



The paleoecology of high-latitude Eocene swamp forests from Axel Heiberg Island, Canadian High Arctic

David R. Greenwood *, James F. Basinger

Department of Geological Sciences, University of Saskatchewan, Sask. S7N 0W0, Canada

(Received March 9, 1993; revised and accepted June 23, 1993)

Abstract

A record of high-latitude (79°55'N) Eocene polar vegetation is preserved on Axel Heiberg Island, Canadian High Arctic, in megafloras in an alternating sequence of swamp-coal, fluvio-lacustrine shale and channel-sand lithofacies of the upper coal member of the Buchanan Lake Formation. Some exposures of the swamp facies contain significant fossil forests represented by autochthonous assemblages of mummified in-situ tree stumps and forest-floor leaf-litter mats. Exposed trunks within a single coal layer represent multiple stands of trees killed and buried at the different times over 500–2000 yr. Stratigraphic examination of peat and coal megafossil floristics of the “level N” fossil forest at the centimetre-scale demonstrates small-scale changes in forest composition and swamp hydrology horizontally, and temporal variation vertically within this layer. A mosaic of taxodiaceous swamp (*Metasequoia* dominant with or without *Glyptostrobus*), a mixed coniferous community, and *Alnus*/fern bog appears to have produced both the leaf mats and the in-situ stumps, with the taxodiaceous swamp the dominant peat-accumulating phase. Taxodiaceous layers are interpreted as areas of standing water which may have experienced seasonal water-level fluctuations. *Alnus*/fern (with or without other broadleaved angiosperms) communities reflect areas of slightly higher peat and hence locally lower water tables, but may also reflect successional processes. The areal extent and position of these different hydrologically-controlled plant communities appears to have changed throughout the interval of accumulation of the peat layer examined.

1. Introduction

Abundant Cretaceous and Tertiary megafloras at high latitudes testify to the presence of extensive forests in areas which today support only tundra. These megafloras have attracted attention due to interest in both the ecosystems they reflect, and in polar climates during periods of Earth history with warmer global temperatures than the present (e.g. Jefferson, 1982; Wolfe, 1985; Francis, 1986, 1991; Spicer, 1990; Crame, 1992). In particular, some commentators have suggested that environments

of past warm periods, such as the Late Cretaceous and the Eocene, may offer insight into potential present global climatic change (Spicer and Corfield, 1992; Wing and Greenwood, 1993).

Arctic and Antarctic megafloras of Cretaceous and Tertiary age represent terrestrial plant communities adapted to a yearly cycle of light and dark, possibly representing precursors of modern deciduous broadleaved temperate and boreal forests (Wolfe, 1980, 1987; Spicer, 1990). However, many Tertiary megafloras from Arctic areas are either poorly described or provide limited information on the ecology of polar forest ecosystems. Detailed analysis of the dynamics and character of Tertiary vegetation, including that from the Arctic, is most

* Present address: Paleobiology Department, MRC NHB 121, Smithsonian Institution, Washington, DC 20560, USA.

readily accomplished through careful integration of taphonomic and phytosociological information. In-situ accumulations of plant megafossils, such as found in “fossil forests”, provide an opportunity for high-resolution studies and, when combined with information from a variety of contemporaneous biofacies, allow reconstruction of local and intraregional vegetational mosaics (Christophel et al., 1987; Taggart, 1988; Greenwood, 1991; Wing and DiMichele, 1992).

A record of high-latitude ($79^{\circ}55'N$) Eocene polar vegetation is preserved on Axel Heiberg Island (Fig. 1), in the Canadian High Arctic Archipelago (Basinger, 1991; MacIntyre, 1991; Greenwood and Basinger, 1993). The Axel Heiberg Eocene megafloras include both allochthonous lacustrine and autochthonous “fossil forest” facies (Fig. 2) which exhibit clear floristic differences reflecting the complexity of the local vegetational mosaic (Basinger, 1991). The distribution of stumps, both horizontally and vertically within the fossil forests of Axel Heiberg, indicates that the exposed trunks within a single coal layer likely represent multiple generations of trees (Greenwood and Basinger, 1993).

Modern taxodiaceous [*Taxodium distichum* (L.) Richard] and tropical angiospermous swamp forests exhibit successional changes in species composition and dominance associated with changing local water tables and nutrient levels (Davis, 1946; Spackman et al., 1969; Moore, 1987; Moore and Hilbert, 1992). Temporal and spatial variation in the floristic character of swamp forests is reflected in the plant fossils and petrographic character of the peats (Spackman et al., 1969; MacCabe, 1984; Moore, 1986, 1987; Collinson and Scott, 1987); however, decay and post-depositional petrographic changes will also influence the representation of swamp species as (mega)fossils (Clymo, 1983; Moore, 1989; Moore and Hilbert, 1992).

Autochthonous forest-floor leaf mats permit more detailed examination of the paleoecology of the Axel Heiberg fossil forests. Studies of modern autochthonous plant assemblages suggest that leaf material will reflect both the spatial arrangement and the productivity of the standing forest (Chaney, 1924; Ferguson, 1985; Burnham et al.,

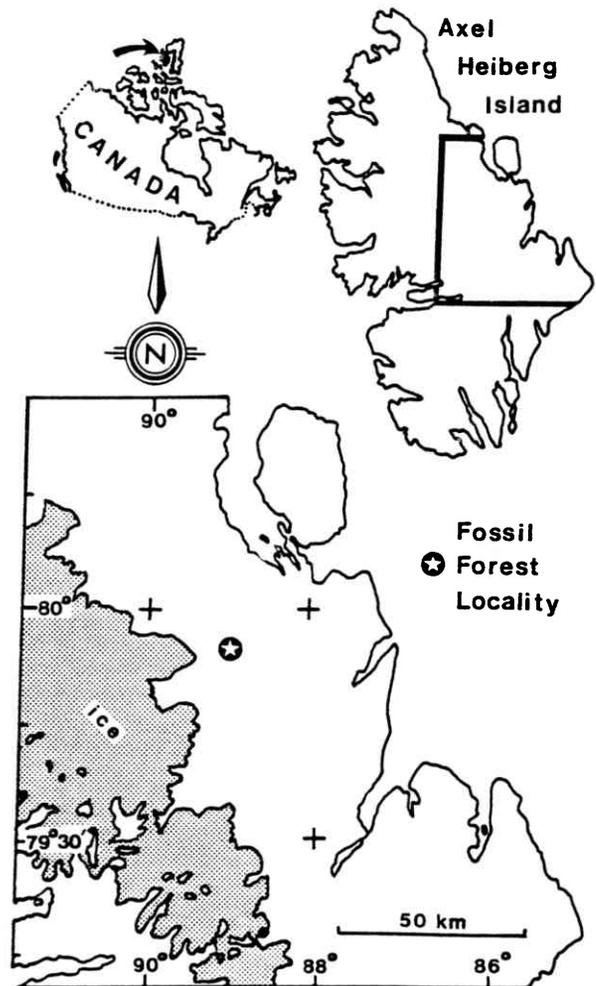


Fig. 1. Location of Eocene megafloral sites of the Buchanan Lake Formation, Axel Heiberg Island: geographical locale of Axel Heiberg Island; area of interest on Axel Heiberg Island; and the location of “Fossil Ridge” area of fossil forests (autochthonous leaf mats *) and mudstone localities (US210 and US188).

1992; Greenwood, 1992; Wing and DiMichele, 1992). Individual “fossil forest” organic layers have been labelled with a letter code (Francis and McMillan, 1987; Francis, 1991). Basinger (1991) noted that some taxa, particularly angiosperm seeds and fruits, occurred in “pockets” within Francis’ (1991) “level *N*”. Greenwood and Basinger (1994) found that floristics of the “level *M*” organic layer varied laterally at the kilometre-scale, and that lithology within the level *M* and *N*

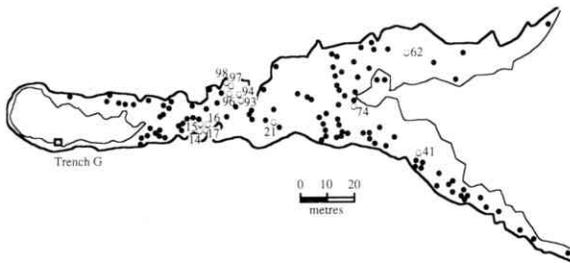


Fig. 2. Sketch map of outcrop of level *N* organic layer and overlying paleosol (where present) showing sample points and adjacent stumps (numbered) for the floristic analysis. Base map from data compiled by Sweda et al. (in prep.); map computer generated by C.L. Greenwood. Stumps (●) not to scale.

organic layers varied vertically and horizontally at the centimetre- to metre-scale. Significant clay partings within the organic layers appeared to reflect a complex record of hydrological changes in the swamp forest community. Stratigraphic sequences over fine time scales (<1000 yr) and the representation of biota are likely to be incomplete (Sadler, 1981; Sadler and Dingsus, 1982; Taggart, 1988). In this report, the autochthonous leaf-litter layer associated with the fossil forest of level *N* (Francis, 1991) is examined in detail. This analysis provides evidence of forest dynamics of this Eocene polar forest community.

