Late Permian to Early Triassic changes in acritarch assemblages and morphology in the Boreal Arctic: New data from the Finnmark Platform

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**ABSTRACT**

The Late Permian extinction interval is in many marine locations characterized by the development of anoxic conditions. The Finnmark Platform is one of few exceptions, as sedimentological and palynofacies evidence indicate oxygenated conditions throughout the event. Changes in acritarch assemblages and morphology were studied in order to better understand the link between acritarchs and environmental conditions. The main taxa are of *Micrhystridium*, *Baltisphaeridium* and leiospheres, while *Veryhachium* and the prasinophytes *Cymatosphaera* and *Tasmanites* were present in low abundances. Increased concentrations of acritarchs, particularly *Micrhystridium*, show that the environmental changes at the start of the extinction event may have resulted in enhanced marine productivity. A shift from *Micrhystridium/Baltisphaeridium* dominance before and during the extinction event, to leiosphere-dominance after the extinction event, indicates a shift towards a more inshore environment. The new data are compared with published Late Permian acritarch records from East Greenland, China and Pakistan. A striking difference between the East Greenland and Finnmark Platform, which are both expanded Upper Permian/Lower Triassic sections, is that the acritarch record from Greenland shows a strong decrease in process length of the acritarch *Micrhystridium*. Together with a change in the acritarch assemblage, this change in morphology was interpreted to represent a decrease in salinity at the site, resulting from increased run-off. The differences between the East Greenland and the Finnmark records are likely due to their palaeo-geographical settings, as the East Greenland section was located in a narrow and elongated basin which was likely more sensitive to evaporation and run-off changes than the Finnmark Platform.

1. Introduction

The Late Permian extinction event impacted ecosystems on a global scale. Especially the marine environment was heavily affected by loss of diversity, resulting from, amongst others, spreading ocean anoxia (e.g. Grice et al., 2005; Shen et al., 2016; Wignall and Hallam, 1992; Wignall and Twitchett, 2002a, 2002b), ocean acidification (e.g. Clapham and Payne, 2011; Clarkson et al., 2015; Hönisch et al., 2012), increase in water temperatures (e.g. Joachimski et al., 2012; Sun et al., 2012) and toxic marine conditions (e.g. Grasby et al., 2011). Marine organic walled microfossils, like acritarchs and prasinophytes, have been found to decrease in number (Twitchett et al., 2001) and in diversity during the extinction event (Lei et al., 2012). Acritarchs are defined as organic walled microfossils of unknown affinity (Evitt, 1963), but here we focus on a group of marine acritarchs, which are thought to represent the cysts of marine algae, and are possible precursors of dinoflagellate cysts (Servais et al., 2004).

Changes in the assemblages and morphology of Late Permian organic walled acritarchs have not been studied well, even though small acritarchs are commonly found in Permian assemblages (Lei et al., 2013a). Studies on Upper Permian sections from the Tethys realm show changes in acritarch assemblages that reflect positive and negative effects of volcanism on marine microplankton communities (Schneebeli-Hermann et al., 2012; Shen et al., 2013). These and other records show the preferential habitat of distinct acritarch groups from nearshore to offshore marine conditions (Lei et al., 2012). Studies on Late Permian and Late Silurian acritarch assemblages revealed that species with longer processes are more abundant in deeper water, and species with shorter processes and leiospheres (which have no processes) are dominant in nearshore environments (Lei et al., 2012; Stricanne et al., 2004). A recent study on changes in acritarch assemblages and morphology in an Upper Permian section in East Greenland (Jameson Land) showed that the process length of *Micrhystridium* on average decreased at the start of the extinction event (Van Soelen et al., 2018). During the extinction event a shift takes place in the assemblages from *Veryhachium/Micrhystridium* to *Micrhystridium/leiospheres.*
Both developments indicate a shift towards more inshore conditions (Van Soelen et al., 2018), even though previous studies showed that sea level was likely rising at the time (Wignall and Twitchett, 2002a, 2002b). Therefore, these changes in acritarch assemblages and morphology are thought to be caused by an increase in run-off, which in turn resulted in water column stratification and lower surface salinities (Van Soelen et al., 2018). Anoxic conditions at this site are thought to directly result from water column stratification, which lead to lower bottom water oxygenation (Van Soelen et al., 2018).

