Palaeoecology of Late Cretaceous polar vegetation preserved in the Hansen Point Volcanics, NW Ellesmere Island, Canada

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Abstract

Mesozoic polar forests represent an extinct biome subject to a polar light regime and elevated atmospheric CO2 levels. In this paper, new Cretaceous fossil plant assemblages are reported from NW Ellesmere Island, Canada at a paleolatitude of 75°N. These occur in a Campanian–Maastrichtian-aged interval of the Hansen Point Volcanics, a unit interpreted as a coastal plain/peat mire complex within an active volcanic setting. Studies of palynomorphs, sterile and fertile foliage, and wood indicate that mire environments were dominated by amber-producing taxodiaceous conifers with other conifers, ginkgos, cycads, angiosperms, ferns, lycopsids, and bryophytes occurring in subordinate numbers. Leaf physiognomic studies imply that most vegetation was deciduous. Occurrence of traumatic rings in the woods, together with a high year-to-year variability in ring width, indicates disturbed growing conditions possibly linked to a combination of frosts, volcanic eruptions, and flooding. Abundant charcoal remains indicate that an additional important disturbance process was wildfire. Results of this study compare closely with those from coeval circum-Arctic fossil sites, and augment our knowledge of the community-scale ecology of the Cretaceous polar biome.

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1. Introduction

During the Cretaceous greenhouse climate phase, conifer/fern-dominated forests grew well inside the polar circle at latitudes as high as 82°N and 75°S (Francis and Frakes, 1993; Spicer et al., 1992, 2002; Falcon-Lang et al., 2001; Falcon-Lang and Cantrill, 2002; Spicer, 2003). These forests must have been adapted to an unusual combination of two environmental parameters not experienced by any extant vegetation: a polar light regime characterized by dark winters and light summers (Read and Francis, 1992) and elevated atmospheric CO2 levels (Berner, 1994;
Nordt et al., 2002). As such Cretaceous polar forests represent an entirely extinct vegetation biome (Spicer and Chapman, 1990).

Interest in the response of modern high-latitude forests to rising CO₂ levels (Beerling, 1999; LaDeau and Clark, 2001) has recently reignited Cretaceous polar forest research. This is because Cretaceous polar forests are believed to represent an extreme end-member of forest adaptation to greenhouse conditions, which could provide an important long-term context for modern global change studies (Beerling, 2000). One exciting consequence of this has been the application to fossil studies of many approaches originally developed to analyze future global change. For example, sophisticated plant physiology experiments and computer climate-vegetation models are now routinely used to analyze aspects of the physiology, ecology, and productivity of Cretaceous polar forest biome (e.g. Beerling et al., 1999, Beerling, 2000; Beerling and Osborne, 2002; Osborne and Beerling, 2002; Royer et al., 2003). As one global change biologist put it, parodying Sir Charles Lyell’s uniformitarian maxim, the future has become the key to the past for palaeobotany (Beerling, 1998).

While such experimental and model results are extremely valuable for drawing generalizations and developing hypotheses, they need to be tested and refined against geological field data. The purpose of this paper is to improve data resolution for the Cretaceous polar biome by reporting new Cretaceous high-latitude fossil plant assemblages located near Emma Fiord, NW Ellesmere Island, Canada (approximate palaeolatitude 75°N, Fig. 1; Wynne et al., 1988). We describe the palaeoenvironmental context, floral composition, taphonomy, and tree growth structures of our fossil assemblages thereby augmenting knowledge of the community-scale ecology of the Cretaceous polar forest biome, and permitting further evaluation of experimental and model results.

2. Geological setting

The fossil plant assemblages were collected on an unnamed peninsula between Emma Fiord and Audhild Bay, NW Ellesmere Island (81°28’ N, 90°02’ W; Fig. 2). They occur in the late Cenomanian–Maastrichtian Hansen Point Volcanics (HPV), an informally named and incompletely mapped unit (Thorsteinsson and Trettin, 1972; Trettin and Parrish, 1987; Embry and Osadetz, 1988), which unconformably overlies the Carboniferous Nansen Formation on the northern margins of the Sverdrup Basin (Ricketts and Stephenson, 1994). This compositionally bimodal unit, which is dominated by basalts, rhyolites and trachytes, may have originated in response to hot spot activity beneath Alpha Ridge during rifting of Canada Basin to the north (Embry and Osadetz, 1988).

Near Emma Fiord, the HPV is probably ca. 500 m thick although widespread normal faulting with throws of 50 m, and possibly greater, has complicated the relationship between the various measured sections (Embry and Osadetz, 1988; MacRae, 1989). Stratigraphic dip is variable, ranging from near horizontal for most of the outcrop area but exceeding 40° close to major faults due to fault drag. The lower 50–300 m of the succession, the focus of this study, is dominated by fossil plant bearing sediments in the
southern part of the study area (sections 1A–1D), and
e intrusive igneous rocks in the northern area with
fewer fossil plants (sections 2A–2C).

The precise age of the Upper Cretaceous beds at
Emma Fiord is uncertain. Palynological data from
southern sections indicate an early to mid-Maastrich-
tian age, based on the presence of *Wodehouseia edmontonicola*, *W. gracile*, *Aquilapollenites bertillon-
tes*, *Triprojectus unicus*, and other taxa diagnostic of
assemblage 7 of Nichols and Sweet (1993), or slightly
younger intervals (see Palynology section below). The
assemblage is very similar to the one described by
McIntyre (1991) from the Expedition Formation on
Axel Heiberg Island. Palynology samples from the
northern field area were barren, probably due to their
high thermal maturity, where vitrinite reflectance
values exceed 1.5% (Csank, 2002).