2. Location of study and methodology

Eocene megaflores on Axel Heiberg Island crop out in an alternating sequence of swamp-coal, fluvio-lacustrine shale and channel-sand lithofacies of the upper coal member of the Buchanan Lake Formation (Ricketts, 1991). Exposures of the swamp facies at the so-called “fossil ridge” locale (Fig. 2) contain significant fossil forests represented by autochthonous assemblages of mummified in-situ tree stumps and forest-floor leaf-litter mats (Francis, 1986, 1991; Basinger, 1991; Greenwood and Basinger, 1993). In earlier reports the leaf-litter layers, or coal layers, have been labelled with a letter code designating stratigraphic position. The fossil forest and associated leaf-litter or organic layer discussed in this report and previous studies (Francis, 1991; Greenwood and

Basinger, 1993) is labelled “level *N*” in Francis’ nomenclature (Francis and McMillan, 1987; Francis, 1991) and this procedure is followed here. Field work in 1991 at the Axel Heiberg Island Fossil Forests examined lithic variation at the centimetre- to metre-scale within level *N*, and floristic variation laterally within level *M* at the kilometre-scale (Greenwood and Basinger, 1993).

Each tree stump within level *N* was individually numbered in a detailed survey (T. Sweda, S. Kojima [Nagoya Univ.] and K. Hyashi [Ehime Univ.] unpubl. data) and these tree numbers are used here as points of reference for later reports. A reconnaissance of the level *N* exposure identified a number of areas to examine demography and local succession (Fig. 2). Seven sites were selected for detailed analysis of floristic variation with depth on the basis of: (1) good surface preservation of megafossils, (2) proximity to tree stumps selected for dendrological identification (Sweda et al., unpubl.), and (3) apparent local succession, based on root system stratigraphy and the presence of several tree stump size classes at the local site. The first site represents one of several vertical sections (trenches A–I) through level *N* discussed in an earlier report (Greenwood and Basinger, 1993), labelled here “trench G”. The remaining sites represent surface trenches cut down into the horizontally exposed leaf mat of the level *N* organic layer.

2.1 Site 1: vertical section at trench G

A vertical section had been cut through the level *N* organic layer (=litter mat), from the basal clay that underlies all of level *N*, through a complete organic layer, to the capping paleosol (Greenwood and Basinger, 1993). Analysis of this, and adjacent sections, in the 1991 field season had identified a complex centimetre-scale lithic stratigraphy with significant laterally discontinuous clay partings. Floristic variation with depth at 1 cm intervals for the trench G complete section was examined by Greenwood and Basinger (1993) and those results are repeated in more detail here. The methodology of sampling for this site and the other sites is explained below.

2.2 Sites 2–7

Several areas (sites 2–7) near particular tree stumps were identified for detailed analysis (Fig. 2). Each site was selected to provide information on areas where stump positions and sizes indicated potential changes in local floristics over the combined lifespan of the stumps present at the site, particularly where multiple generations of trees were indicated. A number of sampling points were identified at each site. Megafossils (needles, shoots, cones, etc.) were sampled at 1 cm depth intervals in vertical sequence at each point, extending from the exposed surface of the litter mat to the basal clay (where accessible). Samples were removed as stratigraphically contiguous squares of leaf mat approximately 10 × 10 cm. A semi-quantitative measure of relative abundance was made for each 1 cm interval by visual assessment of all identifiable megafossil taxa in each sample. Taxa represented by both sterile and reproductive material were scored as one taxon and abundance assessed based on the summed amount of both organ classes, although the presence or absence and gross abundance of reproductive material was recorded. Unfortunately, at some sites recognisable megafossils were only encountered at the surface and so data are not available. Quantitative analyses of the level *N* vertical sections were based on a 5 point abundance scale (whole or equivalent recognisable organs) used in Quaternary megafossil studies (Grosse-Brauckmann, 1986, p. 608). The scale (slightly modified) is given below:

+ = only a few pieces (1–2 specimens) of tissue remains (e.g. angiosperm leaf pieces), representing <1% of material; fruits, cones or seeds of the taxon generally not present.

1 = 1–3% of material; or 3–5 fruits, cones or seeds of the same taxon.

2 = 4–10% of material; 5–14 fruits, cones or seeds.

3 = 10–25% of material; > 14 fruits, cones or seeds.

4 = 25–50% of material.

5 = > 50% of material.

The mudstone megafloras crop out in a separate area from the fossil forests. Multiple sites along an unnamed river to the ENE of Fossil Ridge have been collected over several seasons (Basinger, 1991; Basinger and LePage, unpubl. data).

Collection was from scree and was semi-quantitative in that material of common taxa was selectively collected and curated and can be expected to be under-represented. Two of these sites, US188 and US210, are examined here.

The channel sands, associated with both the fossil forest outcrop and the mudstone outcrop, are sparsely fossiliferous, but locally restricted outcrop may contain small megafossil-rich lenses. Floras from this facies are examined qualitatively.

3. Results

3.1 Swamp facies (organic layers associated with "fossil forests")

Level *N* organic layer, where complete, is typically 40–60 cm in thickness. Over the area where the "fossil forest" stumps are exposed, multiple sample points in level *N* indicated the depth of section was much less (5–22 cm; Figs. 3–7) than measured for the section at trench G (47 cm), indicating that a truncated sequence has been preserved over this area. The thinner section of organic layer from level *N* around the fossil stumps may reflect deflation of the organic layer due to post-exposure aeolian erosion, or more likely represents spatially variable rates of accumulation (Sadler, 1981; Sadler and Dingus, 1982; Clymo, 1984; Cohen, 1985).

The principal megafossil taxa were scored for each sample (and are listed as generic names), although the presence of rare taxa were noted. Conifers dominate the level *N* leaf mat, and systematic work on Pinaceae (e.g. LePage and Basinger, 1991, 1992) and the presence of attached reproductive material for many of the taxa generally indicates the presence of modern genera (Basinger, 1991); however, some taxodiaceous material would appear to represent a species from an undescribed new genus, and so is listed here as "undescribed Taxodiaceae".

Site 1 (vertical section at trench G)

The results for this section were reported by Greenwood and Basinger (1993; see fig. 12

therein). The following detailed observations were made:

(1) the dominance (i.e. score of 5 on the abundance scale) of *Metasequoia* throughout most of the section (except where barren), but not at 17–18 and 9–7 cm depth;

(2) the trend for *Alnus* to be richer lower in the section, particularly between 20–6 cm depth, and always richer or even dominant when *Metasequoia* is not dominant;

(3) most of the other taxa scored in the analysis, (*Glyptostrobus*, *Pseudolarix*, undescribed Taxodiaceae, and *Osmunda*) are restricted to the lower part of the section;

(4) some taxa (e.g. undescribed Taxodiaceae and *Osmunda*) are quite sporadic in occurrence in vertical section (a pattern repeated in horizontal transects), or may be either richest towards the base of the section (*Glyptostrobus*) or the middle of the section (*Pseudolarix*).

Site 2 (tree 96 and environs)

Seven sampling points (A–G) were identified for analysis at this site. Sample points B and C were adjacent to tree 93; points A, D and E to tree 94; and sample points G and F were adjacent to trees 98 and 97. Sample points F, E and C were found to be only fossiliferous at the surface and so no data charts are provided for these sample points. The remaining sample points (A, B, E and G) yielded megafossils over depths varying from 4 to 22 cm from the exposed litter-mat surface (Fig. 3a–d). *Glyptostrobus* was the most common taxon at the surface for sample points B and E, whereas *Metasequoia* was dominant at the surface of sample point G (Fig. 3d). *Pinus* was dominant at the surface of point A. *Metasequoia* decreased in abundance or became absent with depth in three of the sections examined at site B (Fig. 3 a,c,d), although *Metasequoia* seed cones were found at F and 8 cm at point G.

