

## Stratigraphy and floristics of Eocene swamp forests from Axel Heiberg Island, Canadian Arctic Archipelago

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A record of polar Eocene forests is preserved as in situ tree-stump fields and leaf-litter mats in Buchanan Lake Formation sediments on Axel Heiberg Island, in the Canadian Arctic Archipelago. Stratigraphic examination at the centimetre to metre scale of peat-coal lithology and macrofossil floristics in two levels of these fossil forests reflects small-scale changes in forest composition and swamp hydrology horizontally and temporal variation vertically. Root system structure and tree base stratigraphy suggest that exposed tree stumps may not include only coeval individuals of a single forest stand, but rather also individuals representing different phases of the forest through one cycle of the hydrological development of this Eocene polar forest community. Earlier calculations of stand density and biomass, based upon the assumption that all stumps represent coeval trees, may therefore be greatly overestimated. A mosaic of *Alnus* - fern bog, mixed coniferous community, and taxodiaceous (*Metasequoia* - *Glyptostrobus*) swamp appears to have produced both the leaf mats and the in situ stumps, with the taxodiaceous swamp the dominant peat-accumulating phase.

Les sédiments de la Formation de Buchanan sur l'île Axel Heiberg, dans l'archipel de l'Arctique canadien, renferment des champs de souches d'arbres et des tapis de litières de feuilles in situ qui document l'existence d'une forêt polaire à l'Éocène. L'étude stratigraphique, à l'échelle du centimètre au mètre, des unités lithologiques de tourbe-houille et de la flore macrofossilifère représentant deux niveaux de ces forêts fossilisées reflète à petite échelle des changements horizontaux dans la composition des espèces forestières et de l'hydrologie des marais, et verticalement des variations temporelles. La structure du système de racines, jointe à la stratigraphie fondée sur les espèces d'arbres, suggère que les souches d'arbres exposées ne représentent pas uniquement des spécimens contemporains d'un peuplement forestier unique, mais plutôt des spécimens qui appartiennent à différentes phases d'une forêt soumise à un cycle de développement hydrologique qui a affecté cette communauté forestière polaire de l'Éocène. Les évaluations faites auparavant de la densité et la biomasse du peuplement étaient fondées sur l'hypothèse que toutes les souches représentent uniquement des arbres contemporains, par conséquent elles sont fortement surestimées. Une mosaïque formée d'*Alnus* - fougères de tourbière, d'une communauté mixte de conifères et d'un marais à Taxodiacées (*Metasequoia* - *Glyptostrobus*) a vraisemblablement produit les tapis de feuilles et les souches in situ, et c'est dans ce marais à Taxodiacées qu'est apparue la plus importante phase d'accumulation de la tourbe.

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### Introduction

Fossil forests are assemblages of tree stumps preserved in their growth positions at a single stratigraphic level (Jefferson 1982; Francis 1991). Such autochthonous plant fossil assemblages provide information on the stand structure and synecology of ancient forest communities (e.g., Fowler et al. 1973; Jefferson 1982; Collinson and Scott 1987; Francis 1991; Taylor et al. 1991). In contrast with allochthonous fluvio-lacustrine plant fossil deposits, fossil forests preserve patterns of abundance and biomass of forest ecosystems approximately intact, as well as spatial relationships of some of the forest constituents. Recent studies on high-latitude fossil-forest stands indicate stem densities of between 325 and 484 trees/h for Eocene Arctic forests (Francis 1991) and 258 trees/h for Triassic Antarctic forests (Taylor et al. 1991). A key problem in determining stem densities, spatial relationships, and biomass, however, is time-averaging; that is, determining whether the in situ stumps were all alive at the same time and, in turn, killed and preserved at the same time.

If trees from within a single continuously growing forest die at different times and are preserved over a geologically short time interval (500-1000 years), later compression of the swamp-peat may bring tree stumps from different time intervals (i.e., lived and died at different times) into stratigraphic juxtaposition. Subsequent erosion may expose all of these stumps

and give the impression that all of the stumps represent coeval members of a single forest community which were killed and preserved in a single catastrophic event. Evaluation of standing biomass (as stems per hectare) and of stand structure and dynamics, based upon assumptions that stumps are coeval, may therefore be grossly overestimated and may misrepresent species composition and relative abundance.

Leaf litter of modern forests reflects the spatial arrangement, canopy composition, and relative biomass (stem basal area) of the standing forest (Chaney 1924; Ferguson 1985; Greenwood 1991, 1992; Burnham et al. 1992). Therefore, autochthonous fossil leaf litter layers will reflect the spatial arrangement and biomass of the palaeovegetation. Such reconstruction of forest structure is also dependent on whether a litter layer represents deposition within the life of a single forest, or an accumulation of successive stands. Floristic variation from point to point must be determined as being caused by either spatial (lateral facies changes) or temporal (vertical stratigraphic changes) variation (e.g., Taggart 1988; Barrett and Christophel 1990; Greenwood 1991).