In contrast published radiometric data (40Ar/39Ar)
from bracketing volcanic units in both northern and
southern areas at Emma Fiord yield plateau ages
ranging from 76 to 82 Ma (MacRae et al., 1990;
Ricketts and Stephenson, 1994), corresponding to the
early to mid-Campanian (Gradstein et al., 1995), a
significant difference with the earliest Maastrichtian
age determination derivable from the palynological
data (71.3 ± 1 Ma). The reason for the discrepancy
between radiometric and palynological dates is
unknown. One possible explanation (biotic hetero-
chroneity) is that palynotaxa arose later in the biostrati-
graphic reference sections in the Western Interior Basin
than in the Arctic (Hickey et al., 1983), although this
idea has been widely criticized (Kent et al., 1984;
Norris and Miall, 1984). Given the uncertainties, the
megaflora described in this paper can only be assigned
to the Campanian or Maastrichtian stage until further
field and analytical studies resolve the age discrepancy.

Although further mapping is needed to improve the
age determination, based on the palynology and the
terrestrial facies, the Emma Fiord deposits can
probably be correlated with the Expedition Formation
of the Eureka Sound Group in the center of the
Sverdrup Basin (Fig. 3). At the section from which

Fig. 2. Location details of studied sites. (A) Map of Canada showing
location of Ellesmere Island. (B) Map showing Cretaceous outcrops
in NW Ellesmere Island. (C) Detailed map of Cretaceous units in
Emma Fiord region indicating location of logged sections given in
Fig. 4 (modified from Thorsteinsson and Trettin, 1972).
McIntyre (1991) describes closely similar palyno-
morph assemblages to Emma Fiord, the relevant
samples (C111755 to C111783) straddle the boundary
between the Upper Member and Lower Member of
the Expedition Formation, as chosen by Ricketts
(1991, his Fig. 49). This stratigraphic correlation
contrasts with earlier studies based on the radiometric
dates alone that posited a correlation between the
Emma Fiord units and the Upper Kanguk Formation
(Embry and Osadetz, 1988; Ricketts and Stephenson,
1994; Harrison et al., 1999).

However, whether Campanian or Maastrichtian in
age, the Emma Fiord deposits are considerably older
than all previously well studied Early Tertiary fossil
plant assemblages, which occur in the Iceberg Bay
and Buchanan Lake formations on Ellesmere and
Axel Heiberg islands (e.g. Francis and McMillan,
1987; Francis, 1988; Christie and McMillan, 1991;
McIver and Basinger, 1999).

3. Depositional environment

Seven moderate-to-poorly exposed stream sections
were measured at Emma Fiord and lithologically
correlated by means of a distinctive, persistent
ignimbrite datum (Fig. 4). Two major facies associ-
ations were noted: a volcanic association with a
bimodal composition; and a poorly exposed sedimen-
tary association dominated by lignite beds.

The volcanic facies association is lithologically
complex, and its proportional thickness and grain size
increase northwards, implying that it was sourced
from a volcanic center to the north (Embry and
Osadetz, 1988). In the northern region of Emma Fiord
it comprises ca. 90% of the thickness of the
succession while in the southern region, only 20%.
Five main facies occur.

Facies 1 consists of up to 7-m-thick columnar
basaltic units with chilled bases and amygdaloidal
tops, which are laterally continuous over several
kilometres. Locally, individual flow units may be
amalgamated into basaltic successions up to 55 m
thick. Basalts are dark grey to black, and typically
feldspar-phyric or aphyric. These units are interpreted
as the product of repeated subaerial lava flows.

Facies 2 consists of 1–5-m-thick, green, welded,
ignimbrite units containing fiamme’ up to 3 cm in
diameter and plagioclase phenocrysts. This facies is
interpreted as hot, pyroclastic flow deposits (Cas and
Wright, 1987).

Facies 3 consists of 1–2-m-thick, green, fine- to
coarse-grained basaltic tuffs, interpreted as mafic
pyroclastic fall deposits.

Facies 4 consists of orange, feldspar-phyric, silicic
agglomerates and tuffs, interpreted silicic pyroclastic
fall deposits.

Facies 5 consists of up to 10 m thick polymictic,
matrix-supported conglomerates containing sub-
rounded clasts up to 20 cm in diameter. This facies
is interpreted as the product of hyperconcentrated
epiclastic flows.

The sedimentary association comprises 10% of the
succession in the northern region increasing to 80% in
the southern region. It contains five main facies, but
these are relatively poorly exposed compared to the
volcanic units.

Facies 6 consists of up to 10-m-thick, broadly
channelized sheets of clast-supported, chert pebble
conglomerate restricted to the interval immediately
overlying the unconformity with the Nansen For-
mation; some clasts contain macrofossils and micro-
fossils derived from the basement rocks. These units
are interpreted as a fluvially deposited basal
conglomerate.
Fig. 4. Graphic logs of studied sections in Emma Fiord region showing volcanic and sedimentary facies, fossiliferous intervals and radiometric dates (after MacRae, 1989; MacRae et al., 1990).
Facies 7 consists of up to 5-m-thick, charcoal-rich, lignite units interbedded with bituminous shale units, which contain up to 5% dispersed pyroclastic grains (mostly pumice and euhedral feldspar). This facies dominates the southern sections. At some horizons numerous very closely spaced, upright, coalified tree trunks (up to 10 cm diameter and 60 cm high) occur in growth position. Lignites are interpreted as the product of forested peat mires. The occurrence of abundant siliciclastic sediment within the lignites as thin sheets (Facies 9) or dispersed grains suggests that they were rheotrophic mires that were regularly flooded by adjacent drainage systems. The presence of euhedral pyroclastics further suggests periodic disturbance by volcanic ash falls.