Here we present acritarch data for an extended Upper Permian section from the Finnmark Platform. Previous palynological studies at this site indicate excellent preservation of palynomorphs and high sedimentation rates (Hochuli et al., 2010a; Mangerud, 1994). The Finnmark Platform shows intervals with low-density bioturbation in the Griesbachian, following the extinction interval (Bugge et al., 1995). The absence of amorphous organic matter throughout the record indicates that oxygenated conditions persisted at this location (Hochuli et al., 2010a). Since water column stratification and salinity changes are expected to be important factors to have affected the Greenland acritarch record (Van Soelen et al., 2018), the Finnmark section provides an interesting opportunity to study acritarch assemblages and morphology under mixed water column conditions.

2. Geological setting and stratigraphy

The Permian-Triassic intervals were deposited in the southwestern part of the Barents Shelf, offshore northern Norway at approximately 40–45°N (Fig. 1). Detailed information on sedimentology and stratigraphy can be found in Bugge et al. (1995) and Mangerud (1994). The interval used in this study comprises three major units. The two lower units, existing of a clastic material and carbonates respectively, were dated by palynomorphs to the Late Permian (Mangerud, 1994). The lowermost unit exists of shale to sandstone, deposited in a shallow shelf environment (Bugge et al., 1995), during a period of major sea-level rise (Mangerud, 1994). The top of the unit indicates sub-aerial exposure occurred, probably due to tectonically induced sea level lowering (Bugge et al., 1995). Continuing sea-level rise resulted in the deposition of the overlying Late Permian carbonate unit (Bugge et al., 1995; Mangerud, 1994). Clastic sedimentation prograded into the Barents Sea, mostly from the Ural Mountains and Nova Zemlya, but also from the South onto the Finnmark Platform (Bugge et al., 1995), forming a third unit, existing of clastic material and deposited in a marginal marine environment (Mangerud, 1994). This last unit was dated to the

3. Material and methods

3.1. Material

Samples were collected from two parallel cores from the Finnmark
Platform: 19 samples from core 7128/12-U-01 and another 3 samples from core 7129/10-U-01. The two parallel cores have been correlated with each other by Bugge et al. (1995), and we use this correlation to project the samples from core 7129/10-U-01 onto core 7128/12-U-01 (Fig. 2). The two cores contain Late Permian to Early Triassic shelf carbonates and clastic material. For the purpose of this study, only material from shale/siltstone intervals has been used.

3.2. Palynological methods

Samples were prepared for palynological analyses following standard procedures at the palynological laboratory of the University of Oslo. Carbonate and silicate minerals were removed by washing the crushed samples with hydrochloric acid (HCl) and fluoracic acid (HF). After the treatment, samples were first neutralized, and after heavy liquid separation, samples were sieved over 7 μm mesh sieves. The residue was mounted onto glass slides and counted under a Leitz Diaplan microscope. Photos were made with an AxioCam ERC 5 s camera, using Zen microscope software (Zen 2 lite, 2011). A lycopodium tablet was added to untreated samples, with known amount of lycopodium spores, to allow quantification of palynomorphs concentration per gram sediment. The slides were counted for palynofacies and terrestrial and marine palynomorphs. Acritarchs were not identified at species level but were grouped together based on their morphological features. We mostly follow the simplified classification system for the spiny acritarchs Micrhystridium and Veryhachium proposed by Lei et al. (2013b), in which Veryhachium has fewer than 8 processes, and all acritarch with a spherical body and 8 or more processes belong to Micrhystridium breve—group. The M. pentagonale—group includes all specimens with a pentagonal or hexagonal shape and 8 or more processes. Because all types of Veryhachium, and also M. pentagonale, have similar morphological features (a polygonal shape, and relatively long processes (see also Lei et al. (2013b)), they were grouped together. We also made an additional group, Baltisphaeridium, which includes all spiny acritarchs with a large, spherical body size (> 20 μm) and large numbers of processes (> 40 processes on one visible side). A final acritarch group included all aquatic palynomorphs with a spherical body and no discernable processes or spines (leiospheres). In addition, two groups of prasinophytes were distinguished, the Tasmanites and Cymatosphaeridia spp. Of the M. breve—group, body size and process length was measured. Folded or broken specimens were excluded. Body size was calculated from the average of two perpendicular measurements (Fig. 3). Process length is based on the average of the 3 longest processes within one focal plane (following the methodology of Mertens et al. (2012)). This focal plane is chosen as the plane that shows the most, and the best visible processes. The aim was to have a minimum count of 20 aquatic palynomorphs counts, and the measurements of body size and process length per sample of at least 20 specimens. However, as concentrations of aquatic palynomorphs were low in most of the intervals, this target was not met for every sample.