The stand structure and dynamics of some of the fossil forests of Axel Heiberg have been briefly examined (Francis 1991; Basinger 1991). The original study by Francis (1991) was based on the unstated assumption that all of the stumps within a single layer were alive at the same time. Stem densities and biomass estimates were derived by measuring the size and position of all exposed stumps. Preliminary examination of the leaf layers had suggested that lateral variation in species composition reflected local community structure but did not address

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variation with depth within the leaf litter layer (Basinger 1991).

Lithology of peats and low-grade coals can be assessed based on colour and the preservation or absence of recognizable plant macrofossils (Moore 1989; Moore and Hilbert 1992). Differences in coal lithology within a single seam can be attributed to the former existence of a mosaic of plant communities, controlled in part by local hydrological conditions, and the plant types present, as well as subsurface diagenetic processes (McCabe 1984; Moore 1986, 1987; Collinson and Scott 1987; Cameron et al. 1989; Moore and Hilbert 1992). (Modern taxodiaceous swamps in Florida contain mosaics of different plant subcommunities, reflecting differences in local hydrology, substrate, and disturbance history (Davis 1946; Spackman et al. 1969; Collinson and Scott 1987).) Stratigraphic examination of floristic and lithological character within seams will therefore demonstrate differences in the hydrological regime and plant community type within a coeval surface and successional changes over time in vertical section (McCabe 1984; Moore 1986; Cameron et al. 1989).

If the assumption of coeval stumps is valid, then each stump should be rooted at the same stratigraphic level, with roots similarly penetrating the peat substrate. Variation in floristics laterally is likely to have been controlled by local hydrology and therefore may be reflected in local lithological differences within the peat leaf-litter layer. In a similar manner, temporal changes in floristics, controlled by either local hydrological changes or disturbance events, are likely to be reflected by both changes in peat lithology and floristics with depth through the peat layer.

Recent fieldwork, reported here, questions some of the assumptions upon which earlier analyses of the Axel Heiberg Eocene fossil forests were based. A detailed lithostratigraphy (centimetre to metre scale) and spatial changes in floristics of two laterally extensive peat-coal layers are presented. To assess whether these fossil-forest stands represent coeval trees or a succession of stands, root system spatial and stratigraphic organization has been examined. Also considered is the relationship between individual leaf layers and local spatial and temporal mosaics of hydrologic conditions and plant community structure.

### Materials and methods

Macrofloras in Buchanan Lake Formation (upper coal member) sediments preserve a record of near-polar vegetation and environments near the Geodetic Hills on Axel Heiberg Island (Fig. 1) in the Canadian Arctic Archipelago (Basinger 1991; McIntyre 1991). Ricketts (1991) interprets this sequence as a meander plain fed by alluvial fans. The upper coal member of the Buchanan Lake Formation has been dated palynologically as Eocene (Ricketts and McIntyre 1986; McIntyre 1991). Well-preserved taxodiaceous fossil forests are preserved in carbonaceous paludal facies of these sediments (Basinger 1991; Francis 1991). Rickett's (1991) upper coal member of the Buchanan Lake Formation is represented at the fossil forest site by a repeating sequence of lacustrine shales, fluvial and fluviolacustrine sandstones and sandy claystones, paleosols, and peaty coal seams (Fig. 2a) exhibiting varying degrees of humifaction (Ricketts 1991; Goodarzi et al. 1991). Peaty coal layers at the site were originally labelled (e.g., levels M, N, and O) in descending alphabetical series (i.e., M is stratigraphically higher than levels N or O) by Francis (1991), and this convention is continued here. Each major coal layer is

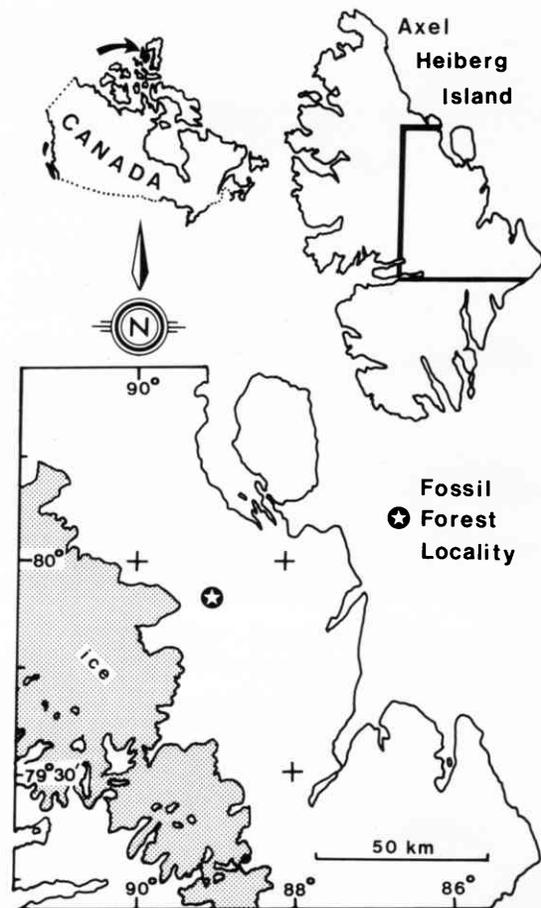


FIG. 1. Location map of the Eocene fossil-forest site, Buchanan Lake Formation, Geodetic Hills area, Axel Heiberg Island, Canadian Arctic Archipelago.

