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Early Cretaceous vegetation and climate change at high latitude: palynological evidence from Isachsen Formation, Arctic Canada

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Quantitative palynology of the marginal marine and deltaic-fluvial Isachsen Formation of the Sverdrup Basin, Canadian Arctic, provides insight into high latitude climate during much of the Early Cretaceous (Valanginian to early Aptian). Detrended correspondence analysis of main pollen and spore taxa is used to derive three ecological groupings influenced by moisture and disturbance based on the botanical affinities of palynomorphs: 1) a mixed coniferous assemblage containing both lowland and upland components; 2) a conifer-filicopsid community that likely grew in dynamic lowland habitats; and, 3) a mature dry lowland community composed of Cheirolepidaceans. Stratigraphic changes in the relative abundance of pollen and spore taxa reflect climate variability in this polar region during the ~20 Mya history of the Isachsen Formation. The late Valanginian was relatively cool and moist and promoted lowland coniferfilicopsid communities. Warming in the Hauterivian resulted in the expansion coniferous communities in well-drained or arid hinterlands. A return to relatively cool and moist conditions in the Barremian resulted in the expansion of mixed lowland communities. This work demonstrates the utility of a multivariate statistical approach to palynology to provide insight into the composition and dynamics of ecosystems and climate of high latitude regions during the Early Cretaceous.

Keywords

Isachsen Formation; Sverdrup Basin; Cretaceous; Canada, Arctic; Palynology

1.0 Introduction

Understanding the behaviour of global climate during relatively warm periods in Earth's history, such as the Cretaceous Period, advances our overall understanding of the climate system and provides insight on drivers of climate change over geologic time. It has been suggested that the Valanginian Age (~139 Ma to 134 Ma; Gradstein et al., 2012) represents the first episode of Cretaceous greenhouse climate conditions with high atmosphere pCO_2 levels and stable, relatively equable warm temperatures that persisted through the Hauterivian and beyond (Lini et al., 1992; Littler et al., 2011). Early Cretaceous greenhouse conditions have been related to Valanginian carbonate platform drowning (Föllmi et al., 1994) and the Paraná-Etendeka continental flood basalts that may have been a source of CO₂ (Channell et al., 1995; Courtillot et al., 1999; Erba et al., 2004). However, the greenhouse hypothesis for the Early Cretaceous (Lini et al., 1992) has been recently questioned (McArthur et al., 2004; Gröcke et al., 2005) and data to support cool climate conditions during the Valanginian have been revisited (Kemper, 1983, 1987; Frakes et al., 1994; Ditchfield, 1997; Podlaha et al., 1998) and are emerging (Price et al., 2000; Alley and Frakes, 2003; Erba et al., 2004; McArthur et al., 2004, 2007; Gröcke et al., 2005; Price and Mutterlose, 2004; Kessels et al., 2006; Price and Bassey, 2013;), with some exceptions (Littler et al., 2011). For example, nannofossil evidence from Europe suggest that the late Valanginian to early Hauterivian interval was cool (Mutterlose and Kessels, 2000; Mutterlose et al., 2003; Kessels et al., 2006). Ditchfield et al. (1997) analyzed belemnites from Spitsbergen and document high $\delta^{18}O_{carb}$ values (low paleotemperatures) for the lower to middle Valanginian and suggest the presence of high latitude ice. Price and Mutterlose (2004), Price and Nunn (2010), and Price and Bassey (2013) use oxygen and carbon isotope data from Valanginian

glendonites and belemnites preserved in polar regions to reconstruct paleotemperatures consistent with transient glacial conditions. The abundance of ice-rafted debris decreases from the Berriasian/Valanginian into the Hauterivian (Kemper, 1987; Frakes, 1992) and glendonites, pseudomorphs after ikaite thought to form in cold sub-aqueous depositional conditions (Kemper, 1987; Frakes and Francis, 1988; Price, 1999), are abundant and widespread in Valanginian strata from the Sverdrup Basin (Kemper and Jeletzky, 1979; Kemper 1983, 1987; Selmeier and Grosser, 2011), Spitsbergen (Kemper, 1983; Rogov and Zakharov, 2010; Price and Nunn, 2010), Siberia (Kaplan, 1978; Rogov and Zakharov, 2010), and northern Alaska (Tarduno et al., 2002), before becoming rare until the latest Aptian (Kemper, 1983, 1987; Schröder-Adams et al., 2014). McArthur et al. (2004) reconstructed changes in seawater temperature from isotopic and chemical signatures of belemnites preserved in Lower Cretaceous strata of East Yorkshire, Northern England, near the confluence of the Tethyan and Boreal realms. They document warming at the base of the Hauterivian to peak temperatures in the middle Hauterivan followed by a decline that persisted into the basal Barremian. This mounting body of evidence suggest that the Valanginian was cool and that a period of warming occurred during the Hauterivian.

Although recent advances in understanding of Early Cretaceous climate change have shed light on the nature and drivers of variability, paleoclimate is less understood in polar regions compared to mid- to low-latitudes (e.g., Pucéat et al., 2003; Price and Mutterlose, 2004; Price and Nunn, 2010) and this is particularly true for the Canadian Arctic (Hopkins, 1971, 1974; Embry, 1985a; Harland et al., 2007; Selmeier and Grosser, 2011; Galloway et al., 2012, 2013; Schröder-Adams et al., 2014). There is a paucity of data overall for the terrestrial realm as most paleoclimate studies have been based on marine material (Spicer and Parrish, 1986; Gröcke et al., 2005; Harland et al., 2007; Selmeier and Grosser, 2011; Galloway et al., 2012, 2013). These few studies suggest that a diversity of coniferous trees occurred in Early Cretaceous high northern latitude forest communities despite long dark winters and summers with continuous sunlight. Polar forests potentially promoted climate feedback effects at regional to global scales through albedo, land surface heat budget, hydrological and carbon cycles (Foley et al., 1994; DeConto et al., 2000; Beringer et al., 2005) and are therefore important to include in global climate modelling (Harland et al., 2007). Constraining the long-term vegetation and climate history of polar regions, especially during extreme warm but variable periods such as the Early Cretaceous, offers a possible analogue for a much warmer future Earth.

In this study we analyze fossil pollen and spores preserved in the Isachsen Formation exposed on Ellef Ringnes Island, Sverdrup Basin (Figures 1, 2), to reconstruct high northern latitude climate and terrestrial ecosystem dynamics during the Early Cretaceous.

2.0 Geologic setting

Sverdrup Basin is a 1300 km by 350 km sedimentary basin that underlies the northern part of the Canadian Arctic Archipelago (Figure 1). The basin began its history with rifting in the Carboniferous to Early Permian, followed by a period of thermal subsidence with episodic uplift of basin margins that lasted into the Cretaceous (Embry and Beauchamp, 2008). Subsidence rate greatly increased in the Early Cretaceous when basaltic volcanism and widespread emplacement of diabase dykes and sills occurred (Balkwill, 1978; Stephenson et al., 1987; Embry and Beauchamp, 2008). The basin then underwent slow subsidence for much of the Late Cretaceous. Sverdrup Basin strata are deformed by structures that developed during episodic flow of Carboniferous evaporites during the Mesozoic (Figure 1; Balkwill, 1978; Boutelier et al., 2010;

Galloway et al., 2013), by Hauterivian to Cenomanian magmatism and faulting (Embry and Osadetz, 1988; Embry, 1991), and by the Eurekan Orogeny (Eocene), which produced high amplitude folds and thrust faults in the northeast basin and gentler folds to the west (Harrison et al., 1999).

The age of Mesozoic strata in Sverdrup Basin are based primarily on ammonites, bivalves, dinoflagellate cysts and foraminifera (Table 1) but paleoclimate studies using pollen and other climate indicators in the Early Cretaceous of the Canadian Arctic are limited (Table 1; Hopkins, 1971, 1974; Wall, 1983; Embry, 1985a; Harland et al., 2007; Selmeier and Grosser, 2011; Galloway et al., 2012, 2013; Schröder-Adams et al., 2014).

Ellef Ringnes Island is located near the axis of the Sverdrup Basin in the Canadian Arctic Archipelago and was situated between paleolatitudes $74 \pm 2^{\circ}$ (standard error) and $79 \pm 1^{\circ}$ in the Early Cretaceous (Wynne et al. 1988; Figures 1,2).

2.1 Isachsen Formation

The Isachsen Formation was first described by Heywood (1957) on Ellef Ringnes Island for a succession of arenaceous strata between two shale-siltstone units (Deer Bay and Christopher formations) (Figures 1, 2). The Isachsen Formation is widespread throughout Sverdrup Basin, ranging in thickness from ~120 m at basin margins to 1370 m on western Axel Heiberg Island (Hopkins, 1971).

Sediments of the Isachsen Formation were deposited in marginal marine/deltaic and fluvial environments during the development of the Amerasia Basin (Embry and Dixon, 1990; Tullius et al., 2014), synchronous with volcanism related to its opening (Embry and Osadetz,

1988; Grantz et al., 2011). The Isachsen Formation is divided into three members (Embry, 1985a). The Paterson Island Member overlies Deer Bay Formation or Mackenzie King Formation with unconformable contact at basin margins and conformable contact in basin centre. The Paterson Island member consists of fine to very coarse-grained sandstone with interbeds of carbonaceous siltstone, mudstone, coal, and volcanic and volcaniclastic/tuffaceous rocks (Embry and Osadetz, 1988; Evenchick and Embry, 2012a, b). Sandstone units are up to 35 m thick and argillaceous intervals between 2 and 10 m thick occur in the 152 m thick type section in the Skybattle Bay C-15 oil and gas well (77°14'N, 105°05'W) (Embry, 1985a). Lowermost sandstones of the Paterson Island Member exposed on Ellef Ringnes Island contain interbedded mudstone and are bioturbated, reflecting deposition in a marginal marine setting (Embry 1985a; Tullius et al., 2014). Shallowing and a northward progradation of paleoshoreline resulted in deposition of cross-bedded, fluvial sandstones. These sandstones grade upward into finer-grained non-marine deposits consisting of fining-upward sandstones interbedded with siltstone, mudstone, and coal deposited in a delta plain setting with overbank and channel environments (Figure 3; Embry 1985a; Tullius et al., 2014). The Paterson Island Member is conformably overlain by interbedded medium to dark-grey mudstone and siltstone of the Rondon Member that were deposited in a marine shelf setting (Embry 1985a; Nøhr-Hansen and McIntyre, 1998; Tullius et al., 2014). The type section in the Skybattle C-15 well is 47 m thick (Embry, 1985a). The Rondon Member is conformably overlain by interbedded fine to coarse-grained sandstone, siltstone, and mudstone with minor coal of the Walker Island Member. The type section of the Walker Island Member in the Skybattle C-15 oil and gas well is 140 m thick (Embry, 1985a). The Walker Island Member on Ellef Ringnes Island is composed of marginal marine, bioturbated sandstones and fluvial sandstones with mud-drapes indicating tidal influence and inferred to have been deposited in a delta front to delta plain environment (Embry 1985a; Tullius et al., 2014). Walker Island Member is conformably overlain by mudstones and fine-grained sandstones of the Christopher Formation.