In three of the sections (Fig. 3b–d) angiosperm remains were most abundant over short intervals in the lower part of the sections, just above clay partings barren of plant remains. Angiosperm seeds were encountered at D, F and 8 cm depth at point G. In contrast to points B, E and G, angiosperms were moderately abundant in the upper

part of the section at point A (Fig. 3a). The megafossil taxa ?*Chamaecyparis* and *Pseudolarix* were not recorded in any of the sections sampled at site 2. *Pinus* and the undescribed Taxodiaceae taxon were only recorded at points A and B, respectively (Fig. 3a,b). A previously unrecorded bipinnate fern was encountered at point E at 3 cm.

Site 3 (trees 14–17)

Three sample points (A–C) were identified near trees 14 and 17 at site 3. Only two of these points (B and C) yielded recognisable megafossils below the litter-mat surface and so data charts are only presented for these sections (Fig. 4a,b). Angiosperms were dominant at the surface (0–1 cm) of all three sample points. *Metasequoia* was a subdominant over this interval, although seed cones were found at 1 cm at both points B and C. Angiosperm leaf remains and *Metasequoia* decreased sharply in abundance with depth in these sections. At points B and C *Glyptostrobus* had a minor abundance peak in the middle of the sections (2 cm depth in both cases). No other conifer taxa were encountered at any of the sample points and no fern remains were recorded.

Site 4 (tree 74)

Three points (A–C) were sampled near tree 74 at site 4. The sections analysed varied in depth from 5 cm (points B and C) to 8 cm (point A). *Metasequoia* was the dominant taxon in each section over much of the vertical interval (Fig. 5a–c), reaching 100% of material at the base of the section at point A. Significant floristic differences were recorded at some depths in the section A. The leaf litter in the section at point B (Fig. 5b) was almost completely composed of *Metasequoia* foliage, with only trace amounts of *Osmunda*, the undescribed Taxodiaceae taxon and *Glyptostrobus* recorded at the 1 cm level. Moderate amounts of angiosperm leaf material was found at the 1 cm level in the section at point C, and significant amounts of *Glyptostrobus* at 3 cm (Fig. 5c).

The top 3 cm of leaf litter in the section at point A was quite rich, recording the following taxa: *Glyptostrobus*, *Metasequoia*, undescribed Taxodiaceae, *Osmunda*, other unidentified ferns, and angiosperms (including a small leaf type; see

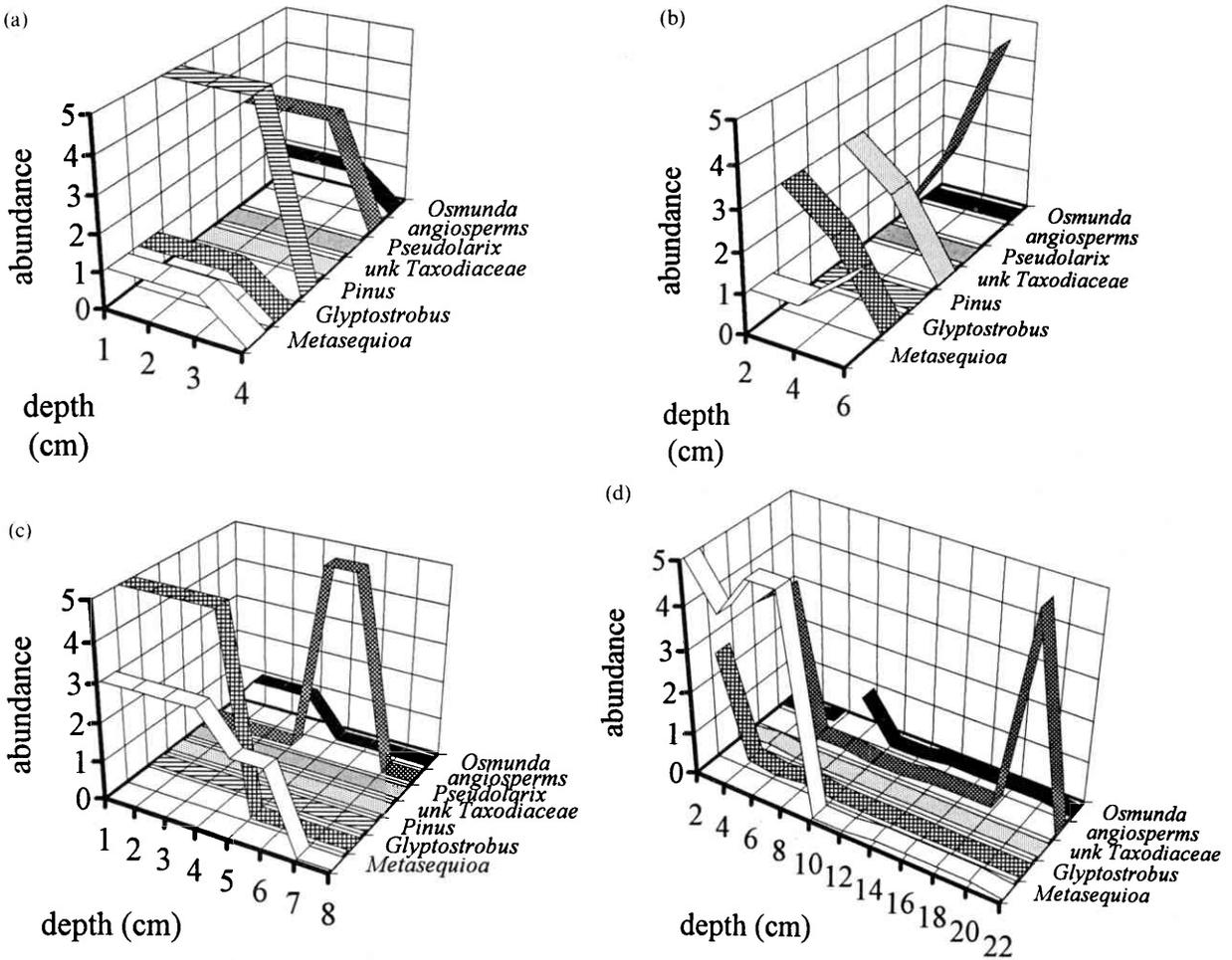


Fig. 3. Relative abundance of principal taxa with depth in vertical section for points near tree 96. (a) Section at point A. (b) Section at point B. (c) Section at point E. (d) Section at point G. Barren intervals (i.e. no taxa scored) correspond to clay partings [Applies to all sections (Figs. 3–7)]

site 7 description). A significant barren interval occurred at 4 cm in the point A section, above which (at 3 cm) a minor peak in angiosperm and *Osmunda* remains was recorded. *Glyptostrobus* was dominant and *Metasequoia* present in lesser amounts in the top 2 cm of the point A section. A significant surface exposure at this site (near A and C) was particularly rich (60–70%) in leaf and cone material of the undescribed Taxodiaceae taxon in association with *Glyptostrobus* (10%).

Site 5 (tree 41 and environs)

Three sample points (A–C) were identified near tree 41 at site 5. The sections analysed (Fig. 6a–c)

varied in depth from 3 cm (point A) to 5 cm (points B and C). Sample points A and B were 1 and 2.5 m from tree 41B respectively (in a line trending ENE), and point C was 0.5 m from tree 41A (WSW). *Metasequoia* was the dominant taxon over much of the section for points B and C (Fig. 6b,c), representing 95% of material at 3 cm depth at point B; however, *Metasequoia* was less abundant at the surface (1–2 cm) than lower in the section (3–5 cm). At point A (Fig. 6a) *Metasequoia* was most abundant at the surface (1 cm), becoming less abundant with depth (2 cm) and absent at 3 cm. *Glyptostrobus* was abundant at point A becoming dominant at 3 cm, but was