about 0.5–2 m thick and may be laterally continuous for more than 2 km (see also Ricketts 1991). In situ stumps comprising “fossil forests” commonly occur within or overlying coal seams. One of the most extensive fossil forests, level N of Francis (1991), is embedded in a coal layer in which mummified leaf litter is clearly recognizable (Figs. 2b and 2c). The fossil forest of level N and the peat layer of level M are considered here (Figs. 2a and 2b).

To test the assumption of coeval fossil-forest stump and litter layers of earlier studies (Basinger 1991; Francis 1991), a series of trenches were dug through vertical edge exposures of the in situ stump-litter layer (level N of Francis' nomenclature) (Fig. 2b) and a trench dug horizontally within the surface exposure of this layer (Figs. 2c and 2d). Samples of the leaf litter-coal (10 × 10 × 5 cm) were collected in vertical sequence within the edge sections to reveal the stratigraphy of the peat leaf-litter layer. The horizontal trench was dug to expose root systems of some tree stumps to reveal their spatial arrangement, laterally and vertically, within the litter layer and any lateral and vertical variation in the microtopography of the peat surface.

The horizontal trench in level N (Figs. 2c and 2d) passed near several small (<10 cm diam.) at peat surface) in situ stumps, a medium-sized stump (>10–30 cm diam.) and a large stump (1 m diameter). An access trench was first dug 40 cm from the stumps and the peat stockpiled at the site. Slabs