Facies 8 consists of up to 1–5-m-thick, channelized, coarse-grained, arkosic sandstone and conglomerate units, which locally contain trough cross-bedding. Close association of these units with the lignite beds suggests they may be fluvial channel deposits, but poor exposure of bed architecture prevents confirmation of this interpretation.

Facies 9 consists of <1-m-thick, normally graded, fine- to coarse-grained, planar-bedded sandstone sheets interbedded with lignite-rich intervals and locally containing abundant foliage compressions; they are interpreted as flood-deposited sandy sheets or crevasse splay deposits.

Facies 10 consists of up to 4-m-thick, light grey, rooted mudstone units containing abundant wood fragments, interpreted as vegetated clastic floodbasin deposits.

Poor exposure of the succession prevents further detailed facies interpretation; however, a few generalizations may be made. The compositionally bimodal nature of the volcanic units is consistent with a continental extensional rift setting (Embury and Osadetz, 1988). Volcanic units were probably sourced from an explosive volcanic center immediately north of Emma Fiord, possibly a continental stratovolcano; the key properties of stratovolcanic deposits observed at our site include the lateral discontinuity of volcanic units over only a few kilometres, the abundance of pyroclastic and epiclastic deposits, and the wide range in compositional and eruptive style (cf. Cas and Wright, 1987). Although crystalline pyroclastics scattered throughout the lignite beds indicate ongoing low-level volcanic eruptions during peat formation, the accumulation of very thick lignite units demonstrates that long periods of quiescence separated major eruptive events as commonly observed for many extant continental stratovolcanoes (Cas and Wright, 1987).

Localized glauconitic sandstone units and beds containing dinoflagellates reported by Embury and Osadetz (1988), but not observed in this study, may indicate marine influence at certain intervals in the section. These data suggest that the floodplain-hosted peat mire complexes that dominated interruption periods were likely formed in a coastal plain setting. This interpretation fits well with regional palaeogeographic reconstructions, which place Emma Fiord on the Sverdrup Basin margin landward of coastal plain, delta plain and open marine facies (Ricketts and Stephenson, 1994).

The identity and distribution of fossil plants within this volcanically influenced coastal plain setting were examined to determine the composition and ecology of the polar forest biome at this site. All the specimens described in the following account are deposited in the Nova Scotia Museum of Natural History (prefix NSM) or the Dalhousie University Earth Science Store (prefix EL87), both located in Halifax, Canada.

4. Palynology

Seven samples from peat mire units (EL87-106, EL87-116, EL87-120), crevasse splay units (EL87-107, EL87-109B) and clastic floodbasin units (EL87-115, EL87-118) in the southern sections were prepared for palynological analysis using standard procedures (Barss and Williams, 1973) and yielded moderately diverse palynofloras comprising ca. 27 genera (Table 1). Three samples analyzed from the dominantly volcanic northern sections (EL87-099, EL87-204, EL87-205) were barren. For each palynoassemblage from the southern sections, 200 specimens were counted and the occurrence of each genus was recorded as either absent, very rare (1–3 specimens), rare (4–10 specimens), common (10–25 specimens), or abundant (25–50 specimens).

As the purpose of this paper is to analyze megafossil palaeoecology rather than determine the age of the section, only a brief summary of the
dominant palynomorph genera is given here. A more detailed systematic and biostratigraphic treatment of the palynofloras will be prepared at a later date. Conifer pollen dominated all samples, of which taxodiaceous pollen was the most abundant component (represented by *Taxodiaceaepollenites* and *Sequoiapollenites*). Angiosperm pollen was the next most common group (including *Aquilapollenites* and other triprojectates, *Cranwellia*, *Triporopollenites* and *Wodehouseia*), followed by common cycads, putative ginkgos, and ferns. Lycopsid, bryophyte and fungal spores occurred in subordinate numbers. No significant differences in palynofloral composition were noted between facies.

5. Foliage compressions

Foliage compressions lacking cuticles occur throughout the Emma Fiord units but were particularly abundant in a crevasse splay unit within a lignite-rich interval at two adjacent sites, a few tens of metres apart (EL87-060, EL87-097). Given the sedimentary setting, the assemblage is likely parautochthonous, probably being stripped from peat mire vegetation by sediment-laden floods (Gastaldo et al., 1995).

Analysis of a collection of 62 specimens show that the assemblage possessed a low species richness (Fig. 5A). Neobotanical studies suggest that the most of the common species within a community will be represented in even small autochthonous leaf-litter assemb-