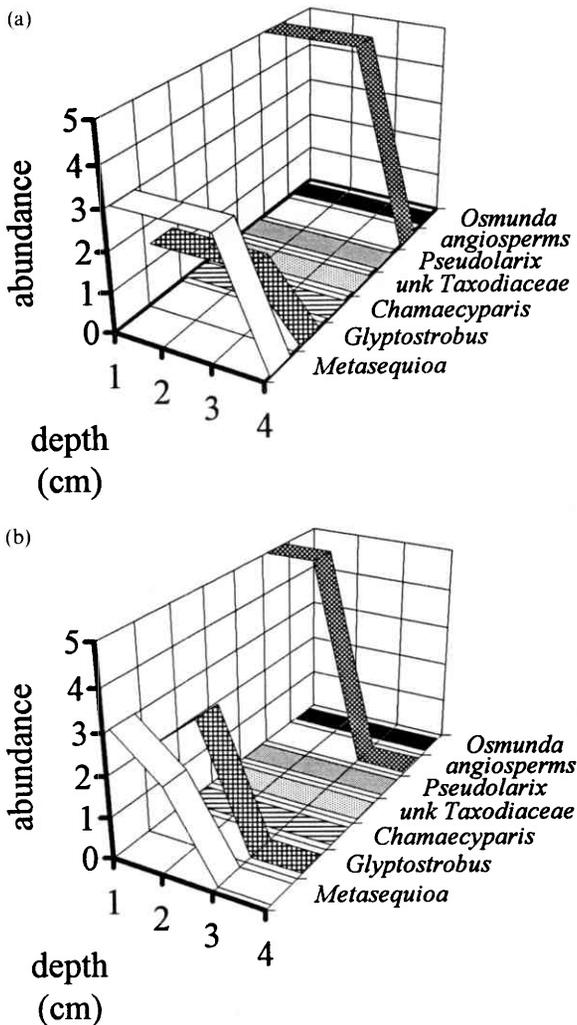


Fig. 4. Relative abundance of principal taxa with depth in vertical section for points near trees 14–17. (a) Section at point A. (b) Section at point B.

lower in abundance in the section at point C becoming much less abundant with depth below 2 cm. *Glyptostrobus* was present as only a trace through most of the section at point B. Material removed during excavation of a trench leading from tree 41B to 41C was rich in *Glyptostrobus* (5) with trace amounts of ?*Chamaecyparis* (+) and small amounts of *Pseudolarix* (1). The upper 3 cm of the section at point C was quite diverse, with the all but one of the scored taxa present at different depths. Angiosperm leaves were recorded

over most of both of the sections at points B and C; however, angiosperms were recorded only as a trace between 2 and 4 cm at point B, but at moderate amounts at 1 cm at point B and over 2 to 4 cm in the point C section. ?*Chamaecyparis* was recorded in trace amounts at points B and C, excepting at 2 cm at point C.

Site 6 (tree 62)

A pit was dug 60 cm southeast of the centre of the large stump of tree 62. Despite the appearance of abundant megafossils on the surface, only trash (unrecognisable megafossil remains) was encountered throughout a 6 cm section examined from this pit. The top 3 cm contained abundant fine roots suggesting that this area was an active soil humic horizon. A trace amount of *Glyptostrobus* leafy twigs was found in this material. Between 3 and 6 cm the leaf-mat was also trash, but at this depth trace amounts of well degraded angiosperm leaves were found.

Site 7 (tree 21)

Five sample points (A–E) were identified near tree 21 at site 7. Only the sections at sample points A, B, D and E were fossiliferous below the litter-mat surface and so data charts are only presented for these points (Fig. 7a–d). The sections analysed varied in depth from 5–7 cm (points A, D and E) to 12 cm (point B). Significant barren intervals (clay partings) were present at 3–4 and 6–7 cm in the point D section (Fig. 7c), at 4 cm in the point E section (Fig. 7d), and at 7 and 11 cm depth in the point B section (Fig. 7b). Preservation of plant megafossils was generally poor for much of section D.

Metasequoia was dominant for the whole section at point E (Fig. 7d), and all but the top 2 cm (0–1 cm) of the section at point A (Fig. 7a), with a peak abundance of 80–90% of material at 3–4 cm depth at point A. Three intervals within the point B section were dominated by *Metasequoia*; 3–4, 9–10, and 12 cm depth (Fig. 7b). *Metasequoia* seed cones were found at 3, 8 and 9–10 cm at point B. Significant other occurrences were a *Glyptostrobus* spike at 1–2 cm in the point E section, an undescribed Taxodiaceae taxon spike at 1–2 cm (and a lesser spike at 6 cm) in the point B section, an

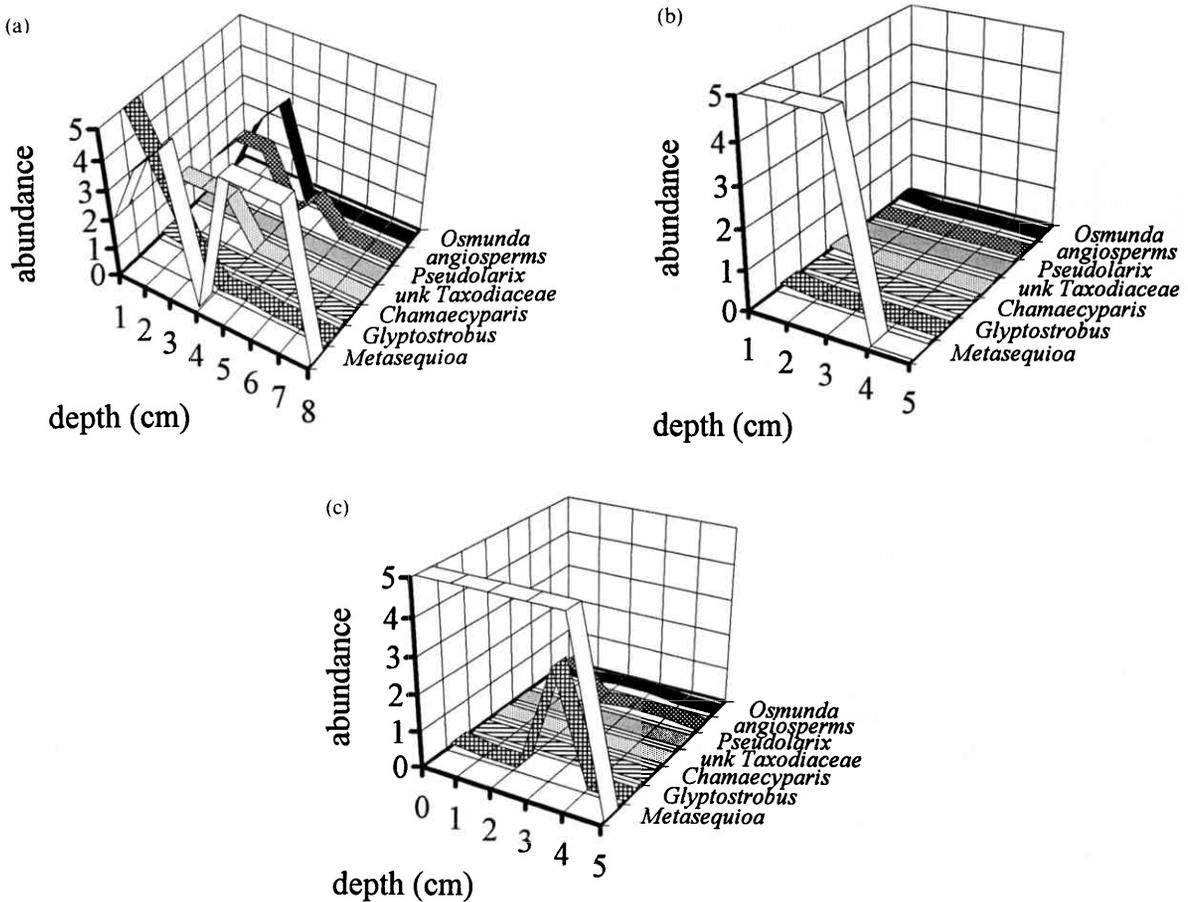


Fig. 5. Relative abundance of principal taxa with depth in vertical section for points near tree 74. (a) Section at point A. (b) Section at point B. (c) Section at point C.

angiosperm spike at the surface (0 cm) of the point A section (and significant abundance scores between 1–3 cm), and an angiosperm spike above a barren clay parting at 2 cm in the point D section. Angiosperm leaves were also abundant at 5 cm in the point B section with lesser spikes at 9 and 12 cm depth in this section (Fig. 7b); in each case 0–1 cm above clay partings. The most common angiosperm leaf-type (at all points at site 7) was a small leaf (non-Betulaceae) about 1 × 2 cm; however, angiosperm diversity was quite high in some sections (especially at point B) with at least 4 types seen, including Betulaceae and ?Juglandaceae, and a narrow leaf (undescribed) at 5 cm at point E. The conifer taxa, *Chamaecyparis*

and *Pseudolarix* were not encountered in any of the site 7 sections.