2.1.1. Biostratigraphy and paleoclimate

Initial palynological research on Isachsen Formation by Hopkins (1971) qualitatively describes palynoflora preserved in samples collected from the bottom of seismic shot hole samples on northwest Melville Island. A stable temperate climate was inferred (Hopkins, 1971). Galloway et al. (2013) quantitatively examined seven well-cuttings samples from Isachsen Formation for pollen and spores as part of a longer stratigraphic succession preserved in the Hoodoo Dome H-37 oil and gas well drilled on southern Ellef Ringnes Island. They suggest that the development of humid and cool high-latitude paleoclimate conditions caused a vegetation shift in the late Valanginian or early Hauterivian. Sedimentological and preliminary palynological analyses of four samples from the Isachsen Formation exposed on Ellef Ringnes Island (and revisited here) are presented by Tullius et al. (2014). Flora (e.g., bisaccate and Cupressaceae-Taxaceae pollen) representative of the relatively cool and moist post-late Valanginian/early Hauterivian climate shift described by Galloway et al. (2013) are abundant.

There is limited fossil evidence for age control from the Isachsen Formation (Table 1). The age of the underlying Deer Bay Formation ranges from Tithonian to Valanginian (Table 1). The age of overlying marine mudstones of the Christopher Formation ranges from Aptian to Albian based on marine macrofossils, foraminifera, and pollen and spores preserved in material from various localities (Table 1). The lower 30 m of the Isachsen Formation on Ellef Ringnes contains Buchia cf. B. bulloides (Lahusen) and "Buchia cf. B. terebratuloides (Lahusen)" (reported by Heywood, 1957; Stott, 1969, but probably Buchia crassicollis (Keyserling) as reinterpreted by Jeletkzy (1973) that are dated as late Valanginian). Late Valanginian bivalves have also been reported in the basal Isachsen Formation rocks on nearby Amund Ringnes Island (Balkwill, 1983). Palynology of un-subdivided Isachsen Formation on Banks, Prince Patrick, and Melville islands suggest a Valanginian to Aptian age for the formation (Hopkins, 1971; Plauchut and Jutard, 1976; Dorenkmap et al., 1976). Pelecypods preserved in Paterson Island Member from an unknown locality suggest a Valanginian to Barremian age for this lower unit of the Isachsen Formation (Balkwill, 1983). Dinoflagellate cysts preserved in the Rondon Member of Isachsen Formation exposed at Glacier Fiord and at Buchanan Lake, Axel Heiberg Island, and from south Sabine Peninsula on Melville Island suggest a Barremian age for this marine unit (Costa, 1984; McIntyre, 1984; McIntyre pers. comm. 1984 in Embry, 1985a, 1991; Nøhr-Hansen and McIntyre, 1998). Based on the age of the Rondon Member and overlying Christopher Formation, the age of the Walker Island Member is inferred to be Barremian to Aptian in age (Embry, 1985a).

3.0 Material and methods

3.1 Samples

Eighteen organic-rich samples from three measured and described outcrop sections of Isachsen Formation were collected in 2010 and 2011 from Ellef Ringnes Island and analyzed for pollen and spores (Table 2; Figures 2, 4). All microscope slides are stored at the Geological Survey of Canada, Calgary, Alberta, on loan from the Geological Survey of Canada, Ottawa. Curation, preparation, and specimen numbers are shown in Table 2 and Figure 6.

Palynological data from four samples reported in Tullius et al. (2014) are built upon here by further inspection of material to achieve minimum pollen and spore counts of 300. Detailed sedimentological descriptions and interpretation of the three sections are presented in Tullius et al. (2014). Geographical locations of samples analyzed for palynology are shown in Figures 2 and 4. Where coordinates were unavailable (samples IS-734, IS-761, IS-1107, DS2-638), locations are estimated. Lithological logs and the stratigraphic positions of samples are shown in Figure 5.

The IS-01 Section captures the Deer Bay to Isachsen formational contact as well as the Isachsen to Christopher contact and is cut by several dip-slip faults that offset strata (Figures 4, 5; Evenchick and Embry, 2012a). Uncertainties in the magnitude of displacement and correlation of marker horizons across the faults result in uncertainties in the true stratigraphic positions of samples between 1000 m and 1500 m (from base of the section). The fault at ~1480 m cuts out at least 100 m of the upper Paterson Island Member, all of the Rondon Member, and base of the Walker Island Member (Figure 4). Eight samples of organic-rich material were examined palynologically from the Paterson Island Member exposed in section IS-01 (Table 2).

Ten samples from Isachsen Formation were examined from the DS-02 Section (Figures 4, 5). This section begins in the Paterson Island Member and extends to the Isachsen-Christopher formation boundary. This section is on the gently folded to monoclinal flank of an anticline and

does not appear to be cut by faults (Evenchick and Embry, 2012a). Five samples from the Paterson Island Member, including three samples from the laterally traceable floodplainmeandering stream facies (Figures 3, 5), were analyzed for pollen and spores. One sample was analyzed from the Rondon Member and four samples were analyzed from the Walker Island Member (Table 2).

Four samples from Isachsen Formation were analyzed from the DS-03 Section (Figures 4, 5; Table 2). This section is in fault contact with diapiric evaporates (Evenchik and Embry, 2012a) and extends to the boundary with the Christopher Formation. The sample lowest in this stratigraphic succession (DS3-23) is near the fault contact with the evaporites. This area is structurally complex and the relationship of sample DS3-23 relative to the three overlying samples is not known. The remainder of section Dumbbells West is structurally unremarkable but differentiation of member lithostratigraphy is not possible (Evenchick and Embry, 2012a).

3.2 Palynological preparation, microscopy, and terminology

Organic-rich samples collected from IS-02, DS-02, and DS-03 sections were prepared for palynological analysis at the Geological Survey of Canada, Calgary, following standard extraction techniques, including washing, acid digestion, oxidation with Schulze's solution, and staining with Safranin O (Table 2). Slurries were mounted with polyvinyl and liquid bioplastic. Observations were made using an Olympus BX61[®] transmitted light microscope with oil immersion at 400x and 1000x magnification. Digital images were captured using an Olympus DP72 camera and Stream Motion[®] software. All microscope slides are stored in the registered collections of the Geological Survey of Canada. Statistical analyses of palynomorphs are based

on counts of unsieved preparations with greater than 300 spores and pollen enumerated per sample (mean 339 ± 24 SD).

Ancient monosulcate pollen are ascribed to a large variety of genera (Jansonius and Hills, 1976) even though modern pollen of the Ginkgoales, Cycadales, and Bennettitales are difficult to differentiate using light microscopy (Samoilovich 1953 translation 1961, p. 36; Hill, 1990). We assign ellipsoid monosulcate pollen where the single longitudinal furrow reaches almost to the end of the pollen grain to the genus Cycadopites Wodehouse. This genus accommodates grains with exines of various texture that have a single longitudinal furrow reaching almost to the end where it gapes open, even when closed in the middle (Wodehouse, 1933; Jansonius et al., 1998). The type species C. follicularis ranges in size from 39-42 µm long and 18-21 µm wide (Wilson and Webster, 1946). We do not distinguish Cycadopites to the species level, as this is rarely possible even with living material (Wodehouse, 1933). We distinguish larger monosulcate pollen (~52 µm long x ~30 µm wide) as Entylissa Naumova 1939 ex Ishchenko 1952, an obligate senior synonym of Gingkocycadophytus Samoilovich 1953. Gingkocycadophytus, and thus Entylissa, accommodates pollen ranging in size from 33-85 µm long and 20-40 µm wide (with one specimen (Ginkgocycadophytus sp. Pl. 111, Fig. 4 Samoilovich 1953 translation 1961) with an "extraordinary" dimension of 117 μ m by 56 μ m) with a single furrow extending the full length of the grain. The furrow may be closed to fully open and occasionally edges overlap (Samoilovich, 1953, translation 1961). Samoilovich (1953, translation 1961, p. 36) acknowledges that the pollen Gingkocycadophytus does not have adequate morphologic characteristics to assign the pollen type to the Ginkgoales or Cycadales and notes that this generic name reflects the similarity of the described pollen to both classes. We differentiate the genus Perinopollenites Couper 1958 from Inaperturopollenites and undifferentiated

Cupressaceae-Taxaceae by the presence of a perinosaccus (Jansonius and Hills, 1976). We use the genus name Inaperturopollenites Pflug & Thomson & Pflug 1953 to refer to pollen with a spherical original shape and with a thin, infrapunctuate exine with many secondary folds (Jansonius and Hills, 1982). Spherical, infrapunctate pollen with an exine that tends to split along a more or less radial line (e.g., Taxodiaceaepollenites Kremp 1949 ex. Potonié 1958) are retained in Cupressaceae-Taxaceae and not differentiated. Other pollen and spore types are also identified to the lowest possible taxonomic level (Table 3).

3.3 Multivariate statistics

The relative abundance of each taxon is based on a pollen and spore sum that includes palynomorphs with affinities to terrestrial land plants. Non-terrestrial palynomorphs, including dinoflagellate cysts, other algae, and acritarchs, are excluded from the pollen and spore sum and omitted from multivariate statistical analyses.

