath of the biotic crisis, as shown by persistently low process lengths to the end of the study interval (Fig. 6). Meanwhile, the ongoing marine transgression likely resulted in the shoreward migration of oxygen deficient waters which explain the development of permanently anoxic conditions higher up in the Wordie Creek Formation (over 0.6-0.7 m from the Fm boundary) (Mettam et al., 2017).

The development of widespread anoxia in the late Permian is usually explained by an expansion of anoxic deep waters onto the shelf (e.g. Grasby and Beauchamp, 2009). However, increased runoff and the development of estuarine circulation provide an alternative explanation for the development of anoxia in some shallow marine environments. Furthermore, low salinity is known to negatively impact biomass and size of modern marine invertebrates (e.g. Westerbom et al., 2002), and, along with higher temperatures and hypoxia, might also be a contributing factor in the size reduction of marine organisms recorded in the aftermath of the late Permian extinction event, such as observed for the bivalve *Claraia* the Permian-Triassic section of East-Greenland (Twitchett, 2007). Low salinity conditions have previously been invoked to explain the dominance of the brachiopod lingulid in post-extinction ecosystems (Zonneveld et al., 2007), because they are able to tolerate a wide range of salinities as well as hypoxia (e.g. Hammen and Lum, 1977). Lingulid fossils are found in many Permian-Triassic (shallow) marine sections (e.g. Peng et al., 2007) and the lowering of salinities in shallow marine settings and spreading anoxia provided ecological space for the lingulids (Peng et al., 2007; Rodland and Bottjer, 2001). It has been suggested that rising sea water temperatures in the Tethys, resulted in strengthened monsoonal activity (e.g. Winguth and Winguth, 2012) and enhanced precipitation and runoff in the areas surrounding the Tethys (e.g. Parrish et al., 1982). Whether this would have had an effect on the study site is questionable, because of its distance to the Tethys and relatively sheltered, inland position. Possibly river systems existed which brought freshwater to the Greenland-Norway basin from the South. It is also possible that rainfall increased locally. Mettam et al., (2017) speculated that changes in circulation patterns may have resulted

341   in onshore winds bringing moist air to the study site. In addition vegetation destruction and soil erosion may

342   also have contributed to enhanced runoff.

343

344   **5.3 Sea water temperature**

345   Besides salinity, increasing water temperatures can also affect process length in dinocysts (e.g. Mertens

346   et al., 2009, 2012) but this relationship is not always evident (e.g. Ellegaard et al., 2002). Sea water temperature

347   reconstructions for the late Permian and Early Triassic exist mainly from carbonate rich sections originating in

348   the Tethys Ocean (e.g. Joachimski et al., 2012; Schobben et al., 2014; Sun et al., 2012). These reconstructions

349   indicate increasing temperatures during the extinction event, and maximums temperatures are reached in the

350   Early Triassic (e.g. Joachimski et al., 2012; Kearsey et al., 2009; Schobben et al., 2014; Sun et al., 2012). Since

351   no water temperature reconstructions exist for the Greenland-Norway basin, at this time, it is not possible to

352   exclude the effects of rising water temperatures on the acritarch morphology. Increasing water temperatures

353   might be partly responsible for decreasing process length in acritarchs, however, a rising sea-level in

354   combination with rising temperatures are not able to explain the changes in the acritarch assemblages, which

355   indicate a shift from more open marine to near-shore conditions. Increased runoff cannot only explain the

356   reconstructed changes in palynofacies and acritarch records, but in addition, a reduction in salinity also has

357   significant implications for palaeotemperature reconstructions calculated from the oxygen isotopes of carbonates.

358   Most Permian-Triassic temperature records are from the Tethys or surrounding areas, where monsoon activity

359   has been proposed to increase (Winguth and Winguth, 2012) and thus salinity is expected to change as well.