3.2 Mudstone and channel-sandstone megafloras

Detailed examination and systematic analysis of the megafloras of the channel sands and mudstones are not presented here. However, generalisations can be drawn from a morphotype analysis and initial generic survey of the main mudstone-facies sites, and particularly US188. These sites provide some insight into diversity and the floristic character of the interfluvial vegetation that was contemporaneous with the taxodiaceous swamps represented in the “fossil forests” and associated

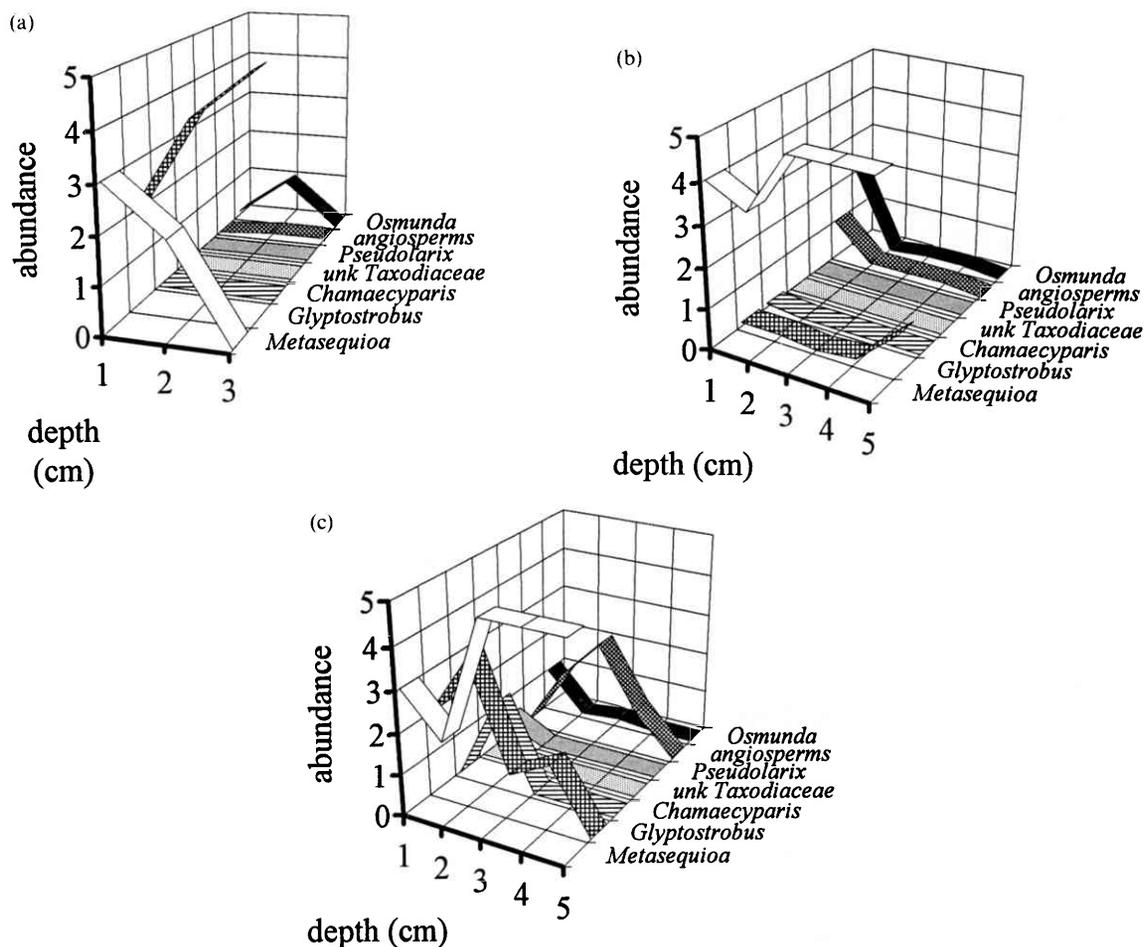


Fig. 6. Relative abundance of principal taxa with depth in vertical section for points near tree 41. (a) Section at point A. (b) Section at point B. (c) Section at point C.

organic layers. Sporadic occurrences of megafossils (principally coniferous seed cones, but also some angiosperm fruits and seeds; Basinger, 1991) in the channel sands allows some understanding of additional plant communities in the regional mosaic.

Basinger (1991) noted the dominance of angiosperms in the mudstone megaforas, compared to the coniferous “fossil forest” organic layers, particularly platanoids, Ulmaceae (cf. *Zelkova*), Betulaceae (*Alnus*, *Betula*), and Juglandaceae. Coniferous foliage (especially *Metasequoia*) and cones were collected at all sites, but were never common in the mudstone floras. Some broadleaved taxa have quite localised stratigraphic and spatial

occurrences, being collected at only 1 or 2 mudstone sites, but not from the same sites in subsequent seasons. For example, leaves of *Ginkgo* have been collected at only one site, and putative leaves of a quercoid (Fagaceae) taxon were collected from site US188 during two separate seasons, but not during intervening collecting seasons at the same site.

Very little mudstone outcrop has been sampled at the Fossil Ridge as its integrity is destroyed by frost action within the thin active layer overlying permafrost. However, ironstone nodules found in the paleosols rarely contain *Alnus* “cones” (Basinger, 1991) and leaf impressions of platanoids and betulaceous leaves. Minor clay-partings within

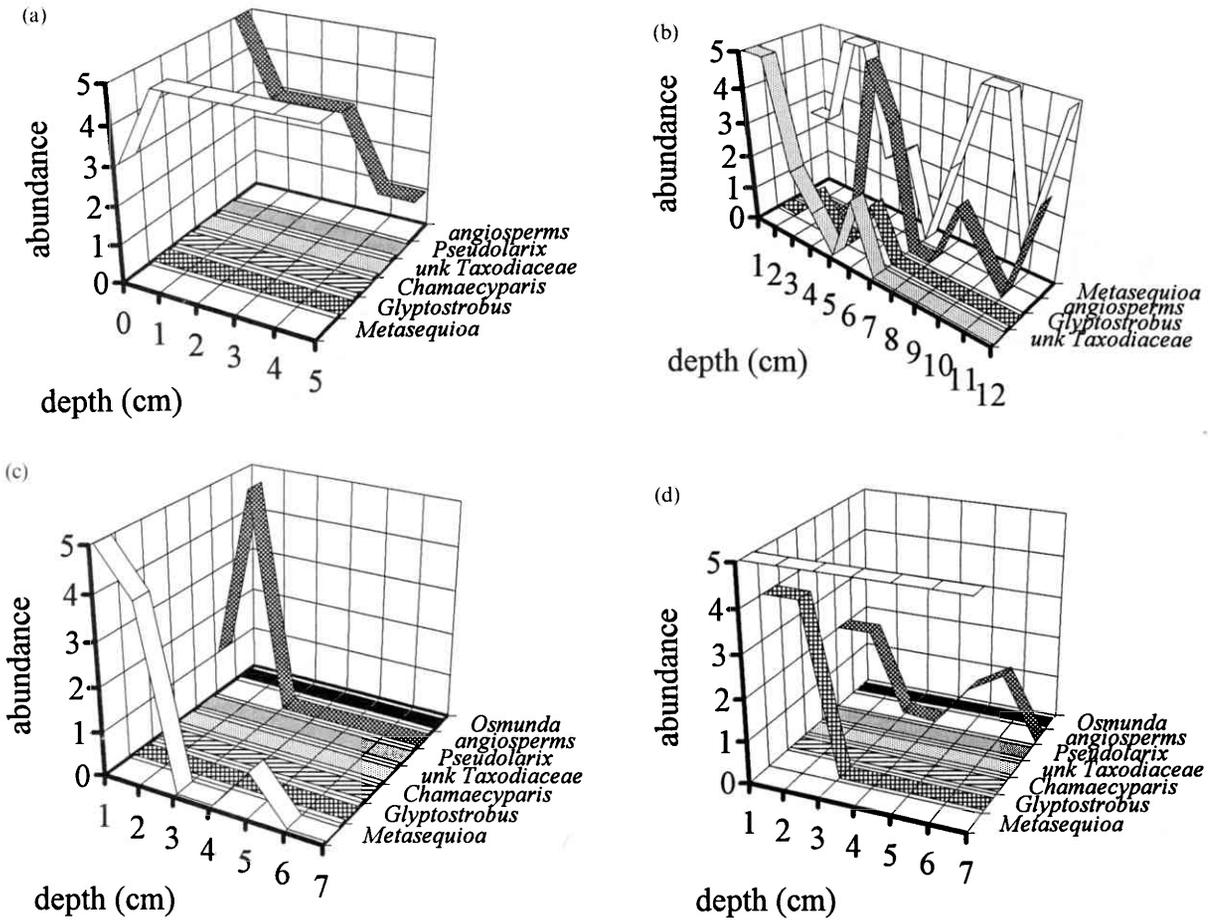


Fig. 7. Relative abundance of principal taxa with depth in vertical section for points near tree 21. (a) Section at point A. (b) Section at point B. (c) Section at point C. (d) Section at point D.

organic layers may be dominated by angiosperm leaves. These occurrences represent taxa encountered in the mudstone floras.