We use two-way cluster analysis (Q- and R-mode) resulting in a cluster matrix to identify samples that cluster together based on palynomorph content to explore if palynoassemblages are unique to a section or part of a section (Q-mode) and to observe which pollen and spore taxa group together (R-mode). Q-mode-defined sample clusters (SC) are shown on the lithological sections to note which facies they occur in. Combined Q-and R-mode cluster analysis was carried out using Ward's minimum variance method and relative Euclidean distance on relative abundance data using the computer program PC-ORD (Fishbein and Patterson, 1993; McCune and Mefford, 2006).

Ordination techniques are commonly used in ecology and paleoecology to determine major gradients in taxa composition. These may be linked to environmental and ecological factors that control assemblage composition. In paleoecological data, ordination is a particularly useful method because fossil assemblages may represent discrete communities, segments of gradients in which taxa are distributed individualistically according to environmental preferences, and/or an association of community signatures transported and preserved in a geologic deposit (Springer and Bambach, 1985; Bambach and Bennington, 1996; Bennington and Bambach, 1996; Holland et al., 2001; Bush and Balme, 2010). Spatial migration of communities can also produce gradients in species composition in time-averaged geologic deposits (Miller, 1988). Detrended Correspondence Analysis (DCA) is a technique that is commonly used in ecological ordination because this method corrects for the arch/horseshoe effects of Correspondence Analysis (Hill and Gauch, 1980). We performed DCA on the relative abundance of taxa having an overall assemblage value of 0.5% or greater to reduce statistical noise (Stukins et al., 2013). In contrast, combined Q and R-mode cluster analysis was performed using all palynomorph data. DCA was done using the Vegan package (v. 2.0-5) in R (v. 2.15.1), with 26 segments and rescaling of axes with 4 iterations (Oksanen et al., 2012). We interpret clusters of taxa observed in the DCA biplot to represent groups of parent plants with similar ecologies that formed an ecological community (Stukins et al., 2013). Sample clusters defined by combined Q-and R-mode cluster analysis are also shown on the DCA biplot.

Taxa preserved in samples from each of the three sections were graphed stratigraphically using the Tilia and TGView computer programs (Grimm, 1993-2001) to view changes over time at an assemblage scale. The relative abundance of plant types (Table 3) and cumulative abundances of members of each of the four ecological groups delineated by DCA are also plotted stratigraphically to observe changes in plant communities over time. Stratigraphically constrained cluster analysis using incremental sum of squares (CONISS; Grimm, 1987) was applied to the relative abundance of all pollen and spores from obligately terrestrial plants to delineate major changes in palynoassemblages over time.

4.0 Results

Palynological preparations of samples collected from the three sections of Isachsen Formation contain numerous pollen and spores assigned to 58 taxa (Table 3; Figure 6). Preservation ranges from exceptional to poor, except for sample IS-1030 that was barren. Thermal alteration of palynomorphs was consistently low (TAI 1+ to 2; Pearson, 1984). Our quantitative analyses are based on an average sample count of 339 ± 24 SD (n=22 samples) pollen and spores with affinities to obligately terrestrial plants.

4.1. Descriptive palynology

Palynoassemblages preserved in Isachsen Formation samples from sections IS-01, DS-02, and DS-03 are dominated by pollen from gymnosperms (Table 3; Figure 7). Pollen attributable to plants belonging to Class Pinopsida compose, on average, 74.34% (\pm 9.56 SD, n=22) of the total pollen and spore sum of each sample. Cupressaceae-Taxaceae (mean 33.93% \pm 14.24 SD) and undifferentiated bisaccate (mean 31.63% \pm 14.61 SD) pollen make up the majority of Pinophytes the samples. Pollen attributable to Division Pteridospermopsida represent a minor component (mean <1%). Pollen attributable to plants belonging to Divisions Cycadophyta/Gingkophyta represent a mean of $4.04\% \pm 1.83$ SD of the total pollen and spore sum of the samples while Eucommidites troedsonii pollen, the only taxon identified attributable to Division Gnetophyta (Tekleva et al., 2006), comprises a mean of <1% of the pollen and spore population of the samples. Filicopsids are the next most common group (mean $17.79\% \pm 8.70$ SD). Gleicheniidites senonicus (mean 5.46 ± 4.40 SD), Deltoidospora hallei (mean $4.95\% \pm 3.19$ SD), and Dictyophyllidites harrisii (mean 2.37 $\% \pm 1.14$ SD) are the main filicopsid spore taxa present in the samples. Lycopodiophytes occur with an average of $0.74\% \pm 0.56$ SD of the total pollen and spore sum of the samples and Bryophytes are also a minor group (mean $1.84\% \pm 1.49$ SD) represented almost entirely by Stereisporites antiquasporites (mean 1.62% \pm 1.21 SD). Nonterrestrial palynomorphs represent a minor component of the total assemblage (mean of samples <1%; although Sigmopollis was not enumerated in all samples). Non-terrestrial palynomorphs include undifferentiated algae, dinoflagellate cysts, Chomotriletes, Sigmopollis, Pterospermopsis, and the acritarch genera Veryhachium and Micrhystridium.

4.2. Multivariate statistical palynology

Combined Q (sample)-and R (variable)-mode cluster analysis demonstrates that four sample clusters can be delineated, labelled Sample Cluster (SC)-1 through SC-4 (Figure 8). We describe each sample cluster in terms of plant classes, except for Pinopsida, which we further distinguish to family and in the case of Pinaceae, to the lowest taxonomic level possible, due to the predominance of pinaceous pollen. Classes and families not labelled are grouped as "other" when representation was less than 10% of the total pollen and spore sum (Table 2). Sample Cluster-1 is characterized by a high relative abundance of bisaccate pollen (mean $60.26\% \pm 3.04$

SD, n=3 samples) and Cycadopsida/Gingkopsida pollen (mean 10.39%±12.00 SD, n=3 samples). Sample Cluster-2 (n=10 samples) is characterized by a mixture of Cupressaceae-Taxaceae and bisaccate pollen with filicopsid spores. Sample Cluster-3 is characterized by a high relative abundance of Cupressaceae-Taxaceae pollen (mean $44.01\% \pm 10.11$ SD, n=7 samples). Sample Cluster-4 is characterized by a high relative abundance of Classopollis classoides pollen (mean 20.09%±1.55 SD) in the two samples that make up this sample cluster. The stratigraphic locations of samples that comprise each sample cluster are shown in Figure 5 to provide insight into any influence of facies on assemblage composition. Sample Cluster-1 (Bisaccate-Cycadopsida/Gingkopsida assemblage) occurs in the DS-3 and DS-2 sections in facies indicative of floodplain and fluvial depositional environments (Tullius et al., 2014). Sample Cluster-2 (Cupressaceae-Taxaceae-Bisaccate-Filicopsid assemblage) occurs mainly in the DS-03 and DS-02 sections; only one sample (IS-1063) in the IS-01 Section represents SC-2. Sample Cluster-2 includes samples from facies indicative of delta plain and fluvial environments. Sample Cluster-3 (Cupressaceae-Taxaceae assemblage) occurs in all three sections from facies indicative of shoreline and fluvial environments. Sample Cluster-4 (Classopollis classoides assemblage) occurs only in the lowermost two samples of IS-01 Section (IS-322 and IS-482) that were deposited in a prodelta to delta front environment (Figures 5, 7). The three stratigraphic sections examined contain broadly similar palynoflora; using combined Q and R-mode cluster analysis we defined sample clusters that for the most part contain samples from each of three sections and do not differentiate based on facies (exception is SC-4) (Figures 5, 7). Therefore, we combine data from samples collected from the three sections for the purpose of the following discussion on age interpretation and paleoecological and paleoclimate reconstruction of Ellef Ringnes Island during deposition of the Isachsen Formation.

Detrended correspondence analysis (DCA) is used to further delineate clusters of taxa to assist in determination of underyling gradients of compositional change. We term these clusters 'ecological groupings' (Stukins et al., 2013). Three ecological groupings (A, B, and C) are identified in the DCA biplot that we interpret as representing paleoecological communities (Figure 9). Ecological grouping A comprises four pollen taxa, three of which have gymnosperm affinities, Ecological grouping B is composed of 12 pollen and spore taxa with gymnosperm, cycad, filicopsid, and bryophyte affinities, and Ecological grouping C is composed of a single pollen taxon, Classopollis classoides.

4.3. Palynostratigraphy

Appendix A shows that few and subtle changes occurred in the relative abundance of palynomorphs throughout the Isachsen Formation. The most complete and intensely sampled DS-02 Section shows a trend of increasing proportions of Cupressace-Taxaceae pollen upsection (from ~20% to ~40-60%). Section IS-01 shows a similar trend where Cupressaceae-Taxaceae pollen increases from ~20% to ~40% with associated increases in undifferentiated bisaccate pollen. Palynomorph abundances in the DS-03 Section show changes in bisaccate pollen composition and an increase in spores toward the top of the section, but these changes are difficult to interpret based on the low sampling resolution and structural complexity of this section. Stratigraphic changes in the relative proportion of the three ecological groupings delineated using DCA are plotted in Appendix A. In Section IS-01 the proportion of taxa composing Ecological grouping A cumulatively increases from ~20% to ~40% up-section in depositional settings that include fluvial, floodplain, and shoreface environments (Figures 5, 10;

Tullius et al., 2014). In Section DS-02 the proportion taxa composing Ecological grouping A increases between ~400 and 650 m in facies indicative of floodplain to fluvial depositional settings while the proportion of taxa that make up Ecological grouping B are abundant in the basal and upper parts of the section. Ecological grouping C shows relatively low abundances in all sections except in the basal two samples of Section IS-01.

5.0 Discussion

Our quantitative, statistical treatment of palynomorphs preserved in three sections of Isachsen Formation exposed on Ellef Ringnes Island provides a palynological 'fingerprint' for this formation that can be used for inter- and intra-basin correlation and insight on high latitude paleoclimate and terrestrial ecology during the Early Cretaceous (Galloway et al., 2012).