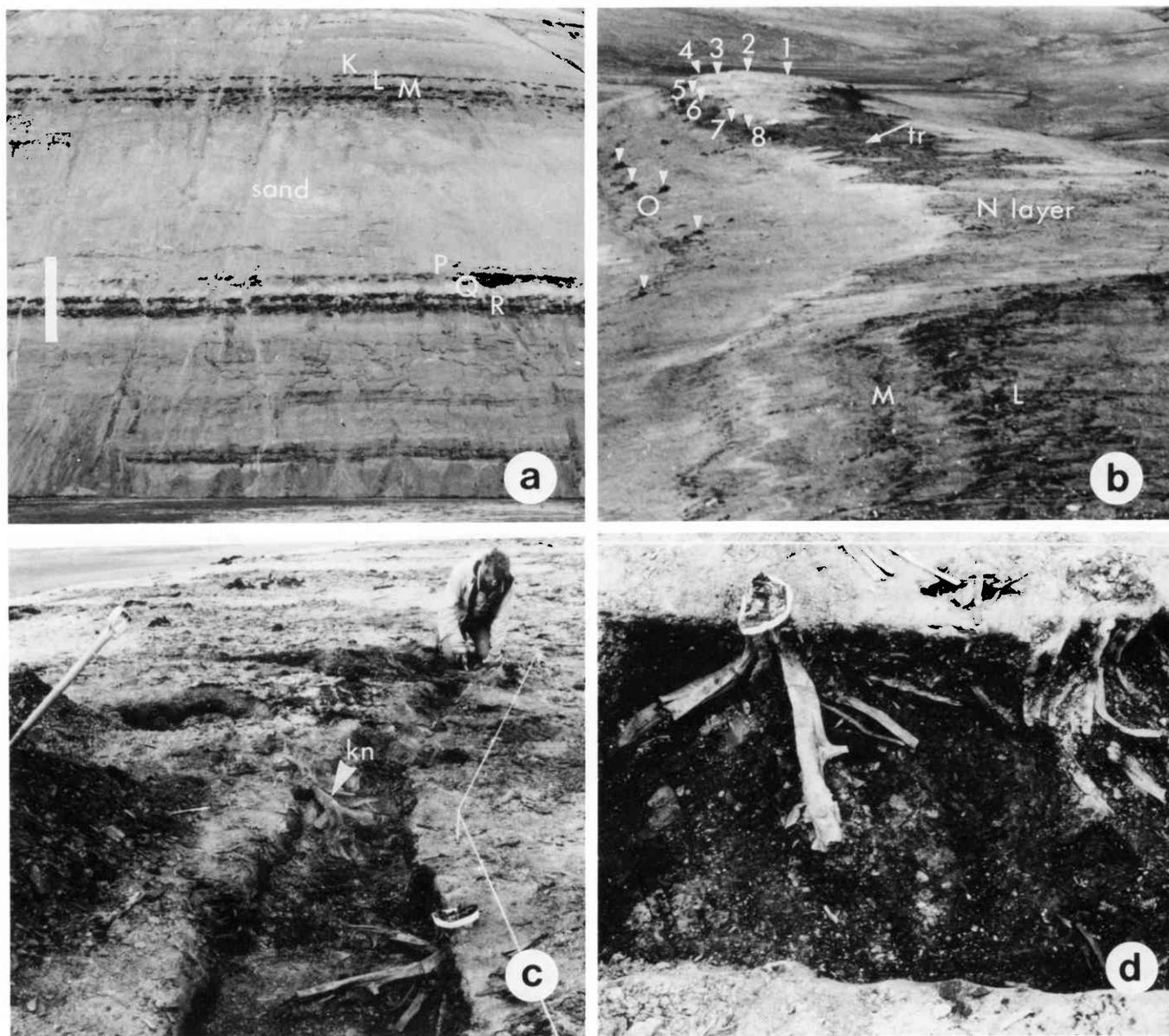


FIG. 2. Stratigraphy of the upper coal member and the fossil forest. (a) Photograph showing alternating sequence of swamp-forest peat-coal layers (K-R), fluvial sandstones, lacustrine shales, and paleosols; fossil-forest site (east ridge, Basinger 1991). Scale bar = 10 m. (b) Photograph showing exposed horizontally lying peat (leaf litter) layer with in situ tree stumps from levels N and O (arrowheads approx. 1 m diam.). The positions of the vertical stratigraphic sections through level N are indicated with arrowheads and the numbers 1-8; tr, position of the horizontal trench. (c) Photograph showing horizontal trench through leaf-litter layer of level N. Note in situ stumps and root systems. kn, position of putative pneumatophore or taxodiaceous "knee." Person for scale. (d) Photograph (detail) of trench showing root systems of in situ stumps (trench width 0.6 m).

of peat, approximately  $20 \times 20 \times 10$  cm, were then sequentially removed along a transect and each sample labelled with its vertical orientation recorded on the sample. After removal of the peat samples, small spatulas and brushes were used to expose the root systems of the in situ stumps.

Detailed examination of the stratigraphic sections exposed by the vertical edge trenches through level N (Fig. 2b, 1-8) were used to assess stratigraphic variation within a 30 m lateral transect. Floristic variation with depth was assessed from samples collected from one of these sections, section 7 (labelled trench G elsewhere), using the procedure outlined below.

A less detailed transect followed the stratigraphically higher

level M laterally for about 1.5 km to assess large-scale variation in floristics. A traverse followed level M horizontally from the fossil forest site proper, along "east ridge" to a point where level M became totally obscured by cover (Fig. 3). Samples of coal,  $10-15 \times 10 \times 5$  cm, were collected from the basal clay-coal contact at about 100-125 m intervals. The coal samples were composed largely of mummified coniferous material (foliage, cones, and other organs), and so macrofossils were extracted by simply dispersing the dry peat manually. Material was sorted according to organ type (cone or other reproductive structure, foliage, etc.). A semiquantitative analysis of the level M transect is presented here using a five point abundance scale (whole or equivalent recognizable

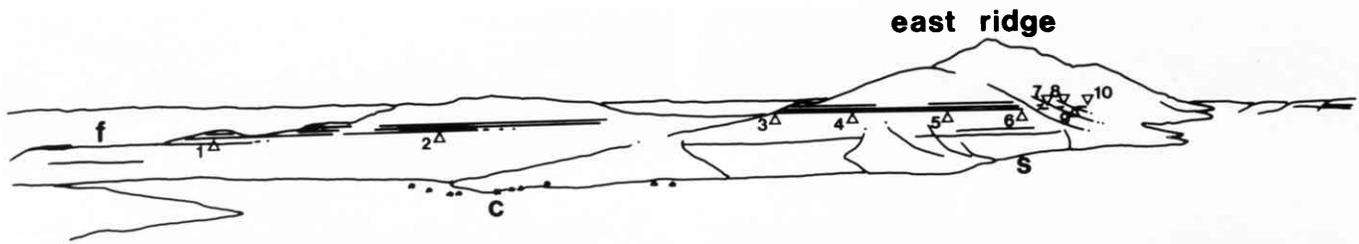


FIG. 3. Sketch of the east ridge and the fossil-forest site (*f*) showing the position of level M and the transect sample points (1–10). Fig. 2a was photographed at *s* and the campsite was at *c*. The distance between each sample point from points 3 to 10 is approximately 100 m and the total distance between *f* and *s* is 2 km.

organs, see below) used in Quaternary macrofossil studies (Grosse-Brauckmann 1986, p. 608).

## Results

### Root systems

The excavation of the horizontal trench revealed intact root systems for the two small stumps and for the medium-sized stump (Fig. 2d); however, no evidence for the root system of the large stump was found in the excavated peat, with only a minimal amount of root material remaining at the peat surface. It would appear that the root system of this individual either rotted after burial, or the individual was dead prior to burial and the root system was already in an advanced state of decay. Clay was found to be domed beneath this large stump as well as other large stumps of level N. The root systems examined were consistent with conifer root systems. The flattened plank-like appearance of the major roots (e.g., Fig. 2d) is probably due to compression, but may also reflect a degree of planarity in the living roots that may be indicative of shallow-rooted trees in swamp conditions (Munaut 1986). A root structure exposed in excavation strongly resembled a pneumatophore (or “knee”; Fig. 4) such as those produced by some Taxodiaceae. This structure was geniculate, resembling the form produced by the modern *Glyptostrobus pensilis* Koch (Fowler et al. 1973), and not conical as seen in *Taxodium distichum* (L.) Rich. Similar structures were found projecting from the unexcavated peat surface.