4. Results

Tables with the total number of acritarchs counted, the relative abundance and average of body size and process length can be found in the supplementary files. Concentrations of all aquatic palynomorphs (Fig. 4A) (acritarchs and prasinophytes) were highest in the Late Permian (below 116 m) with concentrations between 0.6 and $3 \times 10^4$ g^{-1} sediment. Directly at the start of the extinction event, at ~117 m, concentrations strongly increase up to $20 \times 10^3$ g^{-1} sediment, after which there is a sharp drop towards lower values during the extinction event (0.05–0.2 $\times 10^3$ g^{-1} sediment). After the extinction event, concentrations vary between 0.1 and 0.2 $\times 10^3$ g^{-1} sediment, then drop at ~100 m towards a minimum of 0.02 $\times 10^3$ g^{-1} sediment. After which concentrations gradually increase through the rest of the record until ~0.3 $\times 10^3$ g^{-1} sediment. Concentrations of pollen (Fig. 4B) are only relevant in this study to support facies changes; palynology and palynofacies were discussed in detail in Hochuli et al. (2010a).

Veryhachium spp. and M. pentagonale were found in small amounts in some intervals throughout the core (Fig. 4C), and only in one interval (~105 m) made up a maximum of 26% of the assemblage. Baltisphaeridium sp. (Fig. 4D) were only found in the Late Permian interval, in the lower parts of the core, and made up to 80% of the total assemblage. Acritarchs of the M. breve—group were dominant in the lower part of the core, but were replaced in dominance by leiospheres above 104 m (Fig. 4E and F). Tasmanites spp. and Cymatosphaeridia spp. are present in small amounts (up to 20%) throughout the record (Fig. 4G and H). Examples of some aquatic palynomorphs are shown in Fig. 5.

Average body size of M. breve—group varies between 8.9 and 20.0 μm (Fig. 4I). Average body size is stable throughout the lower part of the record (13.3–16.0 μm) and throughout the extinction event, but shift to larger body size (17–19 μm) above 88 m. Even though the acritarch abundance in the top of the record (88–78 m) is low, the change is consistent throughout the three top samples (containing together 10 measured specimens). Similarly, average process length (Fig. 4J) varies between 4.5 and 7 μm in the lower part of the core and shifts towards shorter (3.3–4.8 μm) average length above 88 m core depth, where also relative process length decreases (Fig. 4K).

5. Discussion

5.1. Depositional environment

The late Permian extinction event is characterized by widespread anoxic conditions but intensity and duration varies at a global scale (Bond and Wignall, 2010; Wignall and Twitchett, 2002a, 2002b). It is proposed to be a major factor in the marine extinction (e.g. Wignall and Twitchett, 1996). Most shallow marine Arctic sites, like Jameson Land in East Greenland, or Festningen and Tschermakfjellet on Svalbard, show development of anoxic conditions during the extinction event (Dustira et al., 2013; Wignall et al., 2016). Recently, a high-resolution study of redox conditions at the Fiskegrav section, East Greenland, based on geochemical proxies and sedimentological data revealed stepwise decreasing oxygen availability and eventually establishment of anoxic conditions (Mettam et al., 2017). The Greenland section shows alternating patterns of bioturbated and laminated sediments. Such obvious changes in bioturbation are not found in the Finnmark Platform. Bugge et al. (1995) describes low-density bioturbation, and a few beds that are totally bioturbated higher up in the Griesbachian. Hochuli et al. (2010a) concludes based on the absence of amorphous organic matter, that the depositional environment was well oxygenated throughout the section, without any signs of oxygen deficient conditions. Anoxic conditions would result in increased preservation of amorphous organic matter (AOM), which easily degrades under oxic conditions (Pacton...
et al., 2011; Roncaglia and Kuijpers, 2004; Tyson, 1995). The abundance of AOM proved to be reliable tool for recognizing low oxygen conditions in the late Permian of the Fiskergrav section on Jameson Land, East Greenland (Van Soelen et al., 2018) and agrees with the results obtained from geochemical analyses in Mettam et al. (2017). Absence of AOM in the Finnmark material (based on results by Hochuli et al. (2010a) and results from microscopic analysis of palynological residues used for the present study) thus indicates oxygenated conditions continued during and after the extinction event.