In the US188 florule the dominants (>40% of collected material, >50–70% of outcrop) in successive collections (i.e. samples collected in different years at the same site) were *Betulaceae* (cf. *Betula*) or aff. *Quercus* (Fagaceae), with smaller amounts of *Ulmaceae* (cf. *Zelkova*), magnolids (2 species) and *Cercidophyllum*-complex leaves. Minor though commonly present broadleaved elements in the surveyed site collections included: *Ginkgo*, *Juglandaceae*, aff. *Platanites* and other *Platanaceae*, other hamaleliids, and *Alnus* (*Betulaceae*). Other stratigraphically equivalent sites in the same outcrop as US188 were rich in

either *Cercidophyllum*-complex leaves, or platanooids and other hamaleliids (e.g. US210). Modern forest litter studies have demonstrated that leaves from canopy trees numerically dominate litter, and hence fossil leaf assemblages (Burnham, 1989; Burnham et al., 1992; Greenwood, 1992); it is likely therefore that these megaflores are reflecting forests dominated by *Betulaceae*–*Quercoidae* and *Cercidophyllum*-complex producing canopy trees respectively. Local areas were of moderate to low diversity (typically 10–12 species in 100–200 leaf samples), but site to site variation in species presence indicates a varied and moderately diverse broadleaved-angiosperm forest community. Whether the site to site variation reflects contemporaneous variation in species

membership due to microsite differences, or successional variation associated with the shifting position of the river channels (e.g. Salo et al., 1986), is not clear.

Based on NLR analogy, these broadleaved forests were predominantly if not exclusively composed of deciduous plants. Foliar physiognomy supports this interpretation. The mudstone leaf floras are composed exclusively of leaves with a length to width ratio ($L:W$) close to 1:1 (L/W 1.0), and toothed, lobed or partly lobed forms were common in these floras, as were leaves with their widest point in the lower third of the leaf. Litter collected under tropical to temperate evergreen broadleaved rainforests is dominated by simple entire leaves that have a $L:W > 3:1$ ($L/W > 3.0$) and with the widest point in the middle third of the leaf (Greenwood, 1992; Table 1). Litter collected under dominantly deciduous broadleaved cool temperate and boreal forests is dominated by toothed leaves where the $L:W$ is close to 1:1, with the widest point in the lower third of the leaf, and lobed and partly lobed leaves are common, as seen for the mudstone megaflores (Table 1). Several studies have indicated that $L:W$ reflects aspects of climate (Hall and Swaine, 1981; Christophel and Greenwood, 1988; Wolfe, 1990, 1993; Greenwood, 1992; Gregory and Chase, 1992). Our unpublished data (e.g. Table 1) suggest that Tertiary leaf meg-

aflores dominated by leaves with a $L:W$ close to 1:1 are reflecting deciduous broadleaved forests.

The channel sands associated with both the mudstone floras and the organic layers at Fossil Ridge are only sparsely fossiliferous. Scarce cones and rare foliage of *Pseudolarix*, *Picea*, *Pinus*, other taxa within the Pinaceae, Taxodiaceae and Cupressaceae, and rare *Carya* seeds are the main recognisable megafossils (Basinger, 1991; LePage and Basinger, 1991, 1992). Logs of various sizes also are encountered and rarely in-situ stumps have been found on stabilised point bars. A few exposures of the channel sands at the Fossil Ridge site are richly fossiliferous over very short horizontal and vertical areas of outcrop, representing channel lags. Some of the cones and angiosperm seeds from these channel sands represent taxa also found in the "fossil forest" organic layers, but LePage and Basinger (1992) reported that different species of *Picea* are found in the channel sands and the organic layers (forest floor/swamp facies), respectively.

Channel-sand megaflores generally preserve riparian vegetation (Wing and DiMichele, 1992). However, based on our observations of a number of sites, including areas distal and proximal to the conglomerate wedges of the alluvial fan-meander belt complex defined by Ricketts (1991), it appears likely to us that the coniferous megafossils charac-

Table 1

Summary of mudstone facies megaflores (2 successive collections from the US188 florule); modern litter samples for comparison: Aspen Parkland (Boreal broad-leaved deciduous forest, Namekus Lake, Sask.), Maple-oak-poplar-beech Deciduous Forest (Kingsmere and Pink Lakes, Gatineau National Park, Quebec), Notophyllous Broad-leaved Evergreen Forest (Washpool National Park, New South Wales), and Paratropical-Tropical Rainforest (Mulgrave River, NE Queensland)

Site	Specimens	Morphotypes	L/W^a	% spp. entire ^b
US188 (1990)	115	13	1.6	16.7
US188 (1991)	63	10	1.4	10.0
Namekus Lake	100	9	1.4	0
Kingsmere Lake	106	11	1.5	0
Pink Lake	64	8	1.3	0
Washpool National Park ^c	200	7	3.9	14.3
Mulgrave River ^c	200	20	4.7	95.0

^aMean of all leaf specimens in sample.

^bSimple percent (i.e. leaf species with both entire and non-entire specimens scored as non-entire).

^cSub-samples from original data set of Greenwood (1992, tables xi and xvii).

teristic of the channel sands of the Buchanan Lake Formation also represents the upland (headwater) vegetation of this area in the Eocene.

4. Discussion

The leaf-litter mats (organic layers) of the Geodetic Hills “fossil forests”, Axel Heiberg Island, represent a substantial record of Eocene near-polar forest growth. Greenwood and Basinger (1993) examined two of these organic layers, levels *M* and *N*, and concluded that variation in the floristic character of the level *M* peat layer over the kilometre-scale reflected a *Metasequoia*-dominated swamp forest, but that vertical variation at the centimetre-scale within a 47 cm section through level *N* implied a series of complex shifts between several floristic associations reflecting responses to local hydrological conditions. Greenwood and Basinger (1993) calculated that the organic layer of level *N* represents 500–1000 and probably as much as 2000 yr of accumulation of plant megadetritus, and that multiple stands of the swamp forest are juxtaposed. Patterns of presence and absence and abundance between sites on the level *N* litter-mat, and variation at depth within the forest-floor litter of this Eocene polar forest, have been investigated in more detail here.

Modern autochthonous accumulations of leaf litter in deciduous hardwood forests reflect the canopy biomass and spatial distribution of the standing forest (Burnham et al., 1992). It is reasonable to assume therefore that the observed patterns of vertical and horizontal floristics for the “fossil forest” similarly will reflect forest structure and floristics. However, the study presented here suggests that the incompleteness of the litter mat in vertical sequence from point to point, either through erosion and/or changes in depositional-hydrological character (from peat accumulation to clay), or in-situ decay and compaction within organic layers, contributes much to the observed patterns of floristics (e.g. Spackman et al., 1969; Sadler and Dingus, 1982; MacCabe, 1984; Moore, 1987).

Metasequoia was commonly the dominant mega-

fossil taxon over at least part of any vertical sequence through level *N*, and typically over most of the vertical leaf-mat accumulation. Angiosperm leaf remains were common at all level *N* sites examined, but usually as either trace amounts or at different stratigraphic levels from the main *Metasequoia* abundance peaks. In some instances, angiosperm rich layers were associated with the top of clay partings (e.g. Figs. 3b–d, 7c,d); clay partings correspond to barren depth intervals. Conifer taxa other than *Metasequoia* were sporadic in occurrence between sites, within sites, and at depth within individual sections. In particular, *Glyptostrobus* was present at all sites, but either as a rare or uncommon component of the leaf-mat, or narrowly restricted within the analysed sections. *Glyptostrobus* was usually absent or in low amounts where *Metasequoia* was abundant or dominant. The conifers *Pseudolarix*, ?*Chamaecyparis*, *Pinus* and the undescribed Taxodiaceae taxon were only present at a few sites, and were quite restricted stratigraphically at each site where they were present. These taxa were typically present in low amounts when co-occurring, and more typically one of these conifers was present as the dominant in place of *Metasequoia*, or as the co-dominant either with *Metasequoia* or less commonly, with a second taxon.