360   Permian-Triassic oxygen isotope data for palaeotemperature estimates have been derived from brachiopod shells

361   (Kearsey et al., 2009) or conodont apatite (Joachimski et al., 2012; Schobben et al., 2014), with all studies

362   concluding that temperature rose through the extinction event and that Early Triassic seas were 'lethally hot'

363   (Sun et al., 2012). Oxygen isotope values partially reflect seawater salinity, although this is generally ignored in

364   palaeotemperature studies, because there is currently no independent proxy of salinity change, and so it is

365   assumed that salinity remained constant. If salinity was reduced in shelf seas due to hydrological changes (e.g.

366   enhanced precipitation and run-off), as it appears for East Greenland at least, then all of these studies may have

367   significantly over-estimated Early Triassic temperatures. The actual temperature rise associated with the

368   extinction event would have been lower and below 'lethal' levels, which is more consistent with fossil evidence

369   that the oceans were not completely devoid of life.

370

371   **6. Conclusions**

372   The highest resolution palynological sampling yet attempted for the Fiskegrav location of central Jameson Land

373   has shown significant, millennial-scale changes in marine and terrestrial environments. The biotic crisis,

374   defined by a peak in the spore/pollen ratio, which indicates widespread disruption and collapse of the terrestrial

375   flora, postdates the onset of the carbon-isotope excursion. The spore/pollen peak spans 0.8 m of section, which,

376   on current age estimates, gives an estimation of 1600 to 8000 years for the ecosystem collapse. This is much

377   shorter than previous estimations. The onset of the biotic crisis does not appear to coincide with any obvious

changes in lithology or sedimentary facies, and deposition of the shallow marine shelf sediments appears to have taken place under oxygenated waters. During the latter stages of the biotic crisis, laminated beds begin to appear, indicating periodic anoxic deposition. These laminated rocks contain palynological evidence for a more near-shore setting, which contradicts the widely accepted evidence that globally sea-level was rising during the extinction event. A preferred alternative explanation, consistent with palynological assemblages, is that enhanced runoff, water column stratification and enhanced primary productivity led to the development of anoxic bottom waters. Enhanced runoff would lead to elevated freshwater flux into shallow shelf seas, which would have led to the development of a freshwater wedge, stratification and a reduction in salinity. Acritarch process length is considered here to be a proxy for seawater salinity, and supports these inferred changes. Increased runoff did not immediately lead to anoxia, possibly because precipitation gradually increased during the extinction event until the freshwater flow was large enough to cause water column stratification. Increasing sea water temperatures may have also affected acritarch morphology, and partially be responsible for the reduced process length. However, rising temperatures alone cannot explain the reconstructed changes in the palynofacies and acritarch records. In fact, sea water temperature reconstructions may overestimate the rise in water temperatures during the extinction event, since possible changes in salinity are not included in the calculations.

7. Data availability. The data reported in this paper is available in tables in the supplementary files.

Author contributions. WMK designed the study. RJT provided material. EEvS analysed the samples for palynofacies and palynomorph content and performed measurements on acritarchs. EEvS wrote the paper with input from WMK and RJT.

Competing interests. The authors declare that they have no conflict of interest.

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611   **Figure 1.** Modern map of Jameson Land, East Greenland (adapted from Piasecki, 1984). The location of the

612   studied section is indicated with a red circle. The right panel show the lithology of the Jameson Land section