### Table 1

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Peat facies</th>
<th>Clastic facies</th>
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</thead>
<tbody>
<tr>
<td><strong>Fungi</strong></td>
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</tr>
<tr>
<td><em>Polyporosporites</em></td>
<td>Very rare</td>
<td>very rare</td>
</tr>
<tr>
<td>(one species)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Fusiformisporites</em></td>
<td>Absent to</td>
<td>absent to</td>
</tr>
<tr>
<td>(one species)</td>
<td>very rare</td>
<td>very rare</td>
</tr>
<tr>
<td><em>Multicellaesporites</em></td>
<td>Very rare</td>
<td>very rare</td>
</tr>
<tr>
<td>(one species)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Bryophytes</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Stereisporites</em></td>
<td>Very rare</td>
<td>very rare</td>
</tr>
<tr>
<td>(two species)</td>
<td>to rare</td>
<td>to rare</td>
</tr>
<tr>
<td>unidentified forms</td>
<td>Absent</td>
<td>to rare</td>
</tr>
<tr>
<td><strong>Lycopsids</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Retitriletes</em></td>
<td>Very rare</td>
<td>very rare</td>
</tr>
<tr>
<td>(one species)</td>
<td>to rare</td>
<td>to rare</td>
</tr>
<tr>
<td>unidentified forms</td>
<td>Absent</td>
<td>to rare</td>
</tr>
<tr>
<td><strong>Ferns</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Baculatisporites</em></td>
<td>Rare to</td>
<td>rare to</td>
</tr>
<tr>
<td>(one species)</td>
<td>common</td>
<td>common</td>
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<tr>
<td><em>Hamulatisporites</em></td>
<td>Absent to</td>
<td>absent to</td>
</tr>
<tr>
<td>(one species)</td>
<td>very rare</td>
<td>very rare</td>
</tr>
<tr>
<td><em>Obthusisporites</em></td>
<td>Very rare</td>
<td>very rare</td>
</tr>
<tr>
<td>(one species)</td>
<td>to rare</td>
<td>to rare</td>
</tr>
<tr>
<td><em>Laevigatosporites</em></td>
<td>Common to</td>
<td>common to</td>
</tr>
<tr>
<td>(one species)</td>
<td>abundant</td>
<td>abundant</td>
</tr>
<tr>
<td><em>Polypodiisporites</em></td>
<td>Very rare</td>
<td>very rare</td>
</tr>
<tr>
<td>(one species)</td>
<td>to common</td>
<td>to rare</td>
</tr>
<tr>
<td>unidentified forms</td>
<td>Absent</td>
<td>to rare</td>
</tr>
<tr>
<td><strong>Conifers</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sequoiapollenites</em></td>
<td>Rare to</td>
<td>rare to</td>
</tr>
<tr>
<td>(one species)</td>
<td>common</td>
<td>abundant</td>
</tr>
<tr>
<td><em>Taxodiaceaepollenites</em></td>
<td>Rare to</td>
<td>rare to</td>
</tr>
<tr>
<td>(one species)</td>
<td>abundant</td>
<td>common</td>
</tr>
<tr>
<td><em>Podocarpites</em></td>
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<td>absent to</td>
</tr>
<tr>
<td>(one species)</td>
<td>abundant</td>
<td>common</td>
</tr>
<tr>
<td><em>Abietineaepollenites</em></td>
<td>Rare</td>
<td>rare</td>
</tr>
<tr>
<td>(one species)</td>
<td></td>
<td></td>
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<tr>
<td><em>Alisporites</em></td>
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<td>absent</td>
</tr>
<tr>
<td>(one species)</td>
<td>to rare</td>
<td>to rare</td>
</tr>
<tr>
<td><strong>Other gymnosperms</strong></td>
<td></td>
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</tr>
<tr>
<td><em>Monosulcites</em></td>
<td>Rare to</td>
<td>rare to</td>
</tr>
<tr>
<td>(one species)</td>
<td>common</td>
<td>common</td>
</tr>
<tr>
<td><em>Cycadopites</em></td>
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<td>absent to</td>
</tr>
<tr>
<td>(two species)</td>
<td>common</td>
<td>abundant</td>
</tr>
<tr>
<td><strong>Angiosperms</strong></td>
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<td></td>
</tr>
<tr>
<td><em>Liliacidites</em></td>
<td>Rare</td>
<td>absent to</td>
</tr>
<tr>
<td>(one species)</td>
<td>to common</td>
<td>common</td>
</tr>
<tr>
<td><em>Cranwellia</em></td>
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<td>absent to</td>
</tr>
<tr>
<td>(one species)</td>
<td>to rare</td>
<td>rare</td>
</tr>
<tr>
<td><em>Aquilapollenites</em></td>
<td>Absent to</td>
<td>absent to</td>
</tr>
<tr>
<td>(six species)</td>
<td>abundant</td>
<td>abundant</td>
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### Table 1 (continued)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Peat facies</th>
<th>Clastic facies</th>
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<tr>
<td><strong>Angiosperms</strong></td>
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<tr>
<td><em>Protointegricarpus</em></td>
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<tr>
<td>(one species)</td>
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<td></td>
</tr>
<tr>
<td><em>Triprojectus</em></td>
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<td>absent to</td>
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<tr>
<td>(one species)</td>
<td></td>
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<tr>
<td><em>Mancicorpus</em></td>
<td>Absent to</td>
<td>absent to</td>
</tr>
<tr>
<td>(one species)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Triporopollenites</em></td>
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<td>absent to</td>
</tr>
<tr>
<td>(three species)</td>
<td></td>
<td></td>
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<tr>
<td><em>Wodehouseia</em></td>
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<td>absent to</td>
</tr>
<tr>
<td>(three species)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Paraalnipollenites</em></td>
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<td>absent to</td>
</tr>
<tr>
<td>(one species)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Erdmanipollis</em></td>
<td>Very rare</td>
<td>very rare</td>
</tr>
<tr>
<td>(one species)</td>
<td>to rare</td>
<td>to rare</td>
</tr>
</tbody>
</table>
lages, and usually with similar dominance-diversity characteristics to that of the original community (Burnham et al., 1992). Although our sample size is small, and local transportation has introduced taphonomic complexities not dealt with in Burnham et al.’s (1992) study, the Emma Fiord assemblages, which include taxodiaceous conifers, ginkgos, and angiosperms, are probably representative of the most dominant forest plants. Rare floral elements present in the original community are unlikely to be represented in our samples, however.