5.1 Age interpretation

Pollen and spores preserved in the Isachsen Formation are representative of the Early Cretaceous Cerebropollenites Province of the northern hemisphere (Herngreen et al., 1996). The Cerebropollenites Province is characterized by relatively high abundances and diversities of filicopsid spores (e.g., Gleicheniidites, Cicatricosisporites, Pilosisporites) together with bisaccate and other gymnosperm pollen (e.g., Araucariacites, Inaperturopollenites, Perinopollenites, Classopollis). Cerebropollenites mesozoicus is a common and distinctive element. Many taxa of this province are common to Late Jurassic floras (Herngreen et al., 1996) but the addition of certain taxa (e.g., Aequitriradites, Cicatircosisporites, Trilobosporites, and Foveosporites subtriangularis) indicate a Cretaceous age (Venkatachala and Kar, 1970; Hopkins, 1971; Bose and Banerji, 1984; Taugourdeau-Lantz, 1988). Foveosporites subtriangularis has been interpreted to be an index species for the Hauterivian to late Aptian interval in the eastern North Atlantic (Taugourdeau-Lantz, 1988) and is present in the upper two samples of Section IS-01. Towards the pole, the Arctic sub-province of the Cerebropollenites Province is dominated by bisaccate pollen and spores and contains palynoassemblages with restricted diversity and abundance relative to more southern floras of the Cerebropollenites Province (Hengreen et al., 1996). Other features of the palynostratigraphic record preserved in the Isachsen Formation may refine our understanding of the depositional age of these rocks. On Ellef Ringnes Island, Galloway et al. (2013) document an increase in Cupressaceae-Taxaceae pollen that begins in the upper Deer Bay Formation. Peak abundances of these taxa are reached in lower Isachsen Formation strata preserved in the Hoodoo Dome H-37 oil and gas well. The timing of onset of this floristic event is interpreted as late Valanginan or early Hauterivian when climate became cooler and more humid in high-latitude regions. Documentation of similarly high Cupressaceae-Taxaceae pollen in outcrop samples of Isachsen Formation on Ellef Ringnes Island provides local reproducability of this signal. In Western Siberia, a broadly contemporaneous shift in Taxodiaceaepollenites spp. occurs when this taxon increases in relative abundance (to ~17%) in the middle Hauterivian (Pestchevitskaya, 2008). Shifts in the relative abundance of Cupressaceae-Taxaceae pollen may represent a time significant event for Arctic regions that can be useful in interpreting Early Cretaceous time systems. Further research is necessary to explore the provinciality of this signal.

5.2 Paleoecological interpretations

Considerable uncertainty can exist regarding the botanical affinities of quantitatively important palynomorphs and/or of the ecological tolerances and optima of extinct parent plants. We base our inferences on actualistic principles and assume that certain paleoenvironments supported taxa with broadly similar ecological preferences (Abbink et al., 2004).

5.2.1 Non-terrestrial palynomorphs

Non-terrestrial palynomorphs collectively represent <1% of the pollen and spore sum, reflecting the dominance of input of terrestrial material into the depositional environment (Figure 7). Dinoflagellate cysts are rare or absent in samples. In surface sediments of modern intertidal marshes dinoflagellate and acritarch cysts are present in similarly low relative abundances as observed in Isachsen Formation (~0.2-5.3%, 0.2-1.4%, respectively; Medeanic, 2006). The occurrence of Sigmopollis spp. in some of the samples suggests that at times fresh and/or low salinity environments existed (de Vernal et al. 1989; Matthiessen et al. 2000; Mudie et al., 2010). 5.2.2 Bryophytes

Byrophytes (mosses, hornworts, and liverworts) are a minor group in Isachsen Formation samples (Figure 7) and represented almost entirely by Stereisporites antiquasporites. Mosses usually grow in moist soils typical of humid environments, but can also tolerate periods of drought (Abbink et al., 2004). Bryophyte spores are likely derived from scattered parent plants growing in humid, lowland environments, probably associated with riparian zones alongside rivers and marshes.

5.2.3 Lycopodiophytes

Lycopodiophytes are also a minor group in Isachsen Formation samples (Figure 7). Similar to bryophytes, lycopodiophyte spores can only be used tentatively in paleoecological interpretations due to broad ecological tolerances in modern plants. Most extant lycopsids occur in humid tropical regions, but can also be found in temperate and even polar areas where they often grow in moist settings, such as lowland, river, or tidally-influenced environments. Some Triassic lycopods appear to have been facultative coastal halophytes and inhabited marine shoreline environments in delta systems (Retallack, 1975). In the Mesozoic, lycopodiophytes were components of early successional communities dominated by filicopsids established around coastal or deltaic lowlands with poorly developed floodplains (Dejax et al., 2007; Stukins et al., 2013).

5.2.4 Filicopsids

Filicopsids are a common and diverse group in Isachsen Formation samples (Figure 7). Modern filicopsids flourish in humid and shady environments although a minority are tolerant of full sunlight or grow in open habitats (e.g., Gleicheniaceae and Schizaeceae (Anemia); Crane, 1987; Abbink et al., 2004). Ancient Schizaeceae may have grown in heathland communities (Dettmann and Clifford, 1992, and references therein) but most Early Cretaceous filicopsids are inferred to have grown in moist riparian habitats and as understory components in forests (van Konijnenburg-van Cittert, 2002; Abbink et al., 2004; Dejax et al., 2007; Schrank, 2010). Filicopsids are considered to be the predominant, early colonizing, stress-tolerant floras in the Mesozoic prior to the evolution of angiosperms and grasses (van Konijnenburg-van Cittert, 2002). Filicopsid spores range up to 70-75% in coal samples deposited in humid environments during the Jurassic-Cretaceous in the mid-southern hemisphere (Schrank, 2010, and references therein). Populations of ~20% in coaly mudstones of the Isachsen Formation are low relative to these more southern latitudes, reflecting the likely dryer and cooler conditions on Ellef Ringnes Island during the Early Cretaceous.

5.2.5 Pteridosperms

Vitreisporites pallidus, and possibly some of the undifferentiated bisaccate pollen preserved in Isachsen Formation, may be attributable to pteridosperm parent plants. Vitreisporites pallidus attains a mean relative abundance of <1% of the pollen and spore sum (Figure 7), indicating rare occurrences of parent plants that probably grew in deltaic flood plain to backswamp environments (van Konijnenburg-van Cittert, 1971; Abbink et al., 2004; Dejax et al., 2007; Stukins et al., 2013).

5.2.6 Pinophyta

Class Pinopsida, which includes the families Pinaceae, Sciadopityaceae, Cupressaceae (includes Taxodiaceae; ITIS, 2014), Taxaceae, Araucariaceae, and Cheirolepidaceae represents one of the most important pollen producers in the ecosystems that existed during deposition of Ischasen Formation on Ellef Ringnes Island (Figure 7). Parent plants of bisaccate pollen were likely upland conifers growing in well-drained habitats (Stukins et al., 2013). Cerebropollenites may have affinities with modern Tsuga (Balme, 1995; Shang and Zavada, 2003), which grows in temperate regions where it is restricted to moist, poorly drained slopes (Tesky, 1992). Cerebropollenites may also have affinities to Cupressaceae (Taxodiaceae) (van Konijnenburgvan Cittert and van der Burgh, 1989) or Sciadopitys (Dejax et al., 2007). Only one extant representative of the Family Sciadopityaceae exists (formerly assigned to the Family Taxodiacae; ITIS, 2014). This species (Sciadopitys verticillata (Thunb.) Siebold & Zucc.) is endemic to Japan where it is common in mixed conifer (e.g., Tsuga and Chamaecyparis) and angiosperm forest communities that include filicopsids, lycopodiophytes, and bryophytes growing in cool and moist environments. Sciadopitys plant macrofossils are found in abundance in Middle to Upper Jurassic marine deposits from the northern hemisphere with remains of

Gingko spp. and Pinus spp. (Manum, 1987; Vakhrameev, 1991), suggesting Sciadopitys coexisted with other gymnosperms in the Mesozoic. Cupressaceae-Taxaceae and allies represent the majority of the gymnosperm pollen in Isachsen Formation samples. Perinopollenites elatoides pollen is likely attributable to the Cupressaceae (Taxodiaceae) (van Konijnenburg-van Cittert, 1971; Harris, 1979; van Konijnenburg-van Cittert and van der Burgh, 1989; Balme, 1995). Taxodiacean conifers are interpreted to have been hygrophilous plants that thrived in warm to temperate wet lowland environments (Vakhrameev, 1991; Pelzer et al., 1992; Dejax et al., 2007). Plant macrofossils with affinities to Cupressaceae (Cupressinoxylon) are reported from Aptian-Albian strata of Axel Heiberg and Ellesmere islands in the Sverdrup Basin where mean annual temperature is inferred to have been between 3 and 10 °C (Harland et al., 2007). In modern environments Cupressaceae pollen is generally well dispersed and occurs with frequencies of 10-40% in late Holocene lacustrine and marine sediments where parent plants are dominant vegetation components (Gavin et al., 2005; Galloway et al., 2007, 2009, 2010). Relative abundances of ~34% of Cupressaceae-Taxaceae pollen in Isachsen Formation samples therefore suggests that parent plants were important, even co-dominant, in forests surrounding the central Sverdrup Basin and that climate was cool-temperate and moist.

Araucariacites pollen in Isachsen Formation is likely derived from parent plants belonging to Araucariaceae (van Konijnenburg-van Cittert, 1971; Boulter and Windle, 1993). Inaperturopollenites (also rare) pollen is also considered to have affinities to this family (Balme, 1995). Extant Araucariaceae are well adapted to drought and frequently grow in near shore environments (Abbink et al. 2004). In the Jurassic and Cretaceous, high proportions of Araucariacites pollen are indicative of warm climates with low seasonality (Reyre, 1980; Mohr,

1989) and fossil trees are often associated with near-coastal depositional environments in the geologic record (Harris, 1979; Barale and Flamand, 1982; Vakhrameev, 1991).