Sadler and Dingus (1982) cautioned that short stratigraphic sequences are highly likely to be incomplete, particularly where significant lithological changes occur cyclically within the sequence (such as the shift from peat/coal to clay observed in level *N*). The stratigraphically restricted nature of the litter accumulation of the non-*Metasequoia*-dominated plant associations (i.e. 1–3 cm depth), however, suggests that these communities were short-lived within the period of accumulation of the whole level *N* litter-mat (12–60 cm). Common members of these associations were: ?*Chamaecyparis*, *Pseudolarix*, *Pinus*, various angiosperms (including but not restricted to *Alnus* and other Betulaceae) and the undescribed Taxodiaceae taxon. The limited lateral detection of these associations also implies that they occupied only small areas (2–5 m radius). This may suggest that they reflected gap-phase processes (regeneration after a

canopy tree [= *Metasequoia*] dies). The angiosperm occurrences and some of the diverse conifer associations also may reflect larger scale succession after local flooding, as evidenced by the presence of significant peaks in abundance of some taxa (such as *Alnus*) stratigraphically higher than significant clay partings.

The analysis presented above provides an initial look at a high latitude Eocene forest landscape, and provides some insight into local floristic changes over short time frames within a swamp-forest community. These plant communities have no exact modern analogue as today no forests occur at equivalent high latitudes. The diverse regional mosaic of angiosperm-dominated flood-plain forests, and taxodiaceous swamp forests, with their successional mosaics of Betulaceae, and pinaceous and cupressaceous conifers, is in direct contrast to the modern tundra environment of these areas.

5. Conclusions

The following conclusions were reached:

(1) *Metasequoia* is the dominant contributor to litter accumulation over the time span represented by the most complete sections examined (1000–2000 yr) and is therefore the main canopy dominant of these Eocene polar swamp forests; angiosperms may be present as either a trace or in significant amounts. *Alnus* is commonly the main angiosperm taxon, although several as yet unidentified angiosperm taxa may be common over short vertical intervals.

(2) Lithic variation with depth at different points over the level *N* layer suggests that short-term changes in local swamp hydrology, perhaps representing minor flooding events, occurred at different points at different times during peat accumulation (Greenwood and Basinger, 1993); the association of some episodes of floristic change at depth with the clay partings implies recovery or successional processes occurred within these forests.

(3) The short interval (1–3 cm depth) and short distance (2–5 m) changes in floristics in the level *N* leaf mat implies cycles of change at small scales.

(4) *Glyptostrobus* is uncommon, but where it is present in significant quantities, *Metasequoia* is usually not dominant and angiosperms are either absent or present in low quantities; other taxa, particularly conifers such as *Chamaecyparis*, *Pseudolarix* and an undescribed Taxodiaceae taxon, are present only sporadically. Where present, these other conifer taxa may co-occur, or one conifer taxon may be dominant.

(5) The sequence of presence and absence of floristic associations in vertical sections through level *N*, is different at each point examined. This suggests that some parts of level *N* reflect an incomplete or truncated record of the floristic history, but also that the plant community varied in composition horizontally.

A mosaic of taxodiaceous (*Metasequoia* ± *Glyptostrobus*) swamp forest, mixed conifer forests, and *Alnus* (± other broadleaved angiosperms and *Osmunda*/other ferns) bog, appears to have produced both the leaf-mats and the in-situ stumps, with the *Metasequoia* swamp the dominant peat-accumulating phase. Taxodiaceous layers are interpreted as areas of standing water which may have experienced seasonal water-level fluctuations. *Alnus*/fern communities reflect areas of slightly higher peat and hence locally lower water tables, or may reflect areas of early succession after disturbance. The areal extent and position of these different hydrologically controlled plant communities appears to have changed throughout the interval of accumulation of the peat layer examined.

Detailed reconstruction of the paleoenvironment reflected in the mudstone and channel-sands facies is unwarranted at this stage; however, the mudstone-facies megaflores examined in this present report (US188 and US210; see also Basinger, 1991) reveal temporal and spatial variation in dominance and composition of the floodplain forests of this area of the Arctic in the middle Eocene. Broadleaved deciduous forests containing a moderately diverse assemblage of Betulaceae (cf. *Betula* and *Alnus*), Fagaceae (aff. *Quercus*), Ulmaceae (cf. *Zelkova*), Juglandaceae, *Ginkgo*, platanoids, *Cercidophyllum*-complex plants and other broadleaved plants with modern NLR's that are

deciduous appear to reflect successional or micro-site variation within this floodplain environment.

Acknowledgements

We thank E. McIver and B. LePage (Sask.), L. Savard (Laval), T. Sweda and S. Kojima (Nagoya), and K. Hyashi (Ehime), for field assistance during the 1992 field season, and C. Greenwood and C. Nelson for assistance preparing and analysing mudstone-flora and modern leaf-litter samples. This research was made possible through field support from the Polar Continental Shelf Project, and Natural Sciences and Engineering Research Council (Canada) Operating Grant No. OGP0001334 to JFB, and was completed while DRG was a NSERC International Postdoctoral Fellow at the University of Saskatchewan. DRG also acknowledges the provision of support and facilities during manuscript preparation while a Smithsonian Postdoctoral Fellow at the National Museum of Natural History. We thank also W. DiMichele, B. LePage and E. McIver for their comments on the manuscript.

References

- Basinger, J.F., 1991. The fossil forests of the Buchanan Lake Formation (early Tertiary), Axel Heiberg Island, Canadian high arctic: preliminary floristics and paleoclimate. In: R.L. Christie and N.J. McMillan (Editors), *The Fossil Forests of Tertiary Age in the Canadian Arctic Archipelago*. *Geol. Surv. Can. Bull.*, 403: 39–66.
- Burnham, R.J., 1989. Relationships between standing vegetation and leaf litter in a paratropical forest: implications for paleobotany. *Rev. Palaeobot. Palynol.*, 58: 5–32.
- Burnham, R.J., Wing, S.L. and Parker, G.G., 1992. The reflection of deciduous forest communities in leaf litter: implications for autochthonous litter assemblages from the fossil record. *Paleobiology*, 18(1): 30–49.
- Chaney, R.W., 1924. Quantitative studies of the Bridge Creek flora. *Am. J. Sci.*, 8: 127–144.
- Christophel, D.C. and Greenwood, D.R., 1988. A comparison of Australian tropical rain forest and Tertiary fossil leafbeds. In: R. Kitching (Editor), *The Ecology of Australia's Wet Tropics*. *Proc. Ecol. Soc. Aust.*, 15: 155–162.
- Christophel, D.C., Harris, W.K. and Syber, A.K., 1987. The Eocene Flora of the Anglesea locality, Victoria. *Alcheringa*, 11: 303–323.
- Clymo, R.S., 1983. Peat. In: A.J.P. Gore (Editor), *Mires: Swamp, Bog, Fen and Moor. General studies. Ecosystems of the World*, 4A. Elsevier, Amsterdam, pp. 159–224.
- Clymo, R.S., 1984. The limits of peat growth. *Philos. Trans. R. Soc. London B*, 303: 605–654.
- Cohen, A.S., 1985. The Okefenokee Swamp: a low sulfur end-member of a depositional model for coastal plain coals. In: R.A. Rahmani and R.M. Flores (Editors), *Sedimentology of Coal and Coal-bearing Sequences. Spec. Publ. Int. Assoc. Sedimentol.*, 7. Blackwell, Oxford, pp. 231–240.
- Collinson, M.E. and Scott, A.C., 1987. Implications of vegetational change through the geological record on models for coal-forming environments. In: A.C. Scott (Editor), *Coal and Coal-bearing Strata: Recent Advances. Geol. Soc. Spec. Publ.*, 32: 67–85.
- Crame, J.A., 1992. Review—Late Cretaceous palaeoenvironments and biotas: an Antarctic perspective. *Antarct. Sci.*, 4(4): 371–382.
- Davis, J.H., 1946. The peat deposits of Florida; their occurrence, development and uses. *Bull. Fla. Geol. Surv.*, 30: 1–247.
- Ferguson, D.K., 1985. The origin of leaf-assemblages—new light on an old problem. *Rev. Palaeobot. Palynol.*, 46: 117–188.
- Francis, J.E., 1986. Growth rings in Cretaceous and Tertiary wood from Antarctica and their palaeoclimatic implications. *Palaeontology*, 29(4): 665–684.
- Francis, J.E., 1991. The dynamics of polar fossil forests: Tertiary fossil forests of Axel Heiberg Island, Canadian Arctic Archipelago. In: R.L. Christie and N.J. McMillan (Editors), *The Fossil Forests of Tertiary Age in the Canadian Arctic Archipelago*. *Geol. Surv. Can. Bull.*, 403: 29–38.
- Francis, J.E. and McMillan, N.J., 1987. Fossil forests of the far north. *Geos.* 16(1): 6–9.
- Greenwood, D.R., 1991. The taphonomy of plant macrofossils. In: S.K. Donovan (Editor), *The Processes of Fossilization*. Belhaven, London, pp. 141–169.
- Greenwood, D.R., 1992. Taphonomic constraints on foliar physiognomic interpretations of Late Cretaceous and Tertiary palaeoclimates. *Rev. Palaeobot. Palynol.*, 71: 142–194.
- Greenwood, D.R. and Basinger, J.F., 1994. Stratigraphy and floristics of peat-coal layers of Eocene swamp forests from Axel Heiberg Island, Canadian High Arctic Archipelago. *Can. J. Earth Sci.*, 31: in press.
- Gregory, K.M. and Chase, C.G., 1992. Tectonic significance of paleobotanically estimated climate and altitude of the late Eocene erosion surface, Colorado. *Geology*, 20: 581–585.
- Grosse-Brauckmann, G., 1986. Analysis of vegetative plant macrofossils. In: B.E. Berglund (Editor), *Handbook of Holocene Palaeoecology and Palaeohydrology*. Wiley, Chichester, pp. 591–618.
- Hall, J.B. and Swaine, M.D., 1981. Distribution and Ecology of Vascular Plants in a Tropical Rainforest Vegetation in Ghana. *Geobotany*, 1. Junk, The Hague, 383 pp

