PALYNOLOGY OF THE TRIPORATE POLLEN AND PALEOECOLOGY OF THE TERTIARY FOSSIL FORESTS OF EASTERN AXEL HEIBERG ISLAND, N.W.T., CANADA

by

Juliet McDonald, B.Sc. (Hons.)

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfilment of
the requirements for the degree of

(Masters of Science)

Department of Earth Sciences

Carleton University
Ottawa-Carleton Geoscience Centre
Ottawa, Ontario

The undersigned recommend to the Faculty of Graduate Studies
and Research acceptance of the thesis

"PALYNOLOGY OF THE TRIPORATE POLLEN AND PALEOECOLOGY OF THE TERTIARY FOSSIL FORESTS OF EASTERN AXEL HEIBERG ISLAND, N.W.T., CANADA"

submitted by Juliet McDonald, B.Sc. (Hons.)
in partial fulfilment of the requirements for
the degree of Master of Science

Thesis Supervisor

Chair, Department of Earth Sciences

Carleton University
Ottawa-Carleton Geoscience Centre

Ottawa, Canada
Date

ABSTRACT

The Arctic fossil forests discovered at the Geodetic Hills Locality on eastern Axel Heiberg Island, N.W.T., Canada (79°54' N, 88°57' W) were high latitude, yet warm temperate forests, that have been extremely well-preserved. A palynological investigation of triporate pollen was undertaken using leaf litter samples of the fossil forest sequence obtained from the Buchanan Lake Formation, Eureka Sound Group. This study reveals that the dominant families are the Betulaceae and Juglandaceae, with other less common families including ?Gentianaceae, Myricaceae, Ulmaceae, Santalaceae and rare Caprifoliaceae. Certain triporate pollen types were common in the fossil assemblages; these include: *Alnipollenites verus, Momipites microfoveolatus, Pistillipollenites macgregorii, Trivestibulopollenites claripites* and *Caryapollenites viridifluminipites.* The presence of species such as *P. macgregorii, Momipites coryloides, Plicatopollis* sp. of the *plicata*-type, *Paraalnipollenites* sp. and *Platycaryapollenites* sp. cf. *P. platycaryoides* establish the age of the forest sequence between Early and Middle Eocene, possibly Late Eocene. Mild climatic conditions (warm temperate to slightly subtropical) probably prevailed in the area during the early Tertiary based on the ecological ranges and habitats of modern genera comparable to the observed fossil triporate taxa. A probable scenario for the area is that of a moist lowland area adjacent to a large fluvial system such as a fluvial-floodplain.

The Arctic Tertiary Forest is envisioned to have been composed of deciduous and hardwood trees and shrubs growing on floodplains under moist, warm temperate

conditions similar to those found in present-day southeastern North America and eastern Asia. In nearby cooler upland regions, pinaceous forests were predominant. Numerical analyses support these conclusions. Q-mode cluster analysis revealed two distinct clusters of samples, representing early successional and climax-type forests which occurred in a cyclic pattern. The cycle began with a forest succession from an early stage to a climax-type forest during a stable depositional hiatus, followed by an erosional period (e.g. severe flooding) which eliminated the entire plant community. Such a pattern is consistent with that of a floodplain environment. R-mode cluster analyses have shown distinct clusters of species/taxa that may indicate common floral associations in the fossil forest area.

Assuming an unchanged paleolatitude, the presence of a warm temperate forest at high latitudes is enigmatic. These forests would have had to endure cycles of long dark winters and short summers marked by continuous light. It is likely that the woody plants were photoperiodic ecotypes and developed other biologic adaptations that allowed them to survive in a restricted polar light regime.

ACKNOWLEDGEMENTS

The author wishes to thank the staff at the Canadian Museum of Nature (CMN), Earth Sciences Department for their outstanding and limitless help and advice, use of their palynological facilities (laboratory, microscopy, and photomicrography), without which this thesis could not have been completed.

The author benefitted from stimulating and informative discussion with Drs. D.M. Jarzen (CMN), D. McIntyre (ISPG, GSC), J. Basinger (University of Saskatchewan), and R.G. Day (CMN), R. Rice, P. Born, A. McDonald (all of Carleton University). The manuscript was reviewed in whole by D. Jarzen, D. McIntyre, A. McDonald, O. Dixon (University of Ottawa), R. Patterson, H. Howden, and K. Hooper (latter three of Carleton University); and in part by R.G. Day and R. Rice. Special thanks are also due to R.G. Day and D. Jarzen, who donated much of their time through technical assistance in the palynological laboratory and the darkroom; D. Jarzen (CMN) for free access to his palynological library, the Dan Beju Library and the John F. Grayson Library (all housed in the CMN, Earth Sciences Dept.); R.G. Day for air photos (1:30,000) of the research locality; E. de Kemp, S. Burbidge and A. McDonald (all of Carleton University) for their technical assistance with the Macintosh and PC computer systems; and Dr. Ikuko Webster of Statistical Consulting Centre, Carleton University.