613   and sample depths. (* spore-peak after Looy et al., 2001, marine collapse after Twitchett et al., 2001).
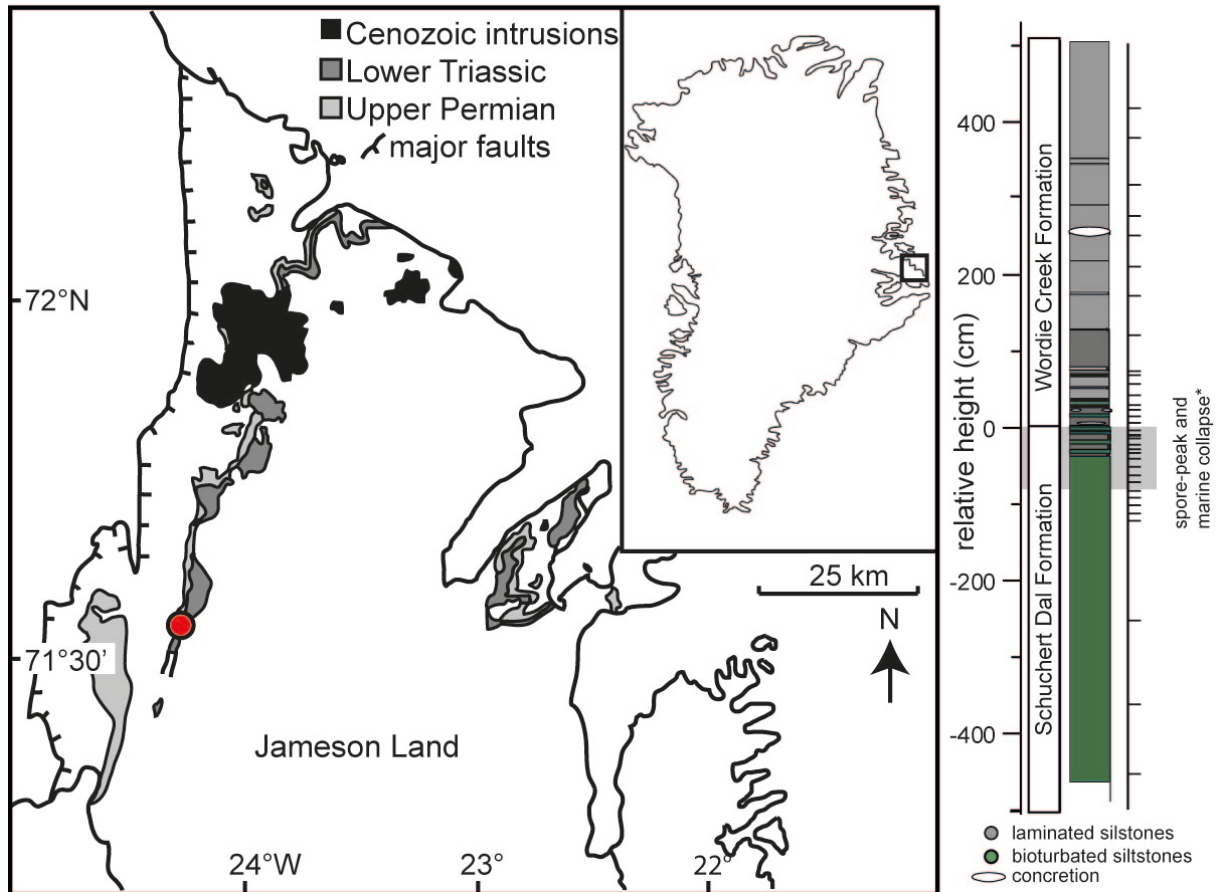
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619 **Figure. 2**. Change in major groups of palynofacies. AOM= amorphous organic matter. The grey shaded box

620 highlights the biotic crisis as defined by the high spore/pollen ratios, which are indicative for the disappearance

621 of forest communities. Green shading indicates data from bioturbated rocks; grey shading indicates data from