The positions of the stump bases were variable within the peat, but the basal level of the peat (possibly representing the establishment microtopography of the preceding paleosol) was also variable. Compaction of the sediments may have contributed to variations in apparent thickness and microtopography of the peat and peat–clay contact. However, it is likely, given the very low compaction ratios of these sediments, that the microtopography of the peat and peat–clay contact reflects original highs and lows in the swamp forest. Similar microtopographic patterns seen in modern peat swamps correlate with small-scale floristic changes, due to differences in water level.

The roots that radiate from the small to medium stumps occur at the mid-level of the peat layer; however, a significant number of large roots and branch roots extend to lower levels. These roots did not appear to penetrate the basal clay. Significantly, the remnants of the large stump root system encountered in the trench, and additional large stumps nearby, stand in relief and appear to sit atop the peat layer. However, excavation beneath these stumps demonstrated that they were underlain by clay, suggesting that they were rooted directly in the preceding clay paleosol. The implication is that the largest



FIG. 4. Closeup of taxodiaceous “knee” noted in Fig. 2c, exposed in the trench through level N. Scale bar = 2.0 cm.

size stumps may represent trees that existed throughout much of the period of peat (leaf litter) accumulation preserved in level N.

### Vertical peat stratigraphy (level N)

Sections through level N revealed interbedding of peaty-coal, clayey-coal, coaly-clay, and clay layers (Fig. 5). The thickness and lateral continuity of distinct layers were variable, with individual layers thinning and thickening, anastomosing, and occasionally disappearing and reappearing (Fig. 6). Individual peat–coal and clay layers within level N were generally between 6 and 30 cm thick.

Net peat accumulation (as thickness) reflects the result of gross productivity (as leaf-fall and root systems, in this case), loss from decay and herbivory, and compaction (Clymo 1983; Moore 1989; Moore and Hilbert 1992). In thick sequences of peat (> 150 cm), total thickness of peat may be a poor reflection of original biomass and the rate of accumulation, as decay and compaction vary with depth (Clymo 1983). Very shallow peats will better reflect accumulation, as compaction is more even and loss through decay is similar at depth. The thickness of each peat layer provides an estimate of accumulation rates, and therefore of the period of peat accumulation. This estimate provides a rough time frame for the fossil forests.

McCabe (1984, 1987) estimates that rates of accumulation

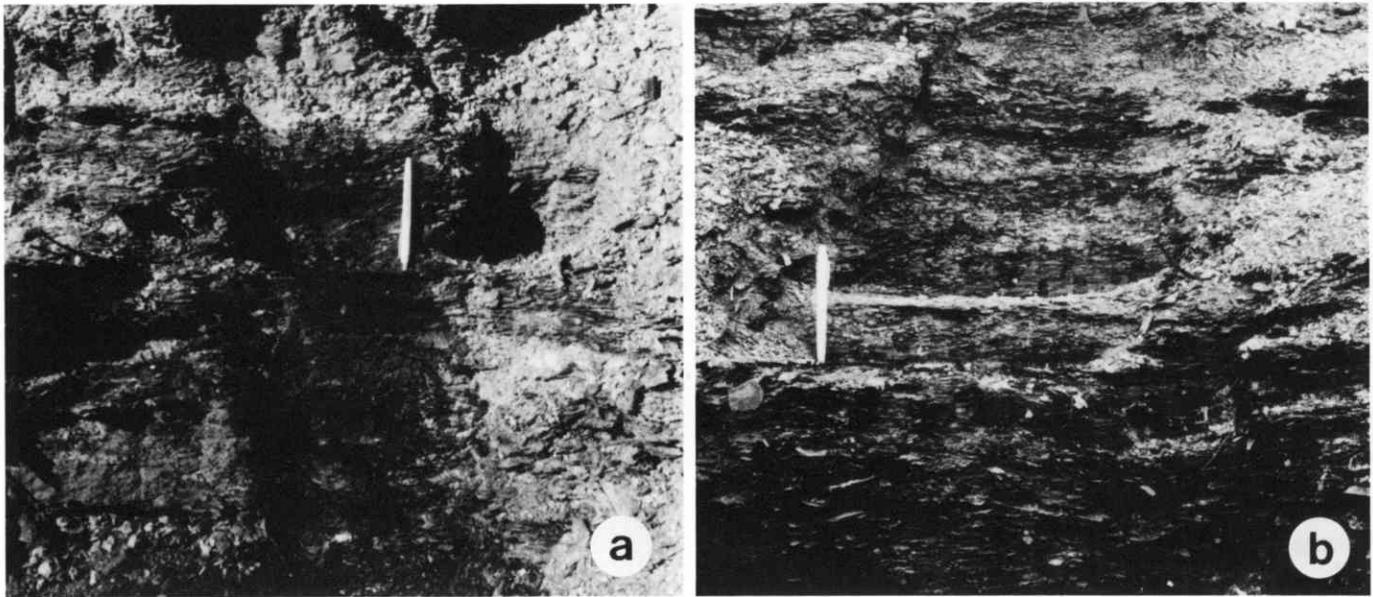


FIG. 5. Photographs of vertical sections through level N. (a) Section 5. (b) Section 7. Peat (leaf mat) layers appear darkest, with coaly-clay layers gray and mineral-clay layers pale. The pen in the photographs is 10 cm in length. See Fig. 6 for an explanation of lithology.