Classopollis pollen is thought to be derived from Cheirolepidiaceans, an extinct group of xerophytic and thermophilous plants (Francis, 1983, 1984; Watson, 1988; Vakhrameev, 1987, 1991). Cheriolepidaceans likely preferred upland arid habitats (van Konijnenburg-van Cittert and van der Burgh, 1996) but may have also thrived in coastal settings (Batten, 1975; Alvin, 1982; Watson, 1988; Vakhrameev, 1987, 1991; Heimhofer et al., 2008) where they may have formed mid to late successional communities (Stukins et al., 2013). Some Classopollis classoides pollen grains in Isachsen Formation samples are preserved in tetrads, a rare phenomenon in the fossil record (Figure 6; Stukins et al., 2013). This preservation suggests little transport of the grains by the fluvial system prior to deposition (Carvalho et al., 2006; Traverse, 2007; Stukins et al., 2013), suggesting that Cheirolepidaceans were components of coastal plain vegetation or, alternatively, had a capacity for flotation that protected them from abrasion (Stukins et al., 2013). Classopollis classoides pollen is common in samples from the lowermost Isachsen Formation in Section IS-01 but are otherwise rare (Figures 7, 10). Abundances of Classopollis classoides pollen near 10% in Deer Bay Formation marine mudstones preserved in the Hoodoo Dome H-37 oil and gas well are interpreted to represent seasonally arid conditions during the Late Jurassic to Early Cretaceous in the Canadian high Artic (Galloway et al., 2013). In this well, Classopollis classoides pollen declines to ~2 to 5% in the uppermost Deer Bay Formation in the Valanginian or Hauterivian and relative abundances remain low throughout the Isachsen Formation (Galloway et al., 2013). Very low abundances (~0-2%; with the exception of ~20% in the lowermost rocks of Section IS-01) of Classopollis classoides pollen in Isachsen Formation could be in response to increasing moisture in the Early Cretaceous that promoted expansion of mid to

late successional conifers such as Cupressaceae at the expense of Cheirolepidaceans and other drought tolerant taxa and/or be an artefact of facies control on the distribution of this pollen. 5.2.7 Cycadophyta

Most fossil pollen grains of the Ginkgoales and Cycadales belong to the genera Monosulcites and/or Cycadopites. Some pollen grains of the extinct Bennettitales may also belong to the Monosulcites/Cycadopites group (Abbink et al., 2004). Gingko biloba, the only extant Ginkgoales, is a deciduous tree that grows in temperate regions. In the Mesozoic, Ginkgoales also grew in temperate regions where they were a diverse group, although some representatives grew in subtropical regions (Abbink et al., 2004). Some Ginkgoales may have been components of lowland vegetation, occupying moist riparian zones (Stukins et al., 2013). Extant Cycadales grow in tropical regions and are adapted for drought, suggesting tolerance of dry summer seasons for Mesozoic ancestors. Similar to Ginkgoales, in the Mesozoic Cycadales were a diverse group that included extinct taxa (e.g., Nilsoniaceae) that grew in lowland, subtropical areas (Abbink et al., 2004 and references therein), but in general Cycadales are interpreted to have been mesoxerophilous plants and probably grew in well-drained upslope habitats (Dejax et al., 2007). Bennettitales may have been restricted to lowland deltaic habitats (van Konijnenburg-van Cittert and van der Burgh, 1989; Dejax et al., 2007) while others grew in drier climates in upland habitats (Watson and Sincock, 1992) or savannahs (Harris, 1973). Regardless of botanical affinity, parent plants of Cycadopites pollen likely grew in drier lowland environments or on upslope, well-drained sites (Abbink et al., 2004; Dejax et al., 2007; Stukins et al., 2013).

5.2.8 Magnoliopsida

The pollen of angiosperm plants are absent from Isachsen Formation samples.

Angiosperm pollen first appears in late Albian-aged strata of the central Sverdrup Basin: two species of tricolpate pollen are reported from uppermost beds of Christopher Formation on Ellef Ringnes and Amund Ringnes islands (Hopkins, 1974). Monocotyledenous pollen are reported from the Cenomanian Bastion Ridge and Strand Fiord formations on Axel Heiberg Island in eastern Sverdrup Basin (Núñez-Betelu et al., 1992), but are absent from underlying late Albian Hassel Formation on Ellesmere Island (Núñez-Betelu et al., 1992) and from Hassel Formation on Ellef Ringnes Island (Galloway et al., 2012). Albian and Cenomanian strata of the Sverdrup Basin contain low abundance and diversity of angiosperm pollen relative to angiosperm pollen occurrences in Alberta and the U.S.A. (Galloway et al., 2012). The late arrival of angiosperm pollen to the Sverdrup Basin and subsequent low diversity relative to more southern latitudes may be due to relatively cool northern continental climate experienced in the Canadian Arctic and/or barriers to angiosperm plant migration. See Galloway et al. (2012) for a discussion.

5.3. Paleoecological analysis

Palynomorph assemblages in Isachsen Formation are preserved in depositional settings, ranging from near shore marine deposits to terrestrial sedimentary environments. Differential transportation and sorting of pollen and spores types during transportation and deposition must be considered, even though the effect is likely negligible in marginal marine to terrestrial depositional settings where palynomorphs are less subject to hydrodynamic processes than in open marine systems (Tyson, 1995; Traverse, 2007; Abbink et al., 2004; Heimhofer et al., 2012). In marine deposits, palynomorph size, shape, density, and buoyancy can result in significant

biases (Tyson, 1995; Traverse, 2007; Heimhofer et al., 2012). This is particularly evident for bisaccate pollen grains that can be transported long distances in air and water (Heusser and Balsam, 1977). However, in sections IS-01 and DS-02 increases in bisaccate pollen occur in facies indicative of fluvial to floodplain settings of the Paterson Island Member (Appendix A).

Robust-walled and ornamented spores can also be differentially sorted relative to thinwalled, non-saccate palynomorphs; the former have been observed to be preferentially deposited proximal to river mouths (Heusser and Balsam, 1977; Tyson, 1995). Similar to changes in the proportion of bisaccate pollen, changes in the relative abundance of relatively robust walled (Ruffordiaspora and Cicatricosisporites spp.) vs. thin walled spores (e.g., Deltoidospora ssp.) do not seem to follow pattern associated with differential sorting. Classopollis pollen occurs mainly in the delta front and prodelta environments of Paterson Island Member in Section IS-01. This signature may be due to increased buoyancy and selective hydrodynamic transport of Classopollis pollen in this marginal marine setting (Stukins et al., 2013) but in general we consider the effects of hydrodynamic sorting to have had a minimal effect on palynomorph abundances and patterns (Heimhofer et al., 2012).

When palynological data are presented on a DCA biplot, taxa present in Isachsen Formation with a total relative abundance of greater than $\geq 0.5\%$ (n=17 taxa, n=22 samples) exhibit groups that can be interpreted as ecological relationships with reference to their botanical affinities (discussed above) (Figure 9). We interpret the main ecological gradients influencing Isachsen Formation floristic communities to have been moisture availability and disturbance on the basis of the botanical affinities of taxa (Stukins et al., 2013). We relate the horizontal (x-axis) plane of the DCA biplot to moisture availability. Moisture availability is a major driver of terrestrial ecosystem dynamics. Large coniferous plants, such as the Cheirolepidaceae and members of the Pinaceae, can tolerate arid conditions, whereas other plants (e.g., many bryophytes and filicopsids) are limited to wet conditions. We infer the vertical (y-axis) of the biplot to represent disturbance based on the botanical affinities of taxa and their position on the plot. A disturbance, such as periodic flooding, can be discrete events or a change in a factor influencing an ecosystem that eventually exceeds a critical threshold and results in a shift from one persistent condition to another (Sparks et al., 1990). Moisture availability and disturbance are main drivers of vegetation dynamics in modern coastal lowland settings (Bledsoe and Shear, 2000) and were also fundamental influences ecosystems during the Mesozoic (Abbink et al., 2004; Stukins et al., 2013).

5.3.1. Ecological Grouping A-Mixed conifer assemblage

This ecological grouping comprises four pollen taxa with coniferous affinities. Perinopollenites elatoides may have affinities to the Cupressaceae-Taxaceae and may be derived from parent plants growing in poorly drained floodplains or moist habitats in upland areas. Inaperturopollenites pollen may have affinities to Araucariaceae and may be derived from lowland vegetation growing in warm environments subjected to drought (Harris, 1979; Reyre, 1980; Barale and Flamand, 1982; Mohr, 1989; Vakhrameev, 1991; Abbink et al., 2004). Assuming Entylissa pollen is derived from parent plants with affinities to Cycadophyta, this pollen is likely derived vegetation growing in drier, upslope environments (Dejax et al., 2007). Bisaccate pollen is the predominant pollen type in this ecological grouping. Bisaccate pollen is commonly inferred to have originated from Pinaceae parent plants with a mesoxerophilous ecology growing in upland and relatively arid or well-drained environments (Barrón et al., 2006; Dejax et al., 2007). Macrofossil evidence from the Early Cretaceous of the Canadian Arctic suggests that Pinaceae were common in high latitude forests, with constituents that may have been similar to modern Pinus, Picea, Larix, and Pseudotsuga (Harland et al., 2007). A component of the bisaccate pollen may therefore have been produced by parent plants with broad ecologies similar to extant Pinus and Picea. Modern Pinus species can grow on soils of fluvial origin and are early pioneers of disturbed habitats but can also form edaphic climax. Modern members of Picea are tolerant of brackish water, can be a pioneer or a late successional tree, and can grow on alluvial soils but prefer moist but well-drained substrates (Griffith, 1992; Carey, 1993). Pteridosperm parent plants that likely thrived in lowlands as a constituent in coastal or deltaic climax communities during the Mesozoic also produce bisaccate pollen (e.g., Alisporites Daugherty 1941) (Abbink et al., 2004; Stukins et al., 2013). Ecological grouping A therefore likely contains pollen from mature upland coniferous communities that grew in well-drained substrate with infrequent disturbance as well as pollen derived from lowland plants adapted to more dynamic environments. Plotting in overlapping space as Ecological grouping A are samples from from facies indicative of deltaplain, floodplain, fluvial, and shoreline settings and cluster in three of the four Sample Clusters (SC) identified using combined Q- and R-mode cluster analysis (Figures 5, 9). No clear facies control is observed. Pollen from upland plants would have been transported to lowland environments as pollen rain and in rivers. 5.3.2. Ecological Grouping B – Lowland conifer-filicopsid assemblage

Ecological grouping B is characterized by spores from filicopsids and bryophytes, namely Deltoidospora hallei, Glecheniidites senonicus, Osmundacidites wellmannii, and Stereisporites antiquasporites, and pollen from conifers, including Cupressaceae-Taxaceae and Araucariacites australis. Filicopsids were the predominant early colonizers of disturbed habitats in the Mesozoic prior to the addition of angiosperms and grasses to high latitude ecosystems (van Konijnenburg-van Cittert, 2002). Stereisporites antiquasporites spores may be derived from parent plants occupying lowland marsh habitats. Cupressaceae-Taxaceae pollen is likely derived from plants occupying poorly drained slope of upland forest environments and/or moist coastal forests (Stukins et al., 2013). Cycadopites pollen also occurs in this ecological grouping and may represent plants growing in riparian zones (Stukins et al., 2013) while representatives of Araucariaceae were likely derived from drier lowland habitats. Together, the pollen and spores that compose Ecological grouping B suggest a parent community growing in a mosaic of wet and more arid lowland environments subjected to varying degrees of disturbance.