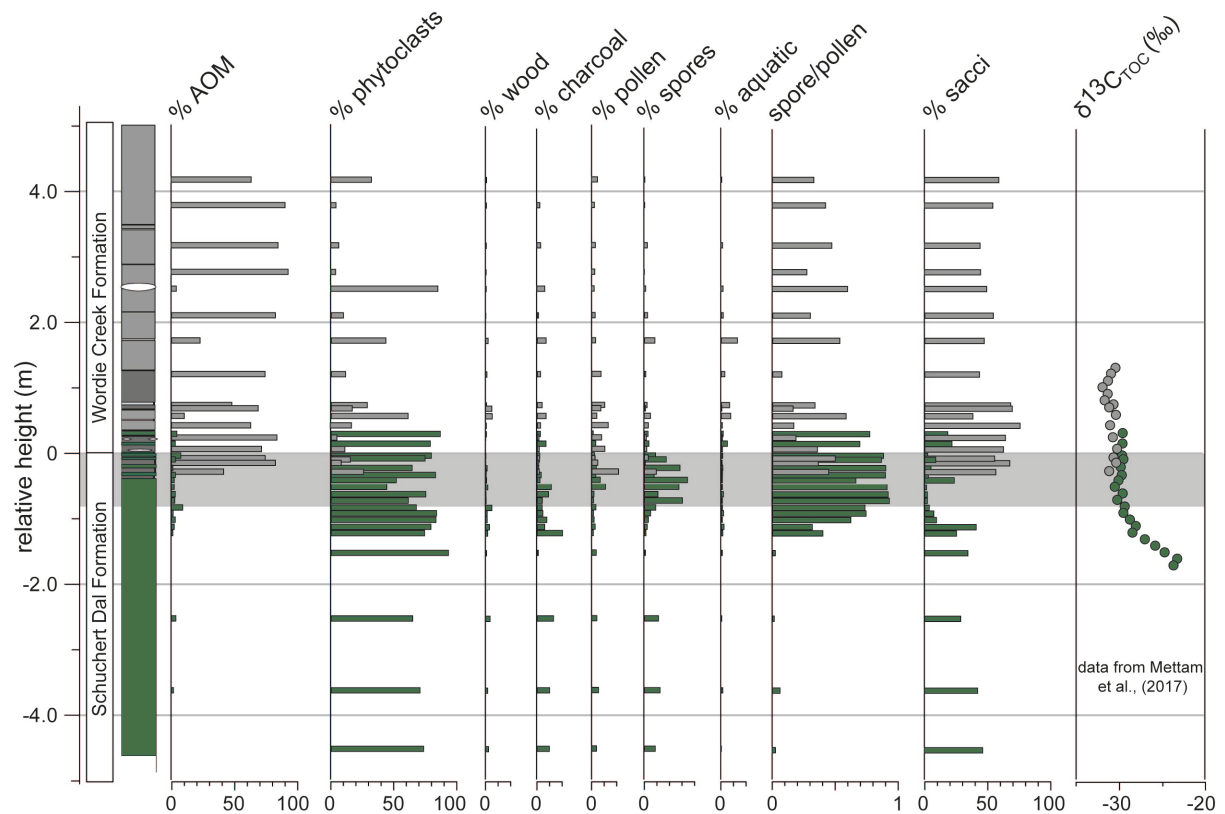622 laminated rocks. Grey horizontal bar indicates the extinction interval, based on high spore: pollen ratios.

632 **Figure 3.** Aquatic palynomorphs plate. A) *M. pentagonale* – group, B) *V. laidii* - group C) *Cymatiosphaera* sp.