Lastly, the author wishes to express indebtedness, gratitude and thanks to her family: especially Andy and Mary; both sets of grandparents, J.S. and P.S. for love, encouragement and moral support. Their patience, time and understanding has allowed me to undertake such a research project.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

LIST OF APPENDICES

LIST OF SPECIES

Species	Page	Plate#-Figure#
1. *Alnipollenites trina*	82	I-4
2. *Alnipollenites verus*	79	I-1,2,3,5,6,7,8,9,10
3. *Alnipollenites* sp. A	84	I-11,12,13,14,15
4. *Annutriporites* sp.	64	IV-5,6
5. *Carpinipites ancipites*	25	I-18; II-4,6
6. *Caryapollenites juxtaporipites*	33	III-3
7. *Caryapollenites viridifluminipites*	32	III-1,2
8. *Caryapollenites* sp. A	38	III-9,10
9. *Caryapollenites* sp. cf. *C. inelegans*	37	III-4
10. *Caryapollenites* sp. cf. *C. veripites*	34	III-5,6
11. *Diervillapollenites* sp.	71	V-7
12. *Momipites coryloides*	42	III-11,12
13. *Momipites microfoveolatus*	44	III-13
14. *Momipites ?tenuipolis*	not described	III-19
15. *Myricipites annulites*	68	V-5,6
16. *Paraalnipollenites* sp.	23	I-16,17
17. *Pistillipollenites macgregorii*	73	V-9,10,11,12
18. *Pistillipollenites* sp. A	77	V-13,14,15,16
19. *Platycaryapollenites* sp. cf. *P. platycaryoides*	39	III-7,8
20. *Plicatopollis* sp. of the *P. plicata*-type	46	III-14,15,17,18
21. *Plicatopollis* sp. A	48	III-16
22. *Santalacites* sp. cf. *S. santaloides*	67	V-3,4
23. *Subtriporopollenites anulatus*	61	IV-17,18
24. *Subtriporopollenites nanus*	63	IV-19,20
25. *Thomsonipollis* sp.	65	V-1,2
26. *Triatriopollenites subtriangulus*	50	IV-4
27. *Triatriopollenites* spp. cf. *T. arboratus*	55	IV-9,10,11
28. *Triatriopollenites* sp. A	52	IV-1,2,3
29. *Triatriopollenites* sp. B	54	IV-7,8
30. *Triporopollenites mullensis*	58	IV-12,16
31. *Triporopollenites* sp. A	60	IV-13,14,15
32. *Trivestibulopollenites betuloides*	28	II-3
33. *Trivestibulopollenites claripites*	29	II-1,2
34. *Ulmipollenites krempii*	88	II-12,13,14,15,16,17
35. *Ulmipollenites tricostatus*	87	II-18
36. *Ulmipollenites undulosus*	85	II-7,8,9,10,11
(non-triporates)		
37. *Polyatriopollenites* sp.	92	V-17
38. *Taxodiaceaepollenites* sp. A	93	V-19
39. *Taxodiaceaepollenites* sp. B	93	V-18
40. *Tiliaepollenites* sp.	94	V-8
41. *Ctenosporites* sp. (fungi)	94	V-20

CHAPTER 1. INTRODUCTION

1.1

Occurrences of fossil forests in the high Arctic have been known since 1878 from reports of plant macrofossils in the Greinnell Land by O. Heer (1878) and the first publication of records from the Greely Expedition to Brainard's "Petrified Forest" near Cape Baird, Ellesmere Island (Greely, 1886). Since the discovery of these petrified forests, a number of expeditions have sought to collect and document these unique localities. In 1955, fossil forests discovered at Hot Weather Creek near Eureka Weather Station, Ellesmere Island, were the target of the first concerted effort scientifically to document these fossil forests during the Geological Survey of Canada's Operation Franklin (Fortier *et al.*, 1963). Subsequent discoveries of many more fossil forests on the Canadian Arctic Islands are also well-documented (see Christie, 1988, for a summary; Christie and McMillan, 1991, for a map of all sites). Recently, a new fossil forest locality was discovered, near Geodetic Hills, eastern Axel Heiberg Island, N.W.T., Canada (79°54' N, 88°57' W; Fig. 1.1). The site has attracted considerable attention due to the fine preservation of wood and other terrestrial plant remains (Basinger, 1986; McMillan, 1986; Francis and McMillan, 1987).

A compilation of the multidisciplinary research and study at the Geodetic Hills locality has produced a single comprehensive volume (Christie and McMillan (eds.), 1991). Studies include tectonics, stratigraphy, paleontology and palynology as well as the economic implications of the natural resources (coal of the fossil forests). This site provides an unique opportunity for paleoenvironment and paleocommunity reconstruction of these unusual high latitude forests.