5.1. Taxodiaceous conifer foliage

Taxodiaceous leafy shoots are the most common compression fossils in the assemblage. Twenty-eight of these specimens (EL87-060.001, 003-008, EL87-060.010, EL87-060.012-015, EL87-097.003-016) are sterile short shoots with slender (1–2 mm diameter), unbranched axes, up to 63–98 mm long, and are of closely similar size and shape (Fig. 5A). One specimen (EL87-097.018) exhibits a side branch and may represent a long shoot. All shoots bear

Fig. 5. Foliage compressions from Hansen Point Volcanics. (A) Slab with randomly oriented plant fragments, scale: 5 cm, EL87-060. (B) Ginkgo cf. G. adiantoides (Heer) Unger, scale: 2 cm, EL87-060.002. (C) Short shoot of Parataxodium sp., scale: 1 cm, EL87-060.001. (D) Trochodendroides cf. T. flabella (Newberry) McIver and Basinger, scale: 8 mm, EL87-060.016. (E) Unidentified angiosperm seed, scale: 2 mm. (F) Mature foliage of Parataxodium sp., scale: 8 mm, EL87-097.017. (G) Parataxodium short shoot attached to mature foliage showing three pollen cones, scale: 8 mm, lost specimen.
monomorphic, bifacially flattened, petiolate, acicular to locally linear-oblong leaves with decurrent bases, arranged with a helical phyllotaxy. Leaves are 11–23 mm long, 1–2 mm wide, spaced 2–3 mm apart along the shoot axis, have a single prominent mid-vein, and an acute or locally obtuse apex. They are inserted at a high angle of divergence (71–83°) in the medial shoot region, but ca. 48° near the apex (Fig. 5C).

A further five specimens (EL87-060.009, EL87-060.011, EL87-097.001–002, EL87-097.017) consist of larger shoots (3–5 mm diameter, 45–79 mm long) which exhibit up to three orders of branching, each orientated in a different plane. These bear appressed, imbricate, helically disposed, lanceolate leaves, which are 2–7 mm long, 2–3 mm wide at the base and taper to an acute apex (Fig. 5F). In some cases, the slender short shoots (described above) are attached to these larger shoots. One of these specimens also exhibits three pollen cones attached to the scaly mature stem by a short pedicel just below the short shoot (Fig. 5G). Pollen cones are 7–8 mm long, 5 mm wide, and consist of at least six helically disposed, peltate cone scales, 3–4 mm long. Ovulate cones are never observed attached to the taxodiaceous foliage. However, two probable ovulate cones (each 17–19 mm long; EL87-097.018-019) and isolated cone scales are associated with these remains (Fig. 5A, F).

These sterile and fertile foliage specimens bear close similarities with the two extant genera of taxodiaceous conifer, *Metasequoia* and *Taxodium*. However, *Metasequoia* differs from our specimens in its decussate phyllotaxy and prominent obliquely joined leaf bases, and *Taxodium* differs in its much lower (<45°) angle of leaf divergence (Chaney, 1950). Specimens with such intermediate characters have been assigned to *Parataxodium*, an extinct taxodiaceous genus (Arnold and Lowther, 1955), which is particularly abundant in Campanian–Maastrichtian strata in circum-Arctic regions (Smiley, 1969; Spicer et al., 1992; Spicer and Herman, 2001). Our specimens differ from two species previously described, *P. wigginsii* Arnold and Lowther, and *P. neosibiricum* Sveshnikova and Budantsev, whose leaves are dominantly linear-oblong with an obtuse, mucronate apex. However, it is presently unclear whether such differences warrant the erection of a new species or simply represent natural intraspecific variability, which is relatively large in taxodiaceous foliage (Chandrasekhar, 1974).

5.2. *Ginkgoalean foliage*

Ginkgoleans are only represented by two specimens (EL87-060.002). These consist of a large, fan-shaped (suborbicular to reniform) leaf, 56 mm long and 72 mm wide, with open dichotomous venation (Fig. 5B). The leaf base is abruptly and narrowly wedge-shaped. There is a pronounced marginally attached petiole, and a small apical notch. As the leaf margin is only partially preserved it is impossible to know whether additional notches existed. Preservation of venation is poor, but veins occur with a typical density of 11–13 per cm.

Using the taxonomic scheme developed by Tralau (1968), our specimens are assignable to the extant genus *Ginkgo* on basis of their margin circumscribing between two-thirds and a quarter of a circle, possessing an apical notch, and exhibiting a vein density of <20 per mm. Without cuticular preservation, a more precise taxonomic assignment is dangerous given the great morphological range seen in individual ginkgoalean species (Czier, 1998). However, in terms of its gross morphological outline, the HPV specimens are very characteristic of the polymorphic species, *G. adiantoides* Unger (Heer). This species, and its various synonyms, are widespread during Late Cretaceous–Early Tertiary times in the circum-Arctic regions (e.g. Hollick, 1930; Kelley et al., 1999; Spicer and Herman, 2001).

5.3. *Angiosperm foliage*

Four well-preserved angiosperm specimens (EL87-060.016–018, EL87-097.017) consist of isolated, polymorphic, microphyllous (ca. 800–900 mm²), elliptical, symmetrical leaves with an obtuse, concave base and an obtuse, rounded apex (Fig. 5D). Leaves are approximately 3.5–4.1 mm long and 3.4–4.3 mm high (length/width ratio ca. 1:1). Leaf margin is partially entire with coarse crenations in the upper half of the leaf. Primary venation is actinodromous, the three primary veins being straight near the base, and diverging at angles of 25–30°. Secondary veins diverge from primary veins at angles ranging from 35° to 80°; higher order venation is not preserved. The
petiole is usually poorly preserved, and marginally attached. A further 19 angiosperm leaf specimens may belong to the same taxon, but venation and leaf margin are too poorly preserved to confirm this (EL87-060.019–037). A few isolated seeds may also be of angiosperm affinity (Fig. 5E).