- Jefferson, T.H., 1982. Fossil forests from the Lower Cretaceous of Alexander Island, Antarctica. *Palaeontology*, 25: 681–708.
- LePage, B.A. and Basinger, J.F., 1991. A new species of *Larix* (Pinaceae) from the early Tertiary of Axel Heiberg Island, Arctic Canada. *Rev. Palaeobot. Palynol.*, 70: 89–111.
- LePage, B.A. and Basinger, J.F., 1992. New species of *Picea* from the Eocene of Axel Heiberg Island, Arctic Canada. *Proc. 4th I.O.P. Conf.*, Paris, August–September 1992, p. 97 (Abstr.).
- MacCabe, P.J., 1984. Depositional environments of coal and coal-bearing strata. In: R.A. Rahmani and R.M. Flores (Editors), *Sedimentology of Coal and Coal-bearing sequences*. Spec. Publ. Int. Assoc. Sedimentol., 7. Blackwell, Oxford, pp. 13–42.
- MacIntyre, D.J., 1991. Pollen and spore flora of an Eocene forest, Eastern Axel Heiberg Island, N.W.T. In: R.L. Christie and N.J. McMillan (Editors), *The Fossil Forests of Tertiary Age in the Canadian Arctic Archipelago*. *Geol. Surv. Can. Bull.*, 403: 83–98.
- Moore, P.D., 1986. Hydrological changes in mires. In: B.E. Berglund (Editor), *Handbook of Holocene Palaeoecology and Palaeohydrology*. Wiley, Chichester, pp. 91–107.
- Moore, P.D., 1987. Ecological and hydrological aspects of peat formation. In: A.C. Scott (Editor), *Coal and Coal-bearing Strata: Recent Advances*. *Geol. Soc. Spec. Publ.*, 32: 7–16.
- Moore, P.D., 1989. The ecology of peat-forming processes: a review. In: P.C. Lyons and B. Alpern (Editors), *Peat and Coal: Origin, Facies, and Depositional Models*. *Int. J. Coal Geol.*, 12: 89–103.
- Moore, T.A. and Hilbert, R.E., 1992. Petrographic and anatomical characteristics of plant material from two peat deposits of Holocene and Miocene age, Kalimantan, Indonesia. *Rev. Palaeobot. Palynol.*, 72: 199–227.
- Ricketts, B.D., 1991. Sedimentation, Eureka tectonism and the fossil forest succession of Eastern Axel Heiberg Island, Canadian Arctic Archipelago. In: R.L. Christie and N.J. McMillan (Editors), *The Fossil Forests of Tertiary Age in the Canadian Arctic Archipelago*. *Geol. Surv. Can. Bull.*, 403: 1–28.
- Sadler, P.M., 1981. Sediment accumulation rates and the completeness of stratigraphic sections. *J. Geol.*, 89: 569–584.
- Sadler, P.M. and Dingus, L.W., 1982. Expected completeness of sedimentary accumulations: Estimating a time-scale dependent, limiting factor in the resolution of the fossil record. *Proc. 3rd North Am. Paleontol. Conv.*, 2, pp. 461–464.
- Salo, J., Kalliola, R., Häkkinen, I., Mäkinen, Y., Niemelä, P., Puhakka, M., and Coley, P.D., 1986. River dynamics and the diversity of Amazon lowland forest. *Nature*, 322: 254–258.
- Spackman, W., Riegel, W.L. and Dolsen, C.P., 1969. Geological and biological interactions in the swamp-marsh complex of Southern Florida. In: E.C. Dapples and M.E. Hopkins (Editors), *Environments of Coal Deposition*. *Geol. Soc. Am. Spec. Pap.*, 114: 1–35.
- Spicer, R.A., 1990. Reconstructing high latitude Cretaceous vegetation and climate: Arctic and Antarctic compared. In: T.N. Taylor and E.L. Taylor (Editors), *Antarctic Paleobiology. Its Role in the Reconstruction of Gondwana*. Springer, New York, NY, pp. 27–36.
- Spicer, R.A. and Corfield, R.M., 1992. A review of terrestrial and marine climates in the Cretaceous with implications for modelling the 'Greenhouse Earth'. *Geol. Mag.*, 129(2): 169–180.
- Taggart, R.E., 1988. The effect of vegetation heterogeneity on short stratigraphic sequences. In: W.A. DiMichelle and S.L. Wing (Editors), *Methods and Applications of Plant Paleocology*. *Paleontol. Soc. Spec. Publ.*, 3, pp. 147–171.
- Wing, S.L. and DiMichele, W.D., 1992. Ecological characterization of fossil plants. In: A.K. Behrensmeyer, J.D. Damuth, W.A. DiMichele, R. Potts, H.-D. Sues and S.L. Wing (Editors), *Terrestrial Ecosystems through Time. Evolutionary Paleocology of Terrestrial Plants and Animals*. Univ. Chicago Press, Chicago, IL, pp. 139–182.
- Wing, S.L. and Greenwood, D.R., 1993. Fossils and fossil climate: the case for equable continental interiors. In: J.R.L. Allen, B.J. Hoskins, B.W. Sellwood and R.A. Spicer (Editors), *Palaeoclimates and their Modelling with Special Reference to the Mesozoic Era*. *Philos. Trans. R. Soc. London B*, 341: 243–252.
- Wolfe, J.A., 1980. Tertiary climates and floristic relationships at High Latitudes in the Northern Hemisphere. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 30: 313–323.
- Wolfe, J.A., 1985. The distribution of major vegetational types during the Tertiary. In: E.T. Sundquist and W.S. Broecker (Editors), *The Carbon Cycle and Atmospheric CO₂. Natural Variations Archaen to Present*. *Am. Geophys. Union Geophys. Monogr.*, 32, pp. 357–375.
- Wolfe, J.A., 1987. Late Cretaceous–Cenozoic history of deciduousness and the terminal Cretaceous event. *Paleobiology*, 13(2): 215–226.
- Wolfe, J.A., 1990. Paleobotanical evidence for a marked temperature increase following the Cretaceous/Tertiary boundary. *Nature*, 343: 153–156.
- Wolfe, J.A., 1993. A method of obtaining climatic parameters from leaf assemblages. *US Geol. Surv. Bull.*, 2040, 73 pp.