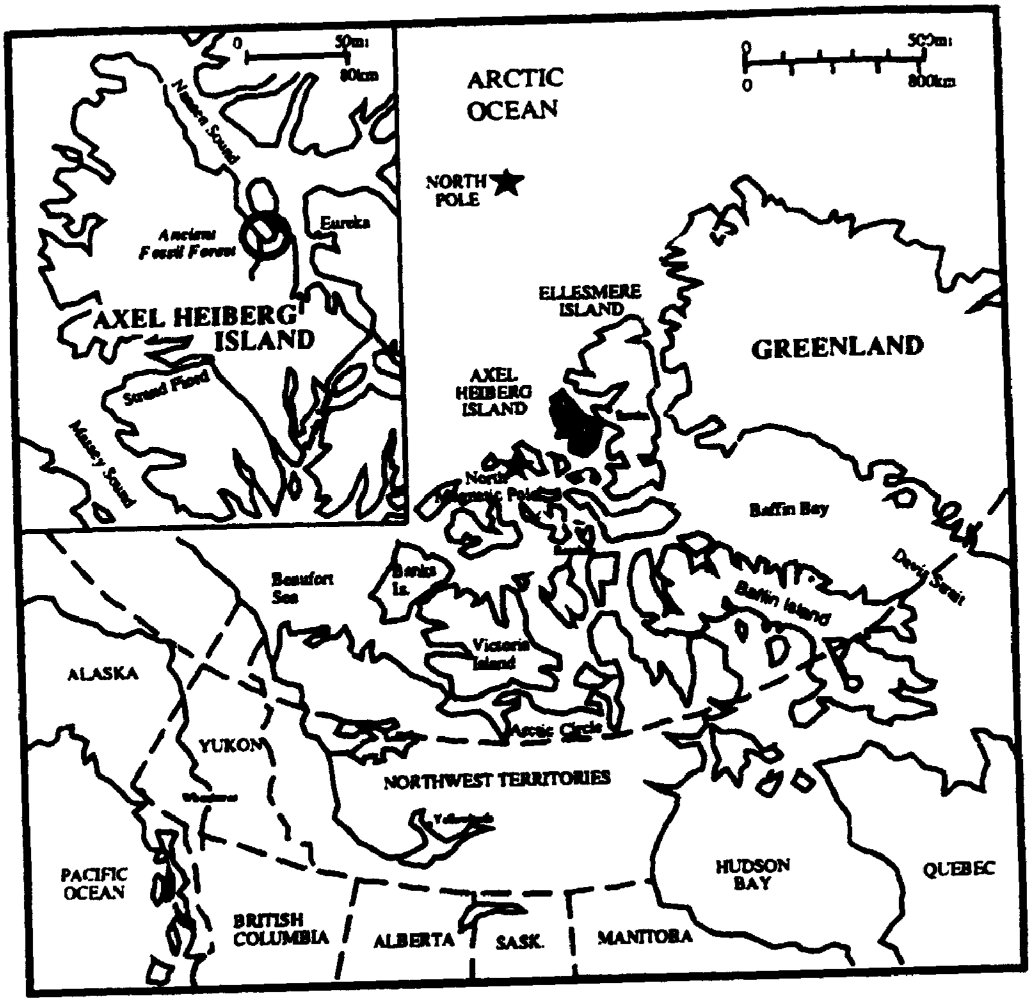


Figure 1.1 Location map (from Basinger, 1986).

1.2 PURPOSE OF STUDY

This thesis presents results of a palynological study of an early Tertiary fossil forest sequence at the Geodetic Hills locality. This research focuses on the triporate palynology, and is an important contribution because it provides the first detailed palynological study at the research locality. Most recent studies in this area have provided only preliminary palynological investigation without adequate systematic treatment or proper descriptions or diagnoses.

The objectives of this study were systematically to describe and document triporate pollen within a part of the fossil leaf layer section at the Fossil Forest Hill site and, secondly, to suggest botanical affinities of the parent plants. A third objective of this investigation was to interpret and discuss the paleoenvironment and paleoclimate. Calculations of the relative abundances of triporate taxa were carried out on each leaf litter horizon or subhorizon to measure temporal plant community changes throughout the section. Multivariate statistics (Q- and R-mode cluster analyses) were also conducted to determine any vegetation distribution patterns. Interpretation of the paleoecology of the area, as presented herein, is based on the pollen distributional data and the clustering data, in conjunction with the other documented palynomorph taxa and sedimentological evidence (Ricketts and McIntyre, 1986; Ricketts, 1986, 1991; Day, 1991; McIntyre, 1991; Kalguktar and McIntyre, 1991).

1.3 PREVIOUS WORK

The Geodetic Hills locality, northeastern Axel Heiberg Island, was discovered by B. Ricketts and P. Tudge in 1985. Basinger (1986), McMillan (1986), and Francis and McMillan (1987) have studied and collected the rich terrestrial plant macrofossils. Early sedimentological works carried out in the region include those by Tozer (1960, 1963), West *et al.*, (1975), Balkwill and Bustin (1975), Bustin (1977, 1982) and West *et al.*, (1981). Ricketts (1986, 1991) has since attempted to work out the stratigraphy and the sedimentology of the Eureka Sound deposits in the eastern Arctic archipelago, his studies particularly emphasized the enclosing sediments of the fossil forest sequence. A stratigraphic scheme based on lithologic units with some biologic imput was developed for the Eureka Sound Group of the Canadian Arctic Islands within the Remus and Strand basins (Ricketts and McIntyre, 1986; Ricketts, 1991). Miall (1984a, 1986) devised a different stratigraphic scheme for the Remus and Strand Fiord basins based on lithostratigraphic units (see Appendix IIB, comparison of stratigraphic schemes).

These fossil forests are unique, occurring in about twenty successions (Francis and McMillan, 1987), possibly as many as 30 (Francis, 1991), each stacked one above the other. Some of the forests are interbedded with medium to fine-grained sands and silts believed to have been deposited in an active fluvial environment (Ricketts, 1986, 1991; Francis and McMillan, 1987). The preserved forest floor litter includes cones, seeds, shed foliage and underbrush as well as the *in situ* trees, associated logs, amber and the soils in which the stumps grew (Basinger, 1986; Francis and McMillan, 1987). Unlike most other fossil forests, the wood and foliage have escaped permineralization and petrification; these materials are preserved in a "mummified state" (Basinger, 1986; Francis and McMillan, 1987). A schematic diagram of the leaf layer succession is shown in Fig. 1.2. It is apparent that a more comprehensive study with specific details and descriptions of each horizon is needed; (see Appendix I for