5.2. Palaeo-environment and sea level

Three groups dominate the acritarch assemblages: Baltisphaeridium, Micrhystridium and leiospheres. Baltisphaeridium spp. have been observed in both Late Permian and Early Triassic material from south China, in both neritic to shelf environments (Lei et al., 2012). Wall (1965) found that both Micrhystridium and Baltisphaeridium dominated the assemblages in inshore and enclosed environments in British sections from the Lower Jurassic. Leiospheres have been found to be more abundant in nearshore environments (Li et al., 2004; Stricanne et al., 2004), and in fluvial-deltaic environments (Zavattieri and Prámparo, 2006). By contrast, Chinese Late Permian records indicate that certain species of Leiosphaeridia are more abundant in open-marine environments, while one species, Leiosphaeridia minutissima, occurs more frequently in a deep and nearshore setting (Lei et al., 2012). Overall, the acritarch assemblages points to a typical shallow marine, nearshore environment. This is supported by palynofacies data of Hochuli et al. (2010a), which shows that particulate organic matter consist for 70–80% out of phytoeasts and 20–30% are terrestrial palynomorphs. Furthermore, amorphous organic matter is rare while aquatic palynomorphs were found in low abundance (Hochuli et al., 2010a). The Late Permian extinction occurred during a period of global sea-level rise (Hallam and Wignall, 1999). At this time, marine carbonate platforms, deposited in open-marine conditions, were covered by prograding clastic deposition coming from the south (Bugge et al., 1995). High sedimentation rates of clastic matter on the platform likely compensated for ongoing sea-level rise, as there are no indications in the acritarch assemblages for a transgression. Veryhachium and M. pentagonale (Fig. 4C), which are indicative for more open shelf/open-marine conditions (Lei et al., 2012), are present with low abundances throughout the record. A temporary increase towards ~25% after the extinction event (~105 m) could be related to sea level rise, but such high abundances are not continued higher up in the core.

A shift in the acritarch assemblage after the extinction event, followed by a shortening of the average process length of the Micrhystridium breve – group after the extinction event (at 88 m core depth), might indicate a change in environmental conditions. The number of acritarchs measured in the top interval is very low (approximately 10 specimens in total between 88 and 78 m core depth), nevertheless, the change is consistent throughout several samples. As shorter processes of acritarchs are associated with more nearshore conditions (Lei et al., 2012; Stricanne et al., 2004), this change could indicate a relative drop in sea-level, as high sedimentation rates continued and the site became shallower. A relative decrease in sea level is supported by an increase in phytoeasts from on average 70% to 80% (Hochuli et al., 2010a), and a gradual increase in pollen concentration from 95 m depth upwards (Fig. 4B). In this clastic interval that is characterized by high sedimentation rates leiospheres become dominant. This is in agreement with the finding that leiospheres are dominant in fluvial-deltaic environments (Zavattieri and Prámparo, 2006).
Fig. 5. Aquatic palynomorphs of Late Permian to Early Triassic sediments from the Finnmark Platform. Samples collected from core 7129/10-U-1 are projected onto core 7128/12-U-01 based on the correlation by Bugge et al. (1995). The samples collected from core 7129 are indicated with arrows to the left of the depth axis, and their corresponding depths are indicated in grey on the depth axis. A) The concentration of all aquatic palynomorphs, note the log-scale for the x-axis B) concentration of pollen, C–H) relative abundances of the different groups of acritarchs and prasinophytes, I–K) measurements of acritarchs of the M. breve – group I) body size per specimen (in grey) and average body size in a sample (black), J) average process length per specimen (grey) and average process length in a sample (black) and K) ratio between average process length and average body size per sample. For I and J) if fewer than 10 acritarchs were measured, the average is not shown. The extinction interval (horizontal bar) is based on a spore peak after Hochuli et al. (2010a) and low concentrations of aquatic palynomorphs.
5.3. Increased marine productivity at the start of the extinction event