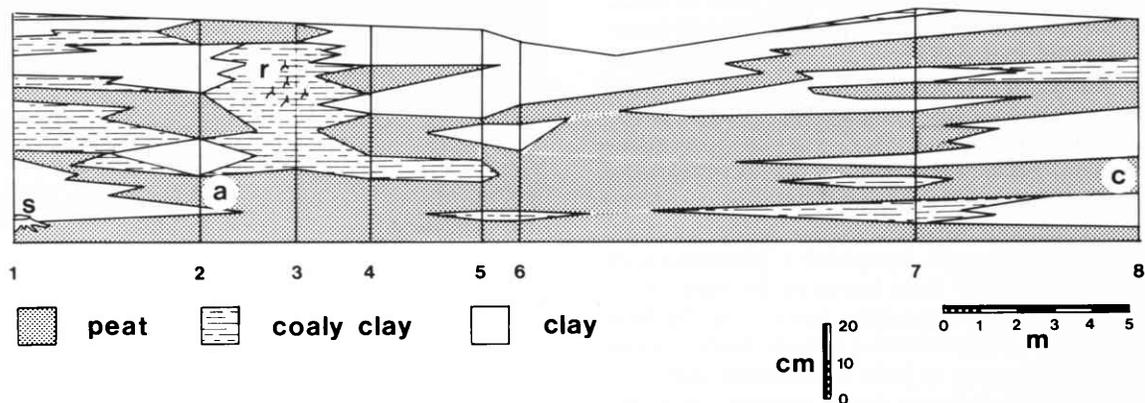


FIG. 6. Composite stratigraphy of level N. Stratigraphy is diagrammatic between measured sections (1–8). Vertical exaggeration  $\times 10$ . Prominent in situ roots (*r*) were observed at section 3 and an in situ stump (*s*) at the base of section 1. The coal layer found between 10 and 20 cm above the base is stratigraphically continuous over the whole lateral transect and is markedly fossiliferous, being dominated by angiosperm leaves (*a*) at section 2, and rich in *Chamaecyparis* (*c*) at section 8. At section 7 (see Table 2) this layer is dominated by *Metasequoia*, with significant amounts of angiosperm leaves, the undescribed Taxodiaceae taxon, and *Glyptostrobus*.

TABLE 1. Accumulation rates of peat in Tertiary and modern peat-forming vegetation

Type of vegetation	Accumulation rate		Source
	Quoted	Years/10 cm	
Mixed podocarp and angiosperm swamp (Miocene)	60 m / $4.8 \times 10^4$ a ( $0.13 \text{ mm} \cdot \text{a}^{-1}$ )	770	Luly et al. 1980
Mixed podocarp and angiosperm swamp (Miocene)	60 m / $10^4$ – $10^5$ a ( $0.6$ – $6.0 \text{ mm} \cdot \text{a}^{-1}$ )	17–170	George 1975
Tropical angiosperm swamp forest (modern)	$2.2$ – $2.8 \text{ mm} \cdot \text{a}^{-1}$	36–46	Anderson 1983
Mixed angiosperm and <i>Taxodium</i> swamp (modern)	$1$ – $2 \text{ mm} \cdot \text{a}^{-1}$	50–100	Gower et al. 1985
<i>Taxodium</i> swamp (modern)	5.9 m / 7000 a ( $0.84 \text{ mm} \cdot \text{a}^{-1}$ )	120	Cohen 1985; Retallack 1990