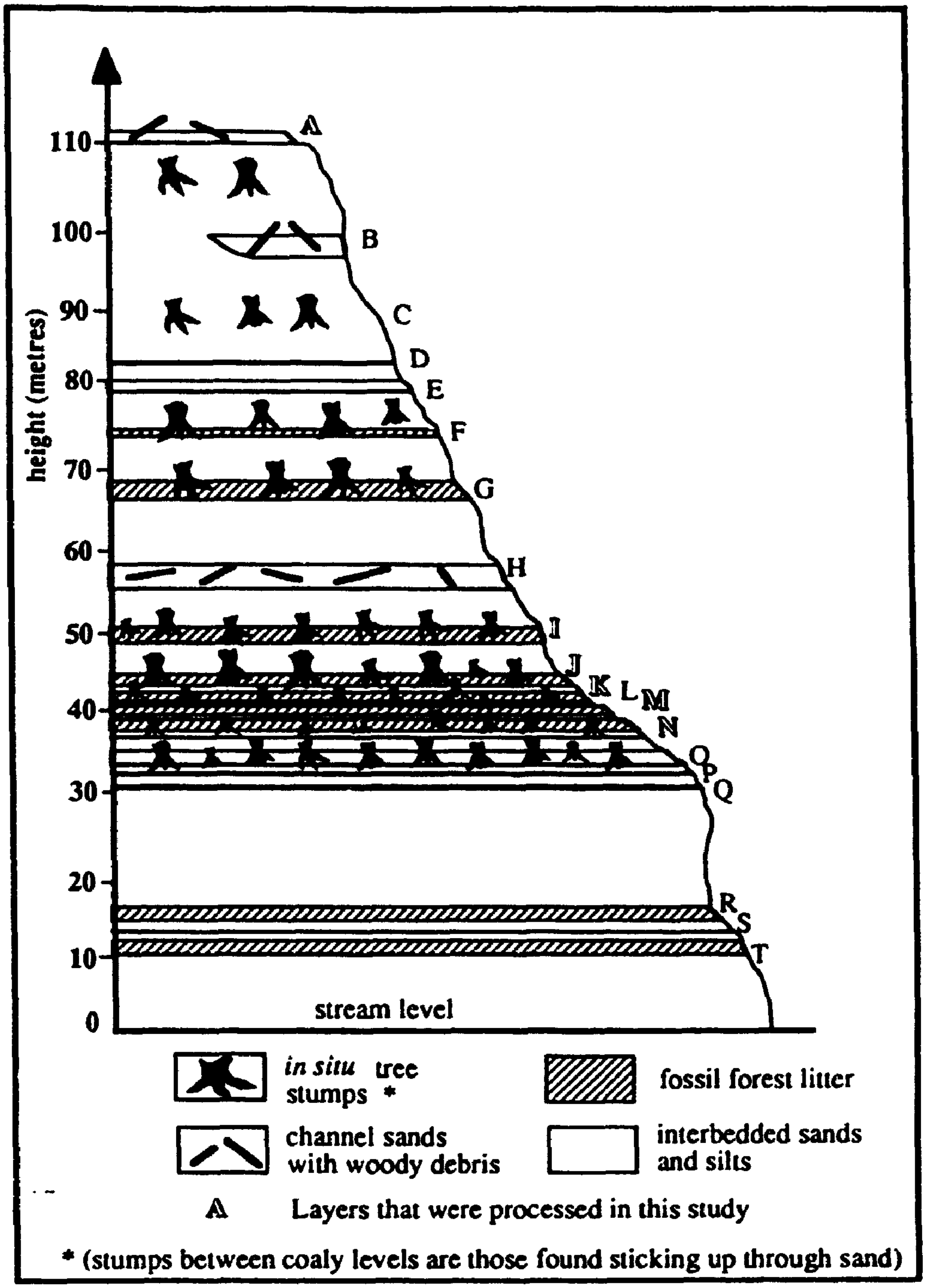


Figure 1.2. Leaf Litter Layer Profile. Measured section through fossil forest levels on Axel Heiberg Island (after Francis and McMillan, 1987); part of the middle, heterogeneous unit (from Basinger, 1991; see Appendix IC) of the upper coal member of the Buchanan Lake Formation (Middle Eocene; from Ricketts, 1991; see Appendix IB).

some leaf litter layer descriptions and stratigraphic schemes for the fossil forest sequence).

Plant remains are most characteristic of this fossil forest site. The plant macrofossils (the stumps, cones, seeds, leaves, fruits, etc.) have been studied by Basinger (1986, 1987, 1991; LePage and Basinger, 1989, 1991). Wood, amber and soil studies have been carried out by Francis (1991); Francis and McMillan (1987) and McMillan, (1986); Obst *et al.*, (1991); Young, (1991); Tarnocai and Smith (1991). It was originally believed that these Arctic Tertiary forests were essentially monotypic, with *Metasequoia* as the dominant floral component (Basinger, 1986, 1991; Francis and McMillan, 1987). Preliminary palynological analysis (pollen, spores, fungal elements) indicates that well-preserved, diverse, spore and pollen floras are present in many leaf layers of the forest interval (Ricketts and McIntyre, 1986; McIntyre, 1991; Day, 1991; Kalgutkar and McIntyre, 1991). This fact contradicts suggestions, based solely on plant macrofossils (Basinger, 1986; Francis and McMillan, 1987), that the forest was monotypic. Based on current knowledge, a deciduous forest is envisioned to have inhabited the area (McIntyre, 1991; Francis, 1991). The palynological and paleobotanical evidence gathered thus far, provides clues to the paleoclimatology of the early Tertiary.