Microphyllous angiosperm leaves of this type are common in Late Cretaceous–Early Tertiary circum-Arctic localities. The taxonomy of such leaves has proved problematic with specimens being assigned to various taxa including *Populus*, *Zizyphus*, *Cocculus*, *Cercidiphyllum*, *Joffrea* and *Trochodendroides*. In their taxonomic review, McIver and Basinger (1993) favored the use of the name *Trochodendroides* for specimens similar to our own material, a genus similar to members of the extant family Trochodendraceae. Our specimens are most closely similar to *T. flabella* (Newberry) McIver and Basinger, although relatively poor preservation precludes definitive attribution to this species.

6. Anatomically preserved woods

Fossil woods are abundant in the Emma Fiord section. Purplish-red-weathering trunks, anatomically preserved by silicification, are particularly common although they mostly occur ex situ in subcrop having been preferentially weathered out of fresh outcrop. Many of these trunks occur associated with lignitic units in section 1A; however, two of the best-preserved examples examined here were found in section 2A and 2B approximately 15–30 m above the unconformity surface in subcrop scree. Analysis of adhering matrix (silicic tuff lithology) indicates that these latter trunks had been derived from acidic ash fall units nearby (Facies 4; EL87-027, EL87-206). Decay of metastable volcanic sediments was probably the source of the mineralizing silica (Jefferson, 1987). Thin sections were prepared along transverse (TS), radial longitudinal (RLS) and tangential longitudinal (TLS) planes, and studied with a petrographic microscope.

Fig. 6. Silicified woods from the Hansen Point Volcanics, all *Piceoxylon* sp., EL87-027. (A) Uniseriate and biseriate opposite tracheid pitting, RLS, scale: 50 μm. (B) Profusely pitted axial parenchyma, TS, scale: 10 μm. (C) Opposite and subalternate tracheid pitting, RLS, scale: 40 μm. (D) Rays with horizontal ducts and pitting tangential walls, TLS, scale: 100 μm. (E) Cupressoid and taxodioid cross-field pits; nature of apertures only observable by scanning up and down through section, RLS, scale: 100 μm. (F) Vertical resin duct, TS, scale: 40 μm.
Charred wood fragments (up to 2.2 cm diameter) were also highly abundant, although only found in peat mire units (Facies 7; EL87-099, EL87-103, EL87-108, EL87-204), where they were scattered across discrete bedding surfaces. Charcoal was prepared using an HNO₃/HF maceration technique (O’Dea, 1996), and examined with a Hitachi S-3200 Scanning Electron Microscope.

Key wood anatomical characters (Phillips, 1948; Greguss, 1955, 1972; Barefoot and Hankins, 1982) were quantitatively described from both silicified and charred woods using the scheme of Falcon-Lang and Cantrill (2000, 2001). In total, 24 charred or silicified specimens were examined of which 79% were taxodiaceous conifers and 21% were pinaceous conifers (Figs. 6 and 7). However, all measurements given in the following descriptions are from the silicified specimens, because the dimensions of charred woods have contracted by up to 30% while burning (Scott, 1989).

6.1. Taxodiaceous woods

A total of 19 taxodiaceous wood specimens were found, the largest and most complete being a 24-cm diameter silicified trunk with a distinctly fluted...
6.2. Pinaceous woods

Six pinaceous woods were found, of which the largest was a 50 cm long and 16 cm diameter silicified trunk exhibiting a 1.6-cm-thick bark rind (EL87-027.1, EL87-099.1, EL87-103.1, EL87-108.1, and EL87-204.1). The following anatomical features were observed:

In RLS, tracheids exhibit uniseriate (53%), biseriate (11%) or triseriate (1.5%) bordered pits, the remaining tracheids being blank (34.5%). Tracheid pits are circular (11 μm diameter) with circular apertures (4 μm diameter), occur in contiguous chains one to nine pits long (mode: 5), and when multiseriate are almost always oppositely arranged (96%) or rarely alternate (4%). Rays are parenchymatous, possess thin, densely pitted horizontal walls, and are composed of cells, up to 260 μm long, 20 μm wide and 14 μm high. Cross-field regions exhibit a mixture of one to four piceoid, cupressioid or taxodioid pits per field. Axial parenchyma is common with densely pitted radial, tangential and transverse walls.

In TLS, tracheid walls locally exhibit spaced, uniseriate pits (8 μm diameter). Pronounced helical tertiary tracheid wall thickening is common in both longitudinal sections; tracheid wall outgrowths demonstrate that this is an anatomical feature of the wood, and not merely taphonomic checking. Rays are 2–35 cells high, dominantly uniseriate (77.7%), but may be biseriate (14.6%) or may contain horizontal resin ducts (7.7%). Horizontal resin ducts (70–120 μm diameter) ringed by 8–14 epithelial cells occur with a density of 0.3 ducts per mm². In TS rare, small axial resin ducts (40–50 μm diameter) ringed by 8–12 epithelial cells occur with a density of 0.3 ducts per mm², and are especially common in the latewood. Growth rings are narrow (mean: 0.96–1.42 mm wide) with marked boundaries defined by 64–72 μm diameter earlywood cells and 10–15 μm diameter latewood cells; there is typically 40–55% latewood (calculated using the method of Creber and Chaloner, 1984). Rays are up to 4.6 mm long, and spaced 125 μm apart when measured close to the ring boundary (i.e. eight rays per mm).
Following Kraüsel (1949) these woods are classified as *Piceoxylon* Gothan. They bear closest similarity to Late Cretaceous specimens of *Piceoxylon thomsoni* from Amund Rignes Island, Arctic Canada (Banaan and Fry, 1957), a species that differs from our specimens in its larger axial resin duct (up to 150 µm) and shorter rays (1–16). Occurrence of axial and horizontal resin ducts indicates that specimens belong to the conifer family, Pinaceae (Greguss, 1955, 1972). Our material may represent a new species; however, given the large range in wood anatomy seen in individual conifer trees along a stump-branch transect (Jane, 1962; Falcon-Lang, in press), we are wary of erecting new taxa on the basis of a limited number of specimens. The combination of prominent helical tertiary wall thickening, and small, irregularly distributed axial resin ducts suggest our specimens may have an affinity to the extant pinaceous genus *Pseudotsuga* (Barefoot and Hanksins, 1982).