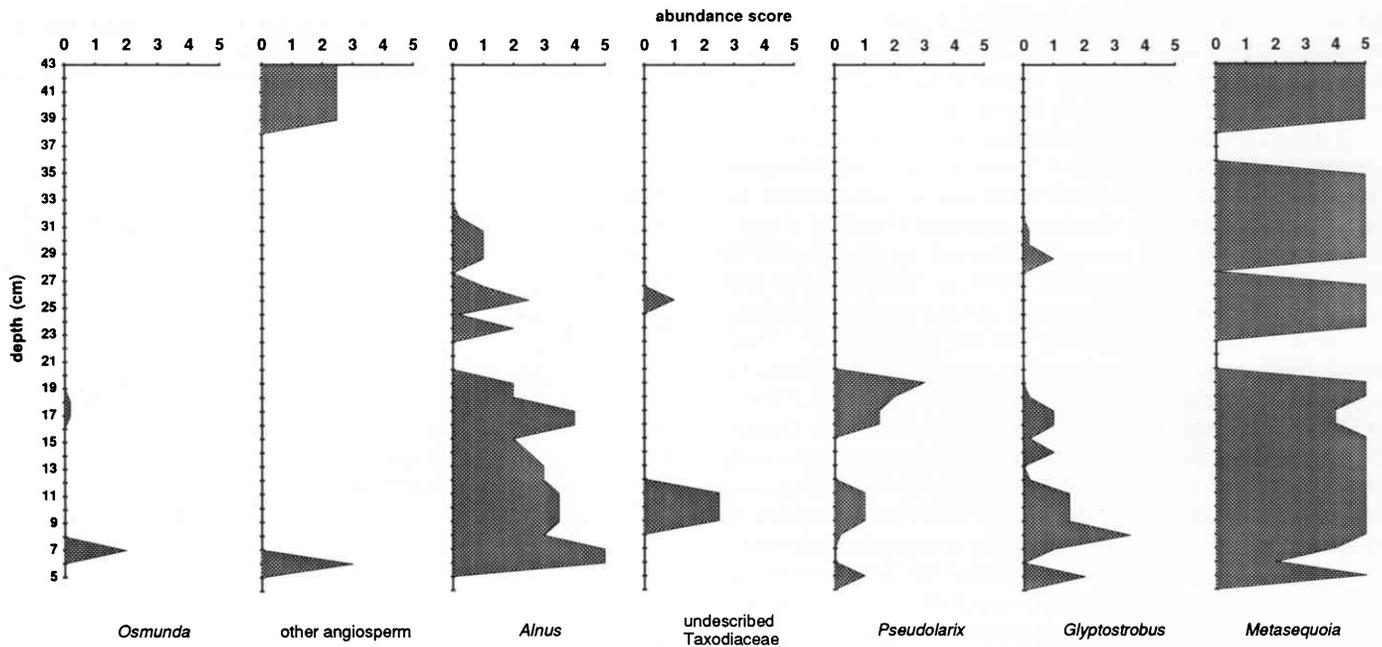


FIG. 7. Floristic composition at centimetre intervals within level N peat through section at section 7. Abundance scale as in Table 2.



FIG. 8. Photograph (detail) of level M showing in situ stump in upper part of the level and root system. The pen lying against the stump is 10 cm in length.

horizon in this topmost layer, suggesting establishment (?and death) of trees at either different times or at different microtopographic positions.

*Horizontal transect (level M)*

The macrofossil taxon most commonly found in abundance in level M (Fig. 3) was *Metasequoia*, represented by both foliage and cones (Tables 3 and 4). *Glyptostrobus* was rare, and remains of other coniferous taxa virtually absent. Very few species were found in individual samples and throughout the transect, indicating a conservative community of low diversity

TABLE 3. Plant associations (common macrofossils) along level M transect (1.5 km), base of section (<25 cm from basal clay), based on field observations

	Sample points									
	1	2	3	4	5	6	7	8	9	10
<i>Metasequoia</i>										
Foliage	×	×	×	×						
Cones	×	×	×							
<i>Glyptostrobus</i>					×					
Other conifer							×			
<i>Alnus</i>					×	×	×			×
Other angiosperm						×				×
<i>Onoclea</i> (fern)					×					
<i>Osmunda</i> (fern)										
No macrofossils								×	×	

TABLE 4. Plant associations (common macrofossils) along level M transect (1.5 km), middle of section (25–50 cm from basal clay), based on quantitative examination of samples

	Sample points									
	1	2	3	4	5	6	7	8	9	10
<i>Metasequoia</i>										
Foliage	5	5	3	5		1	5	5	3	2
Cones	+	1						2–3	+	
<i>Glyptostrobus</i>				+				1		1
Other conifer										+
<i>Alnus</i>	+		2	+	5	5		+	1	3
Other angiosperm	+					1				
<i>Onoclea</i> (fern)					4					1
<i>Osmunda</i> (fern)		+						2	4	
Wood pieces	3	2	5	3	+	2	3	1	3	2

NOTE: Abundance scale as in Table 2.

over a large area. At sample points 5, 6, and 10, thick leaf mats dominated by *Alnus* (Betulaceae) were present (Table 4). The fern remains in level M include *Osmunda* and *Onoclea*. At one sample point, level M was dominated by *Alnus* leaves in association with abundant fern fronds and mummified whole fern plants of *Onoclea*. The amount of woody matter (small branches, bark, etc.) varied between samples. Angiosperm leaves were most commonly preserved as either rare fragments within minor clay partings within otherwise coniferous leaf mats (e.g., sample 9) or as dense mats (e.g., sample 6). *Alnus* was present in all but two samples, but was most common where *Metasequoia* was rare or absent.