1.4 MATERIAL AND METHODS

Leaf mat samples were collected from leaf litter horizons of the fossil forest succession during the field season of 1987 by R.G. Day, (CMN, Earth Sciences Department) and by Dr. L.V. Hills (University of Alberta). Pulverized samples, weighing approximately 10 gm each, from six of the most promising and productive leaf horizons, -- **A, I, J, K (Ka and Kb), M** and **N (Nb only)** -- were processed by R.G. Day. Five samples collected from each horizon (e.g. **A1, A2, A3, A4, A5**) or subhorizon, as in the case of **Nb, Ka** and **Kb** were processed, a total of thirty-five samples from seven (sub)horizons. A slide was made from each sample. The laboratory procedures are outlined in Fig. 1.3.

The lab techniques included the removal of minerals with HCl and HF; oxidation of organics if needed with HNO_3, NH_4OH, K_2CO_3 and HCl; removal of solubles with KOH; flotation with $ZnBr_2$; dispersal of the residue in Darvan and ultrasound treatment (centrifuging and washing in distilled water after each step). Residues were mounted in cellosize on a coverslip and in Krystalon Harleco onto a glass slide. Examination and morphological analysis of the pollen grains were made under oil immersion on a Leitz - Wild M20 Heerbrugg microscope at a magnification of x 1000, photomicrography with black and white film: Kodak T-MAX 100 and Ilford Pan F 80ASA. All specimens illustrated in this thesis and the samples from which they were obtained are in the palynological collection of the CMN, Earth Sciences Department, Ottawa, Canada [catalogue #: locality 226-AHI1 to 35].

All palynomorphs were categorized according to the following groups: polycol(po)rates, tricolpates, tricolporates, tetrads, Taxodiaceae, triporates, spores, bisaccates, monosulcates, fungal elements and polyporates. Relative abundance counts and relative percentages were calculated for each sample (see Appendix III). Generally, only entire specimens were included in the counting of 350 palynomorphs or more for each sample. Relative abundance counts and relative percentages were determined to calculate triporate species abundance and species diversity. Taxonomic diversity of assemblages was determined based on the relative percentages

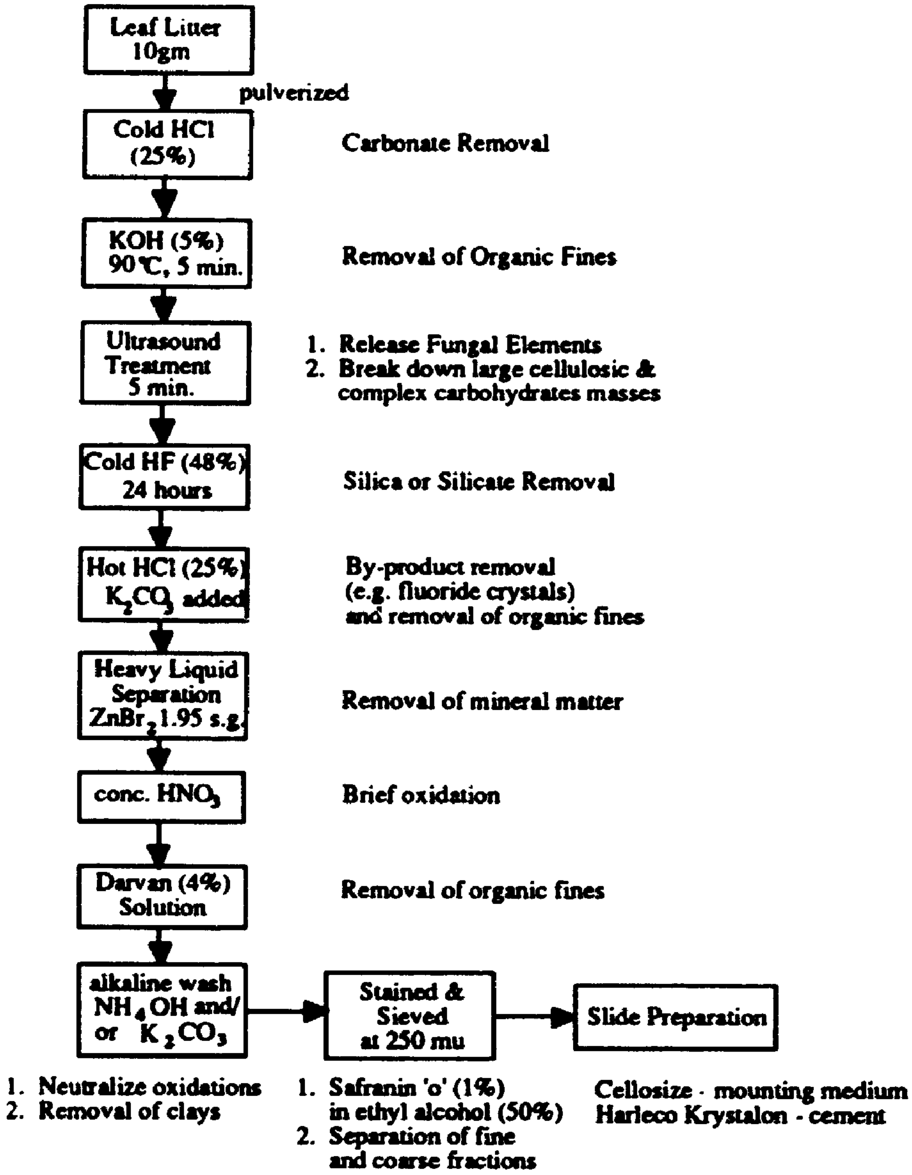


Figure 1.3. Laboratory Techniques used to process fossil leaf litter.

of these groups.