5.3.3. Ecological Grouping C – Lowland conifer assemblage

Ecological grouping C is composed solely of Classopollis classoides pollen. This grouping may represent the distinct ecology of large xerophytic Cheirolepidaceans (Francis, 1983) and a mature community growing in a dry floodplain environment (Stukins et al., 2013). Ecological grouping C is aligned with SC-4 in the DCA biplot, which includes only two samples from facies indicative of delta front to prodelta settings of the Paterson Island Member of Section IS-01 (Figure 5). This ecological grouping may therefore be a biogeochronological signature whereby the high relative abundance of Classopollis classoides pollen in samples IS-322 and IS-482 represents the last point in the stratigraphic succession of abundant Cheirolepidaceans prior to their decline in the late Valanginian/early Hauterivian on Ellef Ringnes Island due to climate change (Galloway et al., 2013) and/or facies control, including increased buoyancy and selective hydrodynamic transport of Classopollis pollen in this marginal marine setting (Stukins et al., 2013).

5.4. Stratigraphic palynology and paleoclimate

Northward movement of Sverdrup Basin from about 45-60 °N during the Late Triassic-Early Jurassic to 60 to >70 °N in the Middle Jurassic and Early Cretaceous led to progressively cooler conditions in the Canadian High Arctic (Wynne et al., 1988; Embry, 1991) although Early Cretaceous climate in the northern hemisphere was still warmer than today (Vakhrameev, 1991; Herman and Spicer, 1996; Littler et al., 2011). Nearest living relative analysis of coniferous wood from the Canadian Arctic suggests that by the Aptian to Albian, climate was cooltemperate (between 3 and 10 °C mean annual temperature; Harland et al., 2007). The consistently strong signal of pollen attributed to Pinaceae, indicative of temperate conditions, and the subordinate amount of pollen attributed to parent plants indicative of relatively warm and dry environments (e.g., Classopollis, Cycadopites, Araucariacites, and possibly also Inaperturopollenites, collectively comprising <10% of the pollen sum) suggest that overall cool and humid conditions prevailed during deposition of the Isachsen Formation on Ellef Ringnes Island.

Small but important stratigraphic changes in the proportions of pollen and spore types composing the three ecological groupings defined by DCA suggest that minor shifts in climate punctuated the overall cool and humid conditions of the late Valanginian-early Aptian of the Canadian Arctic (Appendix A). In the upper Paterson Island Member in Section DS-02 the relative abundance of the conifer-filicopsid assemblage (Ecological grouping B) declines while the proportion of the mixed conifer assemblage (Ecological grouping A) increases (Zone DS-02-B; Figure 10). We interpret the age of these rocks to be Hauterivian based on ages of bounding strata. In Section DS-02 (Zone DS-020B) this change is represented by two samples but the proportion of pollen comprising Ecological grouping A also increases in abundance throughout the more intensely sampled Paterson Island Member in Section IS-01 (Zone IS-01-B; Appendix A), suggesting that this is a real and sustained palynological change.

Drier and possibly warmer climate conditions could have promoted the development and expansion of mature coniferous forests during the Hauterivian in the Sverdrup Basin. More arid climate conditions would be expected to develop under warmer conditions that increased evaporation and evapotranspiration and promoted plants that remained competitive, or thrived, in well-drained or water-limited environments, such as bisaccate pollen producers (Pinus, Picea), at the expense of plants with higher moisture requirements, such as members of lowland coniferfilicopsid bryophyte communities. Harland et al. (2007) report a comparative study of coniferous plant megafossils of the Canadian Arctic and Spitsbergen. They found that morphogenera with affinities to Taxodiaceae (Taxodium?) and Araucariaceae were present only in the Spitsbergen material and infer the greater diversity to reflect warmer conditions in Spitsbergen relative to the Canadian Arctic. In Isachsen Fm samples Araucariacites australis pollen is associated with Ecological group B, the lowland conifer-filicopsid assemblage although this pollen also increases in upper strata of the Paterson Island Member in sections DS-02 (zone DS-02B) and IS-01 (zone IS-01-B), concomitant with the increase in the relative proportion of Ecological grouping A, the mixed conifer assemblage (Appendix A).

The presence of pollen with affinities to Cupressaceae (Taxodiaceae) in Ecological grouping B, along with a diversity of filicopsid spores, suggest that cool-temperate and moist lowland environments were more expansive during the late Valanginian and Barremian to early Aptian than during the more arid and/or warmer conditions we infer to have promoted coniferous communities (Ecological grouping A) during the Hauterivian. Disturbance is also an important influence on vegetation communities and large-scale fluvial systems that deposited the Isachsen Formation would have been an important mechanism of landscape change (Tullius et al., 2014). More vigourous fluvial systems and associated more frequent and intense substrate disturbances would be expected to develop under the wetter and cooler climate conditions we infer for the late Valanginian and Barremian to Aptian intervals. This disturbance would have promoted the expansion of parent plants in the lowland conifer-filicopsid community that were well adapted to environmental disturbance. On Ellef Ringnes Island, a decline in Cupressaceae-Taxaceae pollen and increase in bisaccate pollen represented by two samples in the middle of the Paterson Island Member preserved in the Hoodoo Dome H-37 oil and gas well may be a manifestation of the Hautervian arid and warm event proposed here.

Significant perturbations to global climate occurred during Valanginian to Aptian time when numerous "cool" excursions punctuated otherwise warm Early Cretaceous conditions in the northern hemisphere (McArthur et al., 2004; Gröcke et al., 2005; Kessels et al., 2006). These temperature excursions may have been expressed as glacial episodes in high northern latitudes during the Valanginian (Kemper, 1987; Price and Mutterlose, 2004; Kessels et al., 2006; Price and Nunn, 2010). A subsequent period of warming in the northern hemisphere during the Hauterivian terminated late Valanginian-early Hauterivian icehouse conditions (Pucéat et al., 2003; McArthur et al., 2004; Gröcke et al., 2005; Kessels et al., 2006; Price and Nunn, 2010). A return to cool temperatures occurred in the mid-Barremian (Pucéat et al., 2003; McArthur et al., 2004) and persisted through the Aptian-early Albian interval in high-latitude regions (Harland et al., 2007). These Early Cretaceous climate events are manifested in the Canadian Arctic as changes in terrestrial vegetation whereby the Hautervian warm episode promoted expansion of upland coniferous communities.

6.0 Conclusions

We use a multivariate statistical approach to palynology to provide insight on vegetation dynamics and paleoclimate of the Early Cretaceous. Relatively cool and moist conditions during the late Valanginian and early Aptian promoted disturbance-adapted plants that formed a coniferfilicopsid community in lowland environments. More arid, warm, and stable environmental conditions during the Hauterivian may have promoted expansion of mature coniferous communities. Our paleoclimate inferences for this Canadian high latitude region are consistent with reconstructions from lower latitudes, suggesting at least hemispherical expression of Valanginian cooling and a subsequent warming event in the Hauterivian that influenced polar vegetation.

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Figure captions

Figure 1: A) Geologic map showing location of Sverdrup Basin and Ellef Ringnes Island (after Dewing et al., 2007); B) Jurassic-Cretaceous stratigraphy of Sverdrup Basin (after Embry 1991; Dewing and Embry 2007; Obermajer et al. 2007; Embry and Beauchamp, 2008)

Figure 2: Simplified geologic map of Ellef Ringnes Island (geologic contacts after Evenchick and Embry, 2012a, b). Middle and Early Jurassic units are undivided and no divisions are shown for the Upper Cretaceous Kanguk Fm. Black lines represent locations of measured sections (see Figure 4 for detail). Location of wells with gamma logs shown in Figure 3 also shown and location of Hoodoo Dome well H-37 shown in red (Galloway et al., 2013) Figure 3: Lithostratigraphic cross-section of well and gamma ray logs showing Lower Cretaceous strata of Deer Bay Formation to Upper Cretaceous strata of Christopher Formation from northwest to southeast across Sverdrup Basin. Datum is the top of the Rondon Member within the Isachsen Formation. Most of the Isachsen Formation is laterally continuous across the basin, including over paleotopographic highs such as salt diapirs. Horizontal dimension is not to scale; distances are indicated. Location of wells shown in Figure 2

Figure 4: Map showing locations of samples analyzed for palynology overlain on the map of Evenchick and Embry (2012a). A- Isachsen Central (IS-01) section; B-Dumbbells West (DS-03) Section and Dumbbells East (DS-02) Section. A location for the Rondon member was tentatively identified by Evenchick and Embry (2012a). Based on analysis of well logs and stratigraphy we interpret the Rondon Member to be at DB680 (denoted with *)

Figure 5: Lithostratigraphic sections measured from Ellef Ringnes Island (locations shown in Figures 2, 4) (After Tullius et al. (2014)). Sample clusters defined by combined Q- and Rmode cluster analysis (Figure 8) and discussed in text are shown on measured sections