Although some samples include an abundance of angiosperm leaves, as is apparent from Tables 3 and 4, higher in level M (i.e., >50 cm from the basal clay) peat-coals were composed of either mixed conifer (including *Metasequoia*) or pure *Metasequoia* leaf mats. Mixed conifer layers were commonly succeeded by *Metasequoia*-dominated leaf mats higher in the layer. In situ stumps in level M were uncommon, typically associated with *Metasequoia* leaf mats, and generally occurred from the middle to near the top of level M (Figs. 3 and 8). Cones of *Metasequoia* were present in four samples, being common in only one sample. *Alnus* was present in all but two samples, but was most common where *Metasequoia* was less common, or where *Metasequoia* was absent.

### Discussion

Litter accumulation in modern taxodiaceous swamps is high, producing peat dominated by *Taxodium* foliage (Spackman et al. 1969; Conner and Day 1976; Wing 1984). Nevertheless, modern taxodiaceous swamps in the southern United States contain a mosaic of plant communities reflecting the interaction of hydrology (variations in the water table) and ecology (Davis 1946; Spackman et al. 1969; Conner and Day 1976; Collinson and Scott 1987). Different subcommunities in such swamp mosaics reflect differences in substrate, water level, and successional responses to disturbance. Spackman et al. (1969) have suggested that succession from *Taxodium* forest islands ("Cypress heads") in the Florida swamp-marsh communities to hardwood-dominated forest may be caused by the accumulation of peat and the resulting lowering of the water table. Records of these subcommunities are preserved in the peats. Open-water plant communities commonly produce fine-grained peat lacking obvious plant remains, whereas forested swamps produce coarse-grained peat with obvious leaf and twig remains (Spackman et al. 1969).

The polar Eocene taxodiaceous swamps of Axel Heiberg Island would seem to have had a similar ecological dynamic to modern taxodiaceous swamps, although open-water plant communities appear to have been a more minor component of the ancient swamps. The association of *Onoclea* with *Alnus* leaves in the peats is consistent with the preference of the modern species *Onoclea sensibilis* and *Alnus* spp. for wet soil or marshy forests and is similar to the association of remains of *O. sensibilis* with betulaceous remains and *Metasequoia* foliage in the Paleocene of Alberta (Rothwell and Stockey 1991). It is plausible that the *Alnus*-*Onoclea* association represents hardwood stands or thickets within the taxodiaceous swamp, on local slightly raised or exposed areas of peat.

It seems likely, therefore, that hydrological differences promoted development of a vegetational mosaic of taxodiaceous and betulaceous swamp and bog forests, and that hydrological

evolution of the swamp was complex. The stratigraphic arrangement of root systems in level N may reflect redirection of the roots during the life of these trees, indicating fluctuating water-table levels (Munaut 1986). Repeated patterns of succession of plant communities have not been recognized for the Eocene swamp forests of Axel Heiberg Island. The occasional presence of layers rich in nontaxodiaceous conifers (e.g., *Chamaecyparis*, *Larix*, and *Pseudolarix*; LePage and Basinger 1991; Basinger 1991) indicates the existence of relatively diverse mixed-conifer plant communities within the mosaic. These communities were encountered in level N, but were not seen in the analysis of the level M transect. Nevertheless, the majority of the peat is composed of taxodiaceous litter (principally *Metasequoia*).

The predominance of taxodiaceous peat in the paludal facies of the upper coal member of the Buchanan Lake Formation does not imply that these plant communities were the dominant vegetation of the meander plains. However, *Metasequoia*-dominated forests were by far the widespread vegetation in areas of high net accumulation of peat.

### Conclusions

A succession of coaly layers, representing tree-dominated swamps, is found interbedded with lacustrine shales, fluvial sands, and paleosols within the Buchanan Lake Formation of Axel Heiberg Island. These coals may include well-preserved leaf matter and in situ stumps. Lateral variation in the stratigraphy of these coaly layers indicates that hydrological conditions, and as a consequence the floristic and ecology of the plant communities, may have been highly variable laterally within these swamps. Vertical changes in sediment character within coal layers indicate that hydrological conditions also varied over time, apparently influencing local community composition and structure. Semiquantitative changes in macrofossil taxon abundance (Tables 2-4; Fig. 7) within levels M and N indicate the former existence of a mosaic of taxodiaceous swamp (*Metasequoia*-*Glyptostrobus*), angiosperm-fern (*Onoclea*-*Osmunda*), and mixed coniferous communities. Taxodiaceous swamp was the dominant peat-forming community and must have been intimately associated with areas of soil saturation. Such peat accumulation reflects higher water-table levels and hence suppression of decay and does not necessarily imply higher productivity (Moore 1987).

The thickness of individual coal layers within levels M and N suggests that each represents 500-1000 (or more) years of swamp-forest growth. Individual stumps may represent coeval members of a forest killed and buried contemporaneously, but may also have been shown to be the remains of trees from previous stands. Laterally exposed horizontal layers with in situ stumps may therefore contain superimposed individuals representing different components of the temporal and spatial vegetational mosaic. Inclusion of all stumps in stand-density calculations, based on the assumption that all stumps in such beds are coeval, may substantially overestimate biomass, stand density (stems per hectare), and productivity.

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