Q- and R-mode cluster analyses were also performed. They provide complementary information on the vegetation distribution patterns. R-mode analyses suggest the taxonomic composition of the vegetational distribution patterns indicated by the Q-mode analyses. The relative frequency data were analyzed using the program SYSTAT 2.0, which generated hierarchial dendrograms for cluster analyses. In order to produce clusters, the (dis)similarity between objects is computed based on similarity measures: 1) scale (distance) and 2) linkage (a distance coefficient). The distance is a measure that determines differences between cases/samples. The linkage is a clustering criterion that determines whether a hypothetical partitioning of samples is logical. Similar objects should cluster together and dissimilar ones should segregate. The Euclidean distance was used as a distance measure in this study because it is related to normal distributions. Through sample size normalization, this distance measure (the normalized distance of root mean squares) permits comparison between the clusterings of samples of different sizes. In this case, the samples are arranged on a common scale, allowing different biofacies to be identified (Fishbein and Patterson, *in press*). Ward's minimum variance method (or Ward's linkage) is a multi-amalgamation method used to calculate the distance of an object/cluster from another and to determine whether they should be combined as a cluster in a given step. This method is used as it adjusts for covariance and is believed to be most adequate for determining biogenic diversity (Fishbein and Patterson, *in press*).

Three data sets were considered for cluster analyses: 1) the entire palynomorph assemblage (categorized into morphological groups such as tetrads, triporates, monosulcates, etc.), 2) families with triporate members, and 3) triporate species. Palynomorph data are displayed as co-varying units which correspond to the distribution of the vegetational zones in the study area. It is these relationships that provide the basis for interpreting the fossil palynomorph assemblages.

Ecologicial relationships of the taxa (triporates and non-triporates) were proposed based on the available statistical and distributional data .

Sources of errors.

All samples yielded sufficient palynomorphs for statistical analysis, but there are inherent problems that must be considered. The terms palynomorph abundance, accumulation and productivity are not synonymous, and so, the relationship of the fossil pollen to vegetational types may not be a direct one. Since palynomorphs behave hydrodynamically as sedimentary particles of silt size or less, any pre-burial effects introduce potential sources of error to the numerical analysis.

Many vectors will alter pollen assemblages. Therefore observed relative frequencies in the fossil record may not reflect pollen production of the parent plants or relative frequencies of palynomorphs at the time of deposition. They include: 1) transport mechanisms (wind, animal and fluvial transport to the depositional site), 2) sedimentary characteristics of the palynomorphs (differential deposition, reworking, resuspension, redeposition and sedimentary sorting), and 3) taxonomic considerations of palynomorphs (differential preservation of palynomorphs, productivity of their parent plants and pollen dispersal methods; S.T. Andersen, 1974). The complications introduced by these factors, other taphonomic factors (such as diagenesis), environmental and climatic conditions (e.g. nature of the sedimentary basin, prevailing winds, the time of the year (flowering season) and the hydrologic conditions of the environment), must be taken into account so that consistent and reliable interpretations of the vegetational history may be achieved.

1.5 LITHOLOGY AND STRATIGRAPHY

Previous terminology

The name 'Eureka Sound Group' was first proposed by Troelson (1950) for the predominantly nonmarine, coal-bearing, Cenozoic deposits outcropping on Axel Heiberg and Ellesmere islands. Most of the sediments are sandstones, grey arenaceous to black carbonaceous shales, iron claystones and lignites with plant remains. These sediments, possibly Late Cretaceous or Tertiary in age, were believed to postdate the Eurekan Orogeny (Troelson, 1950). No type area had been designated. Thorsteinsson and Tozer (1957) demonstrated that Troelson's interpretation of post-orogenic deposition was incorrect. The Eureka Sound strata on western Fosheim Peninsula were determined to be synorogenic.

In compliance with North American stratigraphic rules, Tozer (1963) redefined the Eureka Sound Group as a formation and designated the type area from numerous outcrops on the Fosheim Peninsula, Ellesmere Island. The Eureka Sound Formation unconformably overlies Mesozoic strata on Axel Heiberg Island. Souther (1963) independently designated a type section at Strand Fiord, on western Axel Heiberg Island, conformably overlying the Kanguk Formation. This section is currently recognized as the type section for the Eureka Sound unit.

Four informal members were recognized by West *et al.,* (1975), based on lithofacies differences within the Eureka Sound Group in the Bay Fiord area. Other workers (Ricketts, 1986; Miall, 1986) have also tried to establish map unit boundaries but their boundaries do not match those of West *et al.,* (1975), or each other (Miall, 1986, 1988; Ricketts, 1986, 1988, 1991; see Appendix IIA for past stratigraphic schemes).

In his comprehensive paper on the Eureka Sound Group, Miall (1984a) promoted the formation back to group status and formulated a stratigraphic scheme using a lithostratigraphic framework based on genetic depositional systems. Ricketts (1986) also elevated the Eureka Sound Formation to group level and independently introduced a stratigraphic scheme for the Eureka Sound Group based on the general lithologic homogeneity of the rock units and their mappability, and plant microfossils (Ricketts and McIntyre, 1986).