Figure 6: Photomicrographs of pollen and spores captured using differential interference contrast and oil immersion preserved in Isachsen Formation samples from exposures on Ellef Ringnes Island. Sample number, GSC curation number (C-number), GSC Calgary Palynology Laboratory preparation number (P-number), GSC specimen number (pending), microscope (Olympus BX61) coordinate (µm), and England Finder coordinates 1 - Cupressaceae-Taxaceae, IS-946, C-549939, P5244-23B, GSC specimen number 136516, 43872.3x76346.9, M26/1 2 - Perinopollenites elatoides, IS-02, C-549937, P5244-20D, GSC Specimen Number 136517, 39735.9x76346.9, M21/2 3 – Cerebropollenites mesozoicus, DS3-701, C-549932, P-5244-15B, GSC specimen number 136518, 34124.8x73814.3, J16/1 4 – Undifferentiated bisaccate pollen, DS3-701 C-549932, P5244-15B, GSC specimen number 136519, 47739.3x76346.9, M30/1 5 - Classopollis classoides tetrad, IS-02, C-549937, P5244-20D, GSC specimen number 136520, 45079.1x76346.9, M27/2 6 - Classopollis classoides, IS-02, C-549937, P5244-20D, GSC specimen number 136521, 43040.8x72335.1, G25/3 7 – Entylissa, DS3-389.5, C-549930, P5244-13A, GSC specimen number 136522, 60148.9x76346.9, M43/1 8 – Entylissa, DS3-389.5, C-549930, P5244-13A, GSC specimen number 136523, 60595.2x76346.9, M43/2 9 - Cycadopites, DS3-389.5, C-549930, P5244-13A, GSC specimen number 136524, 60646.8x76346.9, M43/2 10 – Cycadopites, DS3-389.5, C-549930, P5244 13A, GSC specimen number 136525, 54661.5x76346.9, M37/1

11 – Microreticulatisporites uniforms, DS3-701, C-549932, P5244-15B, GSC specimen number 136526, 44179.3x76346.9, M26/2

12 – Sigmopollis, DS3-389.5, C-549930, P5244 13A, GSC specimen number 136527, 47201.6x73764, J29/2

13 – Cyathidites australis, IS-322, C-549937, P-5244-20D, GSC specimen number 136528, 28021.5x76346.9, M9/2

14 – Ruffordiaspora australiensis, IS-02, C-549937, P5244-20D, GSC specimen number 136529, 41637.3x74802.6, K24/1

15 –Cyathidites minor, DS3-389.5, C-549940, P-5244-23B, GSC specimen number 136530, 37956.9x75638.3, L20/1

16 – Gleicheniidites senonicus, IS-946, C-549939, P-5244-23B, GSC specimen number 136531, 45625.8x75862.5, L28/4

Figure 7: A- Pie chart showing the relative abundances of pollen and spores from obligately terrestrial plants in each Class identified in samples collected from the Isachsen Formation (all sections), Ellef Ringnes Island. The relative abundance of non-pollen palynomorphs is calculated based on the terrestrial pollen and spore sum. B - Pie chart showing the relative abundance of taxa identified to the lowest possible taxonomic classification of members of the Class Pinopsida, the most abundantly represented plant group

Figure 8A: Combined Q- and R-mode cluster analysis of the relative abundance of pollen and spores from obligately terrestrial plants identified in Isachsen Formation, Ellef Ringnes Island. Four Sample Clusters (1, 2, 3, and 4) are defined based on palynomorph content and delineated by dashed line. Colour coding of Sample Clusters used to show stratigraphic position and facies of samples belonging to each cluster in Figure 5

Figure 8B: Pie charts showing the relative proportion of palynomorph types in each Sample Cluster. Other - <10% sum of means; C-T - Cupressaceae-Taxaceae

Figure 9: Detrended correspondence analysis biplot of pollen and spores occurring with a mean relative abundance of ≥0.5% (n=17) in Isachsen Formation samples from all sections (n=22) (Eigenvalue DCA1=0.209, DCA2=0.068). Three ecological groupings (A, B, and C) of taxa are delineated by solid lines. Sample Clusters 1 through 4 defined by Combined Q- and R-mode cluster analysis are delineated on the biplot and colour coded to be consistent with Figures 5 and 8. SC-1 Bisaccate-Cycadopsida/Gingkopsida assemblage; SC-2 Cupressaceae-Taxaceae-Bisaccate-Filicopsida assemblage; SC-3 Cupressaceae-Taxaceae assemblage; SC-4 Classopollis classoides assemblage

Appendix A

Stratigraphic diagrams of the relative abundances of palynomorphs preserved in three measured sections of Isachsen Formation (A – Section IS-01; B – Section DS-02; C – Section DS-03). Changes in cumulative relative abundance of pollen and spores of Ecological groupings A, B, and C as defined by DCA (Figure 9) also shown. DCA axis 1 (moisture availability) and axis 2 (disturbance) sample scores plotted stratigraphically. Diagrams produced using TILIA (Grimm, 1993-2001). Stratigraphically constrained incremental sum of squares cluster analysis (CONISS; Grimm, 1987) used with visual inspection to delineate informal palynomorph stratigraphic zones for each section

Tables

Table 1: Background information on age determination of Isachsen Formation andbounding strata and summary of paleontological data for the Lower Cretaceous of theSverdrup Basin

| Unit | Age | Based on | Reference(s) |
|---------------|--------------------------|--|------------------------------|
| | determination | | |
| | | Macrofossils, foraminifera, and palynology from various localities | Jeletzky, 1970a, b, 1973, |
| | | | 1974a, b; Hopkins, 1974; |
| | | | Wall, 1983; Nøhr-Hansen |
| | Aptian (126- | | and McIntyre, 1998; Wall in |
| Christopher | 113 Ma ¹) to | | Harrison and Brent, 2005; |
| Formation | Albian (113- | | Davies and Wall in Harrison |
| | 100 Ma) | | and Brent, 2005; Embry and |
| | | | Beauchamp, 2008; Haggart, |
| | | | 2007; Poulton, 2010; |
| | | | Schröder-Adams et al., 2014 |
| | | No age-diagnostic fossils | |
| Isachsen | Barremian | identified but bracketed by | |
| Formation, | (131-126 Ma) | a Barremian age below | Embry, 1985a |
| Walker Island | to Aptian (126- | (Rondon Member) and an | |
| Member | 113 Ma) | Aptian age above | |
| | | (Christopher Formation) | |
| Isachsen | Barremian | Dinoflagellate cysts, Axel | Costa, 1984; McIntyre, 1984; |
| | | | |

| Formation, | (131-126 Ma) | Heiberg and Melville | McIntyre pers comm. 1984 in |
|--------------------|---------------------------|--|---|
| Rondon Meml | ber | islands | Embry, 1985a, 1991; Nøhr- |
| | | | Hansen and McIntyre, 1998 |
| Isachsen | Valanginian | | |
| Formation, | (139-134 Ma) | Pelecypods, Amund | Rollwill 1082 |
| Paterson Islar | nd to Barremian | Ringnes Island | Daikwiii, 1903 |
| Member, | (131-126 Ma) | | |
| | | Palynology, Banks, Prince | |
| | | Patrick, Melville islands; | Jeletzky, 1970a, b, 1973, |
| Linauhdividad | Valanginian | Macrofossils, various | 1975, 1976, 1984; Hopkins, |
| | (139-134 Ma) | localities; Pelecypods, | 1971; Jeletzky in Dorenkamp |
| Farmation | to Aptian (126- | Mould Bay Formation that | et al., 1976; Plauchut and |
| Formation | 113 Ma) | underlies Isachsen | Jutard, 1976; Dorenkamp et |
| | | Formation on Mackenzie | al., 1976; |
| | | King Island; | |
| | | Dinoflagellate cysts 1359- | |
| | | 2012 m, 4460-6600 ft in | |
| | | Hoodoo Dome H-37; | Jeletzky, 1953a, b, 1970a, b, 1974a, b, 1977; Brideaux |
| | Titherien | Palynology and | |
| | | foraminifera, interfingering | |
| Deer Bay | (152-145 Ma) | Awingak sandstones, Prince Patrick Island; Macrofossils, Ellef Ringnes | |
| Formation | | | 1983; Davies, 1983; Embry, |
| | | | |
| | (139-134 Ma) | and Amund Ringnes | Poulton, 2009 |
| | | islands; Foraminifera, | |
| | | eastern Axel Heiberg | |
| | | Island | |
| 1 – Age ranges for | stages based on Gradstein | et al. (2012) | |
Table 2: Samples analyzed for palynology from Isachsen Central Section, Ellef Ringnes

Island^a

| Section ^a | Lithostratigraphy | Sample | Location in | C number ^b | P-number ^c | |
|----------------------|---------------------|----------------------|-------------|-----------------------|-----------------------|--|
| | | name | section (m) | C-number | r-number | |
| | Paterson Island Mbr | IS-322 ^e | 322 | C-549937 | P-5244-20B | |
| | | IS-482 | 482 | C-549938 | P-5244-22B | |
| | | IS-946 | 946 | C-549939 | P-5244-23B | |
| Isachson Contral | | IS-1015 | 1015 | C-549940 | P-5244-24B | |
| | | IS-1030 | 1030 | C-549941 | P-5244-24B | |
| (13-01) | | IS-1063 | 1063 | C-549943 | P-5244-26B | |
| | | IS-1071 | 1071 | C-549944 | P-5244-27B | |
| | | IS-1430 ^e | 1430 | C-549946 | P-5244-28B | |
| | | IS-1450 ^e | 1450 | C-549945 | P-5244-29B | |
| | Paterson Island Mbr | DB-175 | 175 | C-549918 | P-5244-1B | |
| | | DB-347 | 346 | C-549919 | P-5244-2B | |
| | | DB-382 | 382 | C-549920 | P-5244-3B | |
| Dumbhells East | | DB-409 | 409 | C-549921 | P-5244-4B | |
| (DS-02) | | DB-638 | 638 | C-549922 | P-5244-5B | |
| | Rondon Mbr | DB-680 | 680 | C-549923 | P-5244-6B | |
| | Walker Island Mbr | DB-801 | 801 | C-549926 | P-5244-9B | |
| | | DB-818 | 818 | C-549924 | P-5244-7A | |
| | | DB-985 | 985 | C-549928 | P-5244-11B | |
| Dumbbells West | Undifferentiated | DS3-23 | 23 | C-549929 | P-5244-12B | |
| | | DS3-389.5 | 389.5 | C-549930 | P-5244-13A | |
| (DS-03) | | DS3-517 | 517 | C-549931 | P-5244-14B | |
| | | DS3-701 ^e | 701 | C-549932 | P-5244-15B | |