6.3. Amber

Abundant amber consisting of golden to light brown, ellipsoid fragments (0.5–5 mm long) occurs
in the lignite beds. Amber was observed attached to several taxodiaceous wood specimens examined although it could not be confirmed whether or not this was a taphonomic artifact. Nevertheless, it is noteworthy that taxodiaceous conifers were amongst the most prolific amber-producing trees in Cretaceous times as supported by infra-red spectral analysis of some Late Cretaceous Arctic amber (Langenheim et al., 1960; Nicholas et al., 1993; Bellis and Wolberg, 1991). Given the abundant occurrence of taxodiaceous conifers in the HPV and the possible organic connection of amber to taxodiaceous wood, it is likely that this group were main amber-producers at our site.

7. Growth rings in woods

Growth rings in fossil woods provide invaluable data concerning tree ecology and intra-annual to decadal variations in growing conditions (Creber...
Three parameters were analyzed for the two largest wood specimens (EL87-027, EL87-206), which contained sequences 42 and 71 ring increments long, respectively: mean ring width, mean sensitivity, and the nature of growth interruptions (Fig. 8).

7.1. Growth ring width and mean sensitivity

Mean growth ring width, an indicator of annual tree productivity (Creber, 1977; Creber and Chaloner, 1984) was measured for both specimens. Because the width of individual rings varied around the trunk circumference of silicified specimens, ring widths were measured along several radii. In EL87-027 (Piceoxylon), a trunk with an asymmetric cross-section, four opposing radii were measured. Mean ring width varied from 0.96 mm along the shortest radius to 1.42 mm along the widest radius (mean: 1.14 mm; maximum: 5.5 mm; n = 83). In EL87-206 (Taxodioxylon), a partial trunk cross-section exhibiting a pronounced fluted gross morphology, rings were measured along both wide ridges (mean: 1.74 mm) and narrow furrows (mean: 1.58 mm) giving a total mean ring width of 1.66 mm (maximum: 5.3 mm, n = 141; Fig. 9).

Mean sensitivity, a measure of year-to-year ring width variability was then calculated for these data using the formula:

\[ MS = \frac{1}{n-1} \sum_{i=1}^{n-1} \frac{2(x_{i+1} - x_i)}{x_{i+1} + x_i} \]

where \( x \) is ring width, \( n \) is the number of rings in the sequence analyzed, and \( t \) is the year number of each ring (Fritts, 1976). MS values can range from 0 where there is no year-to-year variability to a maximum approaching 2, representing the greatest possible variability. A MS value of 0.3 is usually used to distinguish 'sensitive' ring sequences (MS > 0.3), from 'complacent' ring sequences (MS < 0.3; Fritts, 1976). Sensitive MS values are considered indicative of growth under variable stressful environments (dry, cold or disturbed niches), whilst complacent values imply uniform and favorable growing conditions (Creber, 1977; Falcon-Lang, 2003). Both samples gave sensitive MS values of 0.348 and 0.435, respectively (Fig. 9).

7.2. Growth interruptions

Interruptions to tree growth are also important ecological indicators, and two types of growth interruption were noted in the Cretaceous woods. The first, false rings, consisted of narrow (two to four cells wide), impersistent rings of small (15–20 μm) diameter tracheids. The second, traumatic rings, consisted of impersistent rings of traumatic resin ducts (50–60 μm diameter) and scattered parenchyma cells. Specimen EL87-027 (Piceoxylon) contained nine false rings across 42 ring increments, while Specimen EL87-206 (Taxodioxylon) contained nine false rings and 15 traumatic rings across 71 ring increments (Fig. 8D). Increments containing traumatic rings in EL87-206 were typically narrower than in normal rings (Fig. 9).

8. Discussion

Synthesising data concerning paleoenvironment, floral composition, facies distribution of taxa, plant fossil preservational state, leaf physiognomy, and growth rings in woods allows a community-scale ecological reconstruction to be made.

Megaflora and palynoflora data indicate that laterally and temporarily extensive peat mires and associated floodbasin substrates supported low to medium diversity vegetation dominated by taxodiaceous conifers, together with subordinate pinaceous conifers, ginkgos, cycads, angiosperms, ferns, lycopsods, and bryophytes. Data is of insufficient resolution to determine whether discrete subenvironments possessed different communities; however, a few generalizations may be made. For example, lignite beds containing slender, closely spaced, in situ woody stumps indicate that at least some mire regions supported dense forests rather than open stands. As only coniferous fossil woods were found, conifers were almost certainly the dominant arborescent vegetation in this setting, the largest trunks (up to 24 cm diameter) indicating tree heights of around 15–20 m (Niklas, 1994).

The peat mire forests were probably dominantly deciduous as indicated by limited leaf physiognomic data. As already noted, the most common megafloral element, Parataxodium, bears close similarity to the
deciduous foliage units of extant *Metasequoia* and *Taxodium* (Chaney, 1950). In these modern genera, a resting bud surrounded by scale leaves overwinters, and in the spring produces a determinate shoot, which is shed in the autumn (Liu et al., 1999). The occurrence of *Parataxodium* as isolated shoot units of similar size, at least one clearly preserving scaly leaves near the base, strongly suggests that this plant was deciduous, shedding determinate shoots like extant *Metasequoia* (cf. Arnold and Lowther, 1955). A deciduous phenology is also probable for the gingkoalean specimen because this group is exclusively deciduous today. It is unknown whether the angiosperms were deciduous or evergreen, although their relatively thin leaf lamina may suggest the former phenological condition.