The regional stratigraphy of these deposits (Eureka Sound) is controversial and difficult to resolve and map because of complex facies relations and biostratigraphic problems (Miall, 1984a; Trettin, 1989). The most recent nomenclatural schemes (see Appendix IA) are varied and based on different perceptions of the history of basin development in the Arctic archipelago (Miall, 1986, 1988; Ricketts, 1986, 1987, 1988, 1991). The strata of the fossil forests belong to the Buchanan Lake Formation (Ricketts, 1986) or the Boulder Hills Formation (Miall, 1986). The stratigraphic framework of Ricketts (1986) is used in this study for two reasons: 1) biostratigraphic control in Ricketts' scheme allows palynological data to be directly related to the stratigraphic nomenclature; and 2) Ricketts has studied sediments from the fossil forests considered in this study.

Lithology and Stratigraphy

The Eureka Sound Group is an uppermost Upper Cretaceous to Eocene unit that occurs throughout the Canadian Arctic Archipelago. Exposures of this group extend from Ellesmere Island in the northeast to Banks Island in the southwest, occurring both within and beyond the limits of the Sverdrup Basin. Deposits of the Eureka Sound Group rest conformably on the Upper Cretaceous rocks of the Kanguk Formation in much of the Sverdrup Basin (which occupies the central, northwestern and northern Arctic Islands). In other areas, a transgressive sequence unconformably overlies Paleozoic to Cretaceous rocks or is overlain by post-Eureka Sound thrust plates.

The group is dominated by uniform sections consisting of cyclically interbedded dark shale, mudstone, siltstone, buff to light grey quartzose sandstone, prominent coal seams and coally deposits, with minor amounts of ironstone and local conglomerates. The maximum thickness of the Eureka Sound Group is 3340 m at the southeastern end of Bay Fiord, central Ellesmere Island (Miall, 1984a). Ricketts (1986) has attempted to correlate the Eureka Sound strata on Bylot Island, Amund Ringnes Island, Lougheed Island, Banks Island and at Lake Hazen. Bustin (1977) interpreted four major facies: alluvial plain, delta, interdelta and open marine deposits. Ten significant lithofacies were also identified by Miall (1984a): estuarine, shallow marine-prodeltaic marine, shoreline, distal delta front, proximal delta front-delta plain, high-sinuosity fluvial, low sinuosity fluvial, ephemeral stream, gravelly alluvial fan, and lacustrine.

The lower part of the succession consists of thick intervals of shale, mudstone and siltstone commonly containing marine fossils [e.g. foraminifers (Hornaday in West *et al.*, 1975)]. Conglomerates are a major component of the group locally on northern and eastern Ellesmere Island.

On Axel Heiberg Island, the Eureka Sound Group consists of more than

2500m of non-marine sandstone and siltstone, shale and coal (Geological Survey of Canada Preliminary Map 36 - 1959).

The Eureka Sound Group (within the Remus and Strand Fiord basins), on Axel Heiberg and central Ellesmere islands, is subdivided into four lithologically distinct formations of regional extent (Ricketts and McIntyre, 1986; Ricketts, 1986, 1991): Buchanan Lake Formation; Iceberg Bay Formation; Strand Bay Formation; and Expedition Formation (Fig. 1.4).

The fossil forest succession is included within the Buchanan Lake Formation. It is the youngest and stratigraphically highest unit and is of Middle (or possibly late Middle) Eocene age (Ricketts and McIntyre, 1986; Ricketts, 1991; McIntyre, 1991). This unit consists mainly of a syntectonic diabase pebble conglomerate and lithic sandstones shed from adjacent thrust sheets (Stolz Thrust zone), representing the major period of faulting and folding during the Eurekan Orogeny. There are also minor amounts of sandstone deposited by fluvial processes, commonly by braided rivers, and locally by debris flows (Ricketts, 1986, 1991). The clastic debris of the alluvial fans and braid plains originated from adjacent thrust sheets of Mesozoic and Paleozoic bedrock. Plant macrofossils are contained within a unit of fine-grained channel and floodplain sediments lying conformably on thick conglomerates (Ricketts and McIntyre, 1986; Ricketts, 1991).

The formation was deposited during the final stages of the Eurekan Orogeny, with sediments predominantly supplied by the Early Paleocene or Middle Eocene uplift of the Princess Margaret Arch (Bustin, 1977, 1982; Ricketts, 1986, 1987, 1991). Miall (1984a) proposed that deposition occurred during the early phase of the Eurekan Orogeny of the Late Cretaceous and early Tertiary, believing that the