^aDetailed stratigraphic sections shown in Figure 4 and in Tullius et al. (2014); ^bC-Number – GSC Calgary Curation Number;

^cP-Number – GSC Calgary Palynology Laboratory Preparation Number; ^epreliminary palynology of sample presented in Tullius et al. (2014)

Table 3: Biological nomenclature of spore and pollen taxa identified in Isachsen Formation

| Division | Class | Order | Family | Genus and species | Authority ^a |
|--------------|-----------------------------|--------------------------|---------------------------------|--------------------------------------|---|
| | | | Pinaceae | Undifferentiated bisaccate pollen | |
| | | Pinales | Pinaceae | Laricoidites magnus | (Potonié 1931) Potonié, Thor |
| | | | Pinaceae | Cerebropollenites mesozoicus | (Couper 1958) Nilsson 1958 |
| | | | Tindocac | | |
| | | | Taxodiaceae, Sciadopityaceae | Sciadopityspollenites | Raatz 1937 resp. Thiergart 1 |
| | | | | | ex Potonie 1958 |
| | Pinopsida | | incortao sodis | Inaporturopollopitos | Pflug and Thomson in Thoms |
| | | | | | and Pflug 1953 |
| | | | Araucariaceae | Araucanaciles australis | COOKSON 1947 |
| | | Cupressales | Cupressaceae/ Taxaceae | Undifferentiated | |
| | | | | | |
| | | | Cupressaceae (Taxodiaceae) | Perinopollenites elatoides | Couper 1958 |
| | | | . , | | |
| | | incertae sedis | Cheirolepidaceae | Classopollis classoides | (Pflug 1953) Pocock and Jansonius 1961 |
| | Pteridospermonsida | Cavtoniales | Cavtoniaceae | Vitreisporites pallidus | (Reissinger 1950) Nilsson 19 |
| | | Cupadolas/Cister | incertae sedis | Entvlissa | Naumova 1939 ex Ishchenko |
| | Cycadopsida/ Gingkopsida | Cycadales/Ginkg oales | Cvcadales | Cvcadopites | Wodehouse 1933 |
| | Gnetopsida | incertae sedis | | Eucommidites troedsonii | (Erdtman 1948) Potonié 195 |
| | | | | Cvathidites australis | Couper 1953 |
| | | Polypodiales | Cyatheaceae/ | Cvathidites minor | Couper 1953 |
| | | | Dicksoniaceae | Concavissimisporites parkinii | Pocock 1963 |
| | | | Matoniaceae/ | Matonisporites | B A Couper 1958 |
| Tracheophyta | | | Dicksoniaceae | Matomoponies | 11.A. Oouper 1990 |
| | | Gleicheniales | Gleicheniaceae | Gleicheniidites senonicus | Ross 1949 |
| | | | | Gleicheniidites apilobatus | Brenner 1963 |
| | | | Dipteridaceae | Converrucosisporites | Potonié and Kremp 1954 |
| | | Schizaeales | Schizaeaceae | Ruffordiaspora australiensis | Clifford 1992 |
| | | | | Ruffordiaspora ludbrookiae | (Dettmann 1963) Dettmann Clifford 1992 |
| | | | | Cicatricosisporites cf. C. | (Bolkhovitina) Dettmann 196 |
| | Filicopsida | | | Cicatricosisporites | Potonié and Gelletich 1933 |
| | | | | indetermined | Maliouking 1040 |
| | | | | Klukisporites | Couper 1958 |
| | | | | Klukisporites | |
| | | | | pseudoreticulatus | Couper 1958 |
| | | | | perplexus | Singh 1971 |
| | | | | Trilobosporites sp. | |
| | | | | Concavissimisporites sp. | |
| | | Osmundales | Osmundaceae | Baculatisporites comaumensis | (Cookson 1953) Potonié 195 |
| | | | | Osmundacidites wellmannii | Couper 1953 |
| | | | | Todisporites major | Couper 1958 |
| | | | | Todisporites minor | Couper 1958 |
| | | | | Biretisporites potoniaei | Delcourt and Sprumont 1955 |
| | | Polypodiales | Polypodiaceae/ Blechinaceae | Laevigatosporites ovatus | Wilson & Webster 1946 |
| | | | | Deltoidospora hallei | Miner 1935 |
| | | incertae sedis | | Deltoidospora psilostoma | Rouse 1959 |
| | | | | , | |
| | | incertae sedis | | Deltoidospora psilostoma | Rouse 1959 |

| | | | | Granulationaritaa | A C Ibrohim 1022 |
|--|------------------------------|----------------|-----------------|--------------------------------------|--|
| | | | | Granulatisporites | A.C. Ibranim 1933 |
| | | | | Dictyophyllidites harrisii | Couper 1958 |
| | | | | Pilosisporites verus | Archangelsky and Lloren |
| | | | | Undulatisporites undulapolus | Brenner 1963 |
| | | | | Foveosporites subtriangularis | Brenner 1963 |
| | | | | Plicifera dicarpoides | (Grigorjeva 1961) Ravna 1995 |
| | | | | Gemmatriletes clavatus | Brenner 1963 |
| | | | | Microreticulatisporites uniformis | Singh 1964 |
| | | | | Retitriletes austroclavidites | (Cookson 1953) Döring, Mai and Schulz in Krutzs |
| | Lycopodiopoido | Lycopodialaa | Lyconodiacaca | Lycopodiumsporites expansus | Singh 1971 |
| | Lycopodiopsida | Lycopoulaies | Lycopodiaceae | Lycopodiumsporites indetermined | Delcourt and Sprumont |
| | | | | Leptolepidites verrucatus | Couper 1953 |
| | Isoetopsida | Selaginellales | Selaginellaceae | Neoraistrickia truncata | (Cookson 1953) Potonie |
| | incertae sedis | | | Acanthotriletes varispinosus | Pocock, 1962 |
| | Sphagnopsida | Sphagnales | Sphagnaceae | Stereisporites antiquasporites | (Wilson and Webster 19 Detmann 1963 |
| Bryophyta | Hepaticeae | incertae sedis | | Aequitriradites spinulosus | (Cookson & Dettmann 1 Cookson & Dettmann 19 |
| J - [-] | la contra condia | | | Polycingulatisporites radiatus | Zhang & Grant-Mackie 1 |
| | Incertae sedis | | | Cingulatisporites distaverrucosus | Brenner 1963 |
| incertae sedis | | | | Matthesisporites tumulosus | Döring 1964 |
| Dinophyta | Dinophyceae | incertae sedis | | Dinocysts indetermined | |
| Dinophyta | Dinophyceae | incertae sedis | | Veryhacium | J. Deunff 1954 |
| Chlorophyta | Chlorophyceae | Chlorococcales | Hydrodictyaceae | Pediastrum | Meyen 1829 |
| Chlorophyta or Chomotriletes is incertae sedis (affinity Algal) | Charophyceae | Zygnematales | Zygnemataceae? | Chomotriletes | Naumova 1939 ex Naum |
| incertae sedis | | | | Algae indetermined | |
| Group Acritarcha | Subgroup Acanthomorphitae | incertae sedis | | Micrhystridium | Deflandre 1937 emend. 1970 |
| Group Acritarcha | incertae sedis | | | Pterospermopsis | W. Wetzel 1952 |
| | | | | | |

^aTaxonomic authorities not included in the references



Diapirs, piercement
structures



Figure 3 Galloway et al.



500m

Figure 4A Galloway et al.



Figure 4B Galloway et al.





Figure 6 Galloway et al.



10 µm

Figure 7 Galloway et al.



Pinopsida

All palynomorphs

Relative abundance of pollen and spore sum (n=22 samples) *Relative abundance non-pollen palynomorphs not included in main pollen and spore sum Sigmopollis not included because semi-quantitative data Does not add to 100 due to rounding





Cycadopites Laricoidites magnus Cupressaceae-Taxaceae Todisporites major Retitriletes austroclavidites Entylissa Entylissa Vitreisporites pallidus Gleicheniidites senonicus Deltoidospora hallei Osmundacidites wellmannii Stereisporites antiquasporites Biretisporites potoniaei Dictyophyllidites harrisii Indetermined pollen and spores Araucariacites australis Trilobosporites sp. Cvathidites minor Cyathidites minor Concavissimisporites sp. Cicatricosisporites Plicifera dicarpoides Granulatisporites Lycopodiumsporite expansus Perinopollenites elatoides Lycopodiumsporites Acanthotriletes varispinosus Acanthotriletes Varispinosus Inaperturopollenites Laevigatosporites ovatus Ruffordiaspora australiensis Neoraistrickia truncata Distaltriangulisporites perplexus Matthesisporites tumulosus Todisporites minor Cingulatisporites distaverrucosus Sciadopityspollenites Eucommidites troedsonii Eucommidites troedsonii Klukisporites pseudoreticulatus Klukisporites Cyathidites australis Baculatisporites comaumensis Cerebropollenites mesozoicus Converrucosisporites Pliratella Plicatella Cicatricosisporites pseudotripartitus Germatriletes clavatus Germatriletes clavatus Classopollis classoides Foveosporites subtriangularis Undulatisporites undulapolus Deltoidospora psilostoma Leptolepidites verrucatus Pilosisporites verus Microreticulatisporites uniformis Concavissimisporites parkinii Matonisporites Gleicheniidites anilobatus Gleicheniidites apilobatus Ruffordiaspora ludbrookiae Polycingulatisporites radiatus Aequitriradites spinulosus



Figure 8B Galloway et al.



Assemblage

Assemblage



Supplementary Material Appendix A A



Supplementary Material Appendix A B

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Supplementary Material Appendix A C

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