Growth rings in the woods of taxodiaceous and pinaceous conifers provide further qualitative evidence about paleoclimate and the type of vegetation biome represented by the Emma Fiord assemblages. Modern data from the International Tree-Ring Data-bank show that the maximum mean ring width attainable at a particular site is constrained by climatic parameters, especially Cold Month Mean Temperature (Falcon-Lang, 2003). The maximum mean ring width at Emma Fiord is 1.66 mm. Based on uniformitarian assumptions, these growth ring data suggest temperate conditions at Emma Fiord during the Late Cretaceous.

This interpretation is augmented by evidence of traumatic rings in one of the trunk specimens. The two most common causes of traumatic ring formation are hard frosts, which cause cellular contraction, dehydration and ice crystal formation in the cambium, thereby killing and deforming differentiating tracheids (Glerum and Farrar, 1966), and wildfire, which overheats the cambial zone resulting in similarly deformed tracheid cells (Brown and Swetnam, 1994). Although fire was evidently common in the Emma Fiord forests (see later), the occurrence of multiple (up to four) traumatic rings in single annual growth increments, suggests that frost was the most probable causal agent of these features; it is unlikely that a single tree would be burned four times in a single season, and survive (Chandler et al., 1983). Multiple frost rings are sometimes observed in single annual rings of *Pseudotsuga* growing in cool temperate, northern British Columbia (Reich and Vanderkamp, 1993). In addition to regional climate, the occurrence of regular volcanic eruptions may have accentuated frost ring formation by periodically reducing sunlight and hence temperature (LaMarche and Hirschboeck, 1984). Modern conifer families possess variable tolerance to frost. Pinaceous conifers can tolerate very hard frosts (in the range –20 to –70 °C) before xylem damage occurs, whereas taxodiaceous conifers can only tolerate frosts of –10 to –35 °C (Sakai and Larcher, 1987). These data may explain why frost rings formed in *Taxodioxylon* but not *Piceoxylon*. They may further indicate that temperatures during the late growing season periodically fell below –10 °C (the frost tolerance threshold of modern taxodiaceous conifers), and that conditions were cool temperate. However, given that trees were growing under elevated CO₂ levels (Nordt et al., 2002), ice nucleation may have occurred at slightly warmer temperatures in Late Cretaceous times as indicated by experimental data (Terry et al., 2000; Beerling et al., 2001).

Mean sensitivity (MS) ranges from 0.348 to 0.435 in the Emma Fiord woods and indicate that the trees grew in a disturbed niche. Without additional data, it is impossible to determine the source of ecological disturbance at our site. However, in addition to frost, flooding and volcanism, a fourth major disturbance factor was clearly wildfire, as indicated by the widespread occurrence of charcoal (Scott, 1989). Wildfires may have been promoted by the abundance of resin-producing trees (as indicated by amber; Langenheim et al., 1960) and a putatively elevated atmospheric oxygen concentration (ca. 26%; Berner and Canfield, 1989). Combined, these factors would have made the taxodiaceous vegetation particularly flammable (Chandler et al., 1983), like compositionally similar, coeval Cretaceous vegetation from a range of palaeolatitudes.

In summary, the Emma Fiord data suggest the existence of dominantly deciduous, temperate, low to medium diversity, fire-prone taxodiaceous conifer forests on the volcanically disturbed alluvial plain and peat mire environments of NW Ellesmere during latest Cretaceous times. This ecological reconstruction compares very closely with Campanian–Maastrichtian sites in northern Alaska, northern Russia, and northern Kamchatka at palaeolatitude ranging up to 85°N which possessed similar fire-prone, peat-forming,
deciduous taxodiaceous forest represented by a low diversity megaflora and a moderately diverse palynoflora (Frederiksen et al., 1988; Spicer and Parrish, 1990a,b; Spicer et al., 1992; Herman, 1994; Parrish and Lamberson, 1998).

Parrish and Spicer (1988) suggested that this circum-Arctic vegetation, which is depauperate relative to earlier and later floras, may be suggestive of a latest Cretaceous climatic cool phase. This interpretation has since been supported by estimates of atmospheric composition that indicate CO2 levels generally declined in latest Cretaceous times from 1200 ppm in the early Campanian to 650 ppm in the mid-Maastrichtian (Ekart et al., 1999; Nordt et al., 2002). The findings of this paper further support the occurrence of a latest Cretaceous cool mode, demonstrating the existence of depauperate, cool temperate forests at high palaeolatitudes in Arctic Canada.

9. Conclusions

(1) Cretaceous conifer-dominated fossil plant assemblages occur in a Campanian–Maastrichtian interval of the Hansen Point Volcanics, near Emma Fiord, NW Ellesmere Island, Arctic Canada at a palaeolatitude of 75°N.

(2) Analysis of megaflora and palynoflora assemblages in 10 sedimentary and volcanic facies indicates that forests dominated by taxodiaceous conifers, with subordinate pinaceous conifers, ginkgos, cycads and ferns, grew in a coastal plain/peat mire complex within an explosive volcanic setting.

(3) Tree ring data suggest growth under a temperate climate characterized by the occurrence of growing season frosts, while analysis of leaf physiognomy indicates that most of the vegetation was deciduous. Abundant fossil charcoal indicates that wildfire was a very important disturbance process in these polar forests.

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References


Boyd, A., 1992. Revision of the Late Cretaceous Pautut flora from West Greenland; Gymnospermopsida (Cycads, Cycadeoideas,


LaDeau, S.L., Clark, J.S., 2001. Rising CO2 levels and the fecundity