633 D) and E) leiospheres F)-I) *M. breve* -group J) *M. pentagonale* - group K)-M) M. breve - group N)

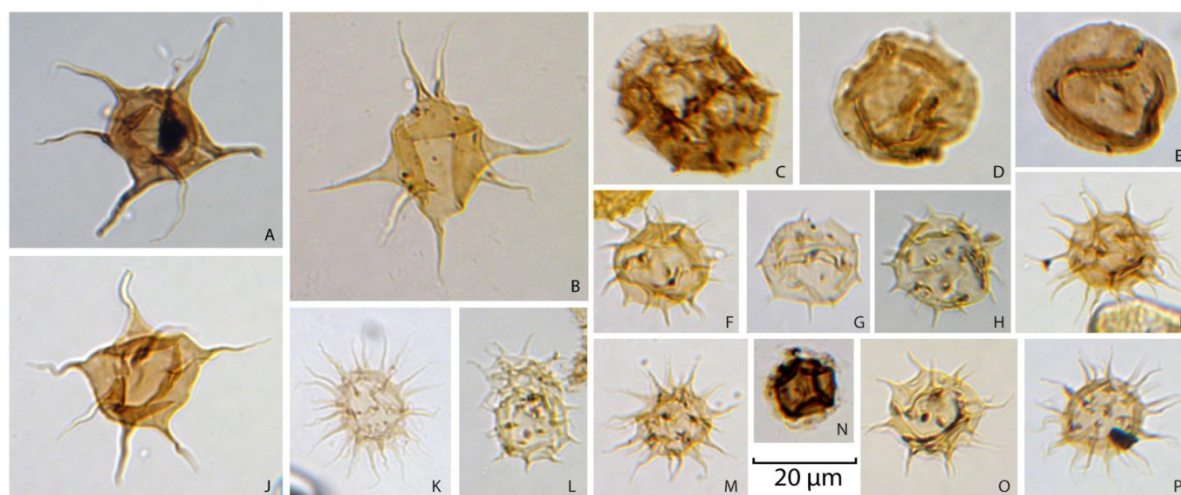634 *Cymatiosphaera* sp. O) and P) *M. breve* -group