At the start of the extinction event the concentrations of aquatic palynomorphs strongly increase for a short interval (Fig. 4A). As concentrations of pollen are relatively low in this interval (Fig. 4B), the ~20× increase in the acritarch concentrations is neither the result of palynomorph condensation nor the result of decreased sedimentation rates. Rather, the high aquatic palynomorph concentrations indicate a strong increase in marine productivity. This acme is mainly caused by an increase of acritarchs in the M. breve – group, which make up ~99% of the aquatic palynomorphs in this interval. The high concentrations at the start of the extinction event are followed by a period of low marine productivity during the event (Fig. 4). The acme is in line with earlier findings that prasinophytes and also acritarchs can behave as “disaster species” as they proliferate at times when other organisms are absent (Tappan, 1980; Van de Schootbrugge et al., 2007).

Increased concentrations of organic walled marine phytoplanктon have been observed at the end-Permian biotic crisis, for example in the Boreal realm (Twitchett et al., 2001), in the Tethys realm (Schneebeli-Hermann et al., 2012; Shen et al., 2013) and at the end-Triassic biotic crisis (Van de Schootbrugge et al., 2007). Both events are thought to result from release of atmospheric CO₂ from volcanism, methane hydrate dissociation and/or organic matter metagenesis (e.g. Cui et al., 2013; Hesselbo et al., 2002; Svensen et al., 2009). Possibly elevated pCO₂ levels and ocean acidification caused a decrease in calcification, thereby allowing organic walled phytoplanктon to thrive (Hönisch et al., 2012). Also increased nutrient availability from volcanic ash may have increased marine productivity (Shen et al., 2013). It is thought that an acme of prasinophytes at the end-Triassic was caused by reduced salinity and increased nutrient conditions as a result of enhanced run-off (Bonis et al., 2010). Increased weathering and erosion during the Late Permian and Early Triassic indicate that the late Permian extinction event is also associated with increased run-off (e.g. Algeo and Twitchett, 2010; Sephton et al., 2005). Similarly, acritarch and palynomorphs from Jameson Land, East Greenland, also indicate a rise in run-off just before the end of the Permian extinction event (Van Soelen et al., 2018).

5.4. Comparison of records from the Finnmark Platform with Greenland and South China

The most detailed acritarch records for the late Permian are from South China (e.g. Lei et al., 2013b; Shen et al., 2013), with several acritarch-records covering the Late Permian extinction event and the Permian-Triassic boundary. The assemblages in South China are comparable to the assemblages found in the two boreal Arctic sections (Jameson Land and Finnmark Platform), with Mixhystridium and Verhachium being the most abundant genera (Lei et al., 2012, 2013b; Van Soelen et al., 2018, and this study). Diversity strongly decreased in the late Permian, with only few species surviving into the Early Triassic (Lei et al., 2012, 2013b). Shen et al. (2013) concludes that volcanism strongly affected the acritarch assemblages in South China, with a positive effect from the additional nutrients resulting from ash input, and a negative effect due to the increase in toxic metals. Acritarchs with short processes, like M. breve showed the smallest decline and were the most abundant group in the Early Triassic (Shen et al., 2013, summarized in Fig. 6). These results are in agreement with our findings from the Finnmark Platform and East Greenland, where Mixhystridium was the most dominant acritarch during and following the extinction event, in addition to leiospheres. Acritarchs with short processes may have been less affected by the extinction event as they had a preference for neritic inshore-shelf environments, which acted as biotic refugia (Shen et al., 2013). Both the Greenland and Finnmark locations are shallow marine environments and may have had less hostile environments during the extinction event allowing stress-tolerant acritarch groups to survive (Shen et al., 2013).

An important difference between the Greenland and Finnmark sections is the development of anoxic bottom water conditions in the Greenland section, first as alternating pattern between low oxygen and oxic conditions, then turning fully anoxic after the extinction event (Mettam et al., 2017). Also the relative process length (in ratio with body size) decreased gradually starting before and continuing during the extinction event, after which process length remained relatively short (results of the Greenland section are summarized in Fig. 6). Since sea level was rising (Wignall and Twitchett, 2002a, 2002b), the decreasing process length is not indicative for a shift from a distal to a proximal setting in this setting. Instead, the gradual shortening of the processes was interpreted to reflect a decrease in salinity, following enhanced run-off due to an intensification of the hydrological cycle during the extinction event (Van Soelen et al., 2018). Such a relationship between process length and salinity has been found in experiments with modern dinoflagellate cysts (e.g. Mertens et al., 2009, 2012), and it is thought that the longer processes facilitate clustering with other cysts or particles in the water column, thereby helping the cysts to sink to the sea floor (Mertens et al., 2009). The inferred increase in run-off also explains the development of anoxic conditions in the Greenland section, as the water column became stratified and bottom water became anoxic (Van Soelen et al., 2018). In contrast, the processes length of the acritarch Mixhystridium in the Finnmark acritarch record remains stable throughout the extinction interval, and only higher up in the record the process length decreases somewhat. Since there is also no obvious change in redox conditions at the site during the studied interval (Hochuli et al., 2010a), water apparently remained well mixed and salinity was not affected at this location.

The difference in redox conditions between Greenland and Finnmark can possibly be explained by their palaeogeographical setting. The clastic sediments of the Greenland section were deposited in a narrow, semi-enclosed, north-south oriented basin (Stemmerik et al., 2001; Wignall and Twitchett, 2002a, 2002b), while the Finnmark section was deposited on an open shallow shelf (Bugge et al., 1995; Mangerud, 1994). The basin between Norway and Greenland was likely to be more sensitive for changes in precipitation and run-off, which would have quickly resulted in a freshwater surface layer, water column stratification and low bottom water conditions. Before the start of the extinction event, the relative process length is longer in the Greenland section compared to the Finnmark section (Fig. 6). Possibly high evaporation rates during the warm and arid Late Permian (Kiehl and Shields, 2005) caused hypersaline conditions in the semi-enclosed basin before until intensification of the hydrological cycle caused the salinity to drop and the water column to stratify. Palynofacies and/or organic geochemical studies in sections and wells from the Salt Range in Pakistan (Schneebeli-Hermann et al., 2012), the Perth Basin (Thomas et al., 2004) and Bonaparte Basin (Gorter et al., 2009) in Australia revealed a similar pattern of regional differences in redox conditions across the Permian-Triassic boundary on the southern Tethyan shelf depending on local palaeogeography.

6. Conclusions

In general, the number of aquatic palynomorphs is very low in the section. A strong increase in Mixhystridium concentrations before the start of the extinction event suggests that the organic phytoplankton profits, at least for a short period, from changing environmental conditions related to the extinction event, like ocean acidification, decreased salinity and/or increased nutrient availability. The generally low concentrations of acritarchs, which are dominated in the assemblage by Mixhystridium, Baltisphaeridium and leiospheres, indicates the material throughout the record to be deposited in a shallow marine, nearshore setting. A change in assemblage from Mixhystridium/ Baltisphaeridium to leiosphere dominance after the extinction interval, followed by a relative drop in process length in the top of the record (< 88 m), suggests the site became even shallower. Since the extinction
event happened during a period of global sea-level rise, the relative sea-level drop at the Finnmark Platform is best explained by the very high sedimentation rates of clastic material transported from the Ural Mountains and Nova Zemlya, which compensated for sea-level rise. The records of process length of Finnmark Platform differ from a section in East Greenland, where process length decreased. Sediments of the Finnmark section remain bioturbated throughout the core, which shows that the water column remained mixed. By comparing the Finnmark and East Greenland records, it appears that the East Greenland section was more sensitive for evaporation and runoff changes than the Finnmark section was.

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Appendix A. Supplementary data

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