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Figure 4. Aquatic palynomorphs. The figure showsconcentration of all aquatic palynomorphs andrelative abundance specific acritarch and prasinophyte groups. Arrow indicate intervals with low counts (<20). Green shading indicates data from bioturbated rocks; grey shading indicates data from laminated rocks. Grey horizontal bar indicates the extinction interval, based on high spore: pollen ratios.
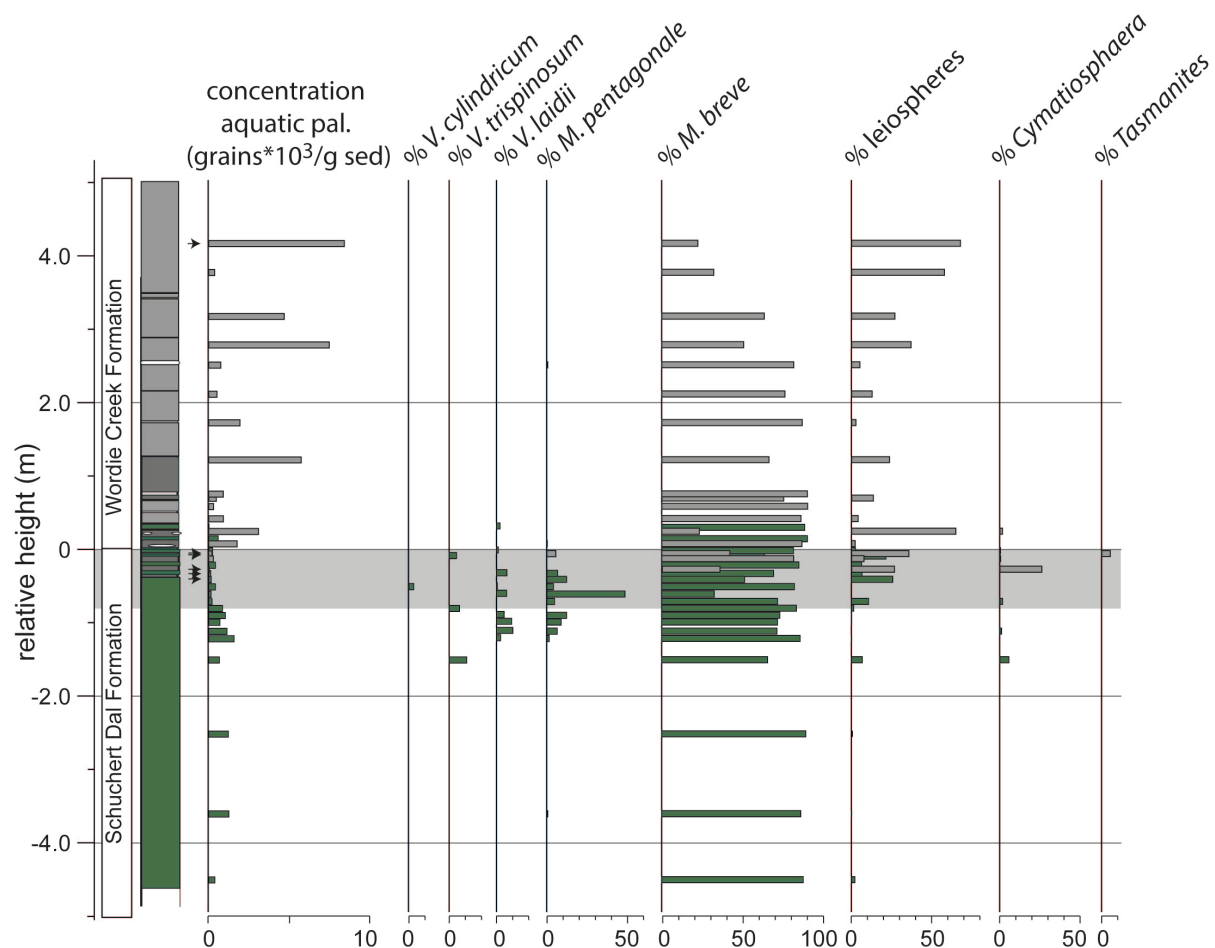
646   **Figure 5.** Size-frequency of body diamter (left) and proces length (right).
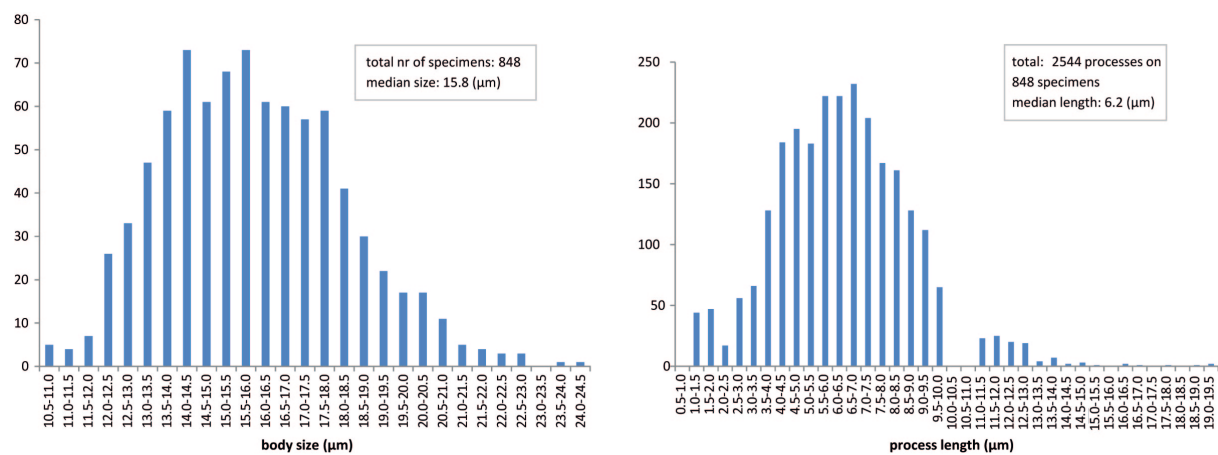
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Figure 6. Changes in acritarch abundance and morphology. In the panel on the left are the main groups of

651   aquatic palynomorphs summarized. On the right: body size, process length, and process length relative to body

652   size. Where are low counts? Green shading indicates data from bioturbated rocks; grey shading indicates data

653   from laminated rocks. The grey bar indicates the extinction interval, based on high spore:pollen ratios. The five

654   small black arrows indicate in which samples the number of specimens used for measurements was low (4-16

655   specimens). Grey horizontal bar indicates the extinction interval, based on high spore: pollen ratios.

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