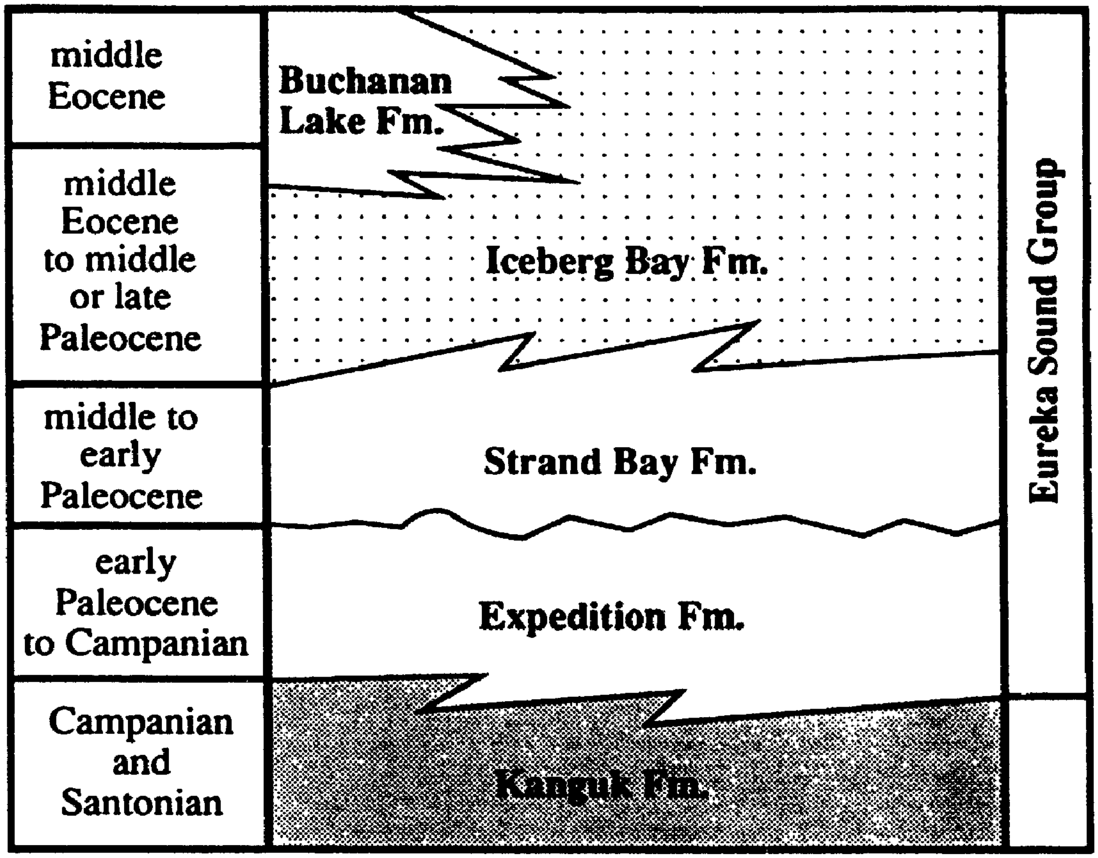


Figure 1.4. Formations of the Eureka Sound Group (from Ricketts, 1986).

orogenic activity ended, possibly in the Oligocene.

Ricketts (1991) summarized the lithostratigraphy of the fossil-forest-bearing strata, Geodetic Hills area, recognizing four mappable units, from the fossil forest site west to the hanging wall of Stolz Thrust. This simple scheme comprises of four map units in ascending order: the *lower coal member*, the *conglomerate member*, the *conglomerate-sandstone member*, and the *upper coal member* (Ricketts, 1991; see Appendix IB). The fossil forest beds are contained in the upper coal member (as described in Ricketts, 1986; Ricketts and McIntyre, 1986; Ricketts, 1991). Barely lignitic coal appears in seams enclosed by mudstones. The mudstones contain a rich, well-preserved flora of Middle Eocene age (Ricketts, 1986; Ricketts and McIntyre, 1986; McIntyre, 1991) and are interpreted as fine-grained channel and floodplain sediments (Ricketts and McIntyre, 1986; Ricketts, 1991). Basinger (1991) further subdivided the fossil forest succession, that is contained in Ricketts' *upper coal member*, into three subunits which were based upon observed trends of the occurrence of plant macrofossils (see Appendix IC). The bulk of the leaf litter mats processed for this study are derived from the middle layer of Basinger's scheme (Day, *pers. comm.*, 1991).

1.6 GEOGRAPHY AND GEOLOGY

Geography

Axel Heiberg Island is part of the Queen Elizabeth Islands of the eastern part of the Canadian Arctic Archipelago. It is underlain mainly by late Paleozoic to Recent sediments of the Sverdrup Basin, a 13 km thick sequence of carbonate, evaporite, clastic, volcanic and intrusive rocks (Balkwill, 1978), which obscures much of the Franklinian Geosynclinal Belt (Balkwill, 1978; Embry and Osadetz, 1988).

Miall (1986) proposed that the Sverdrup Basin was made up of many sub-basins, one of which, the Remus basin, is the location of the fossil forest area. However, the map of the paleogeography of the eastern Canadian Arctic Islands during the Middle Eocene (Buchanan Lake Formation; Fig. 1.5) compiled by Ricketts (1991) illustrates the Eurekan synorogenic intermontane basins in the region. The forests are located within the Axel Heiberg intermontane basin (Ricketts, 1991), delineated by large frontal thrusts or uplifts. The major Eurekan arches and uplifts are also indicated.

The fossil forest locality under study is found near Geodetic Hills, eastern Axel Heiberg Island (79°54' N, 88°57' W). A well-preserved fossil forest succession in Middle Eocene strata is located within the Buchanan Lake Formation of the Eureka Sound Group, (Ricketts and McIntyre, 1986; Ricketts, 1986, 1991). On site, well-exposed leaf-mat beds have been recorded in three different ridges, informally named Fossil Forest Hill, East Hill and South Hill, at the Geodetic Hills locality (Fig. 1.6). Day (1991) observed the leaf litter mats to range from 10 cm to 50 cm in thickness. The Fossil Forest Hill site will serve as the focus for the study herein.

Geology

Eureka Sound beds have been mapped over the years at widely scattered localities in the Canadian Arctic Islands. These deposits are preserved in a number of structural depressions, some of which coincide with the original depositional basins or sub-basins (Miall, 1986). Locally, these deposits consists of more than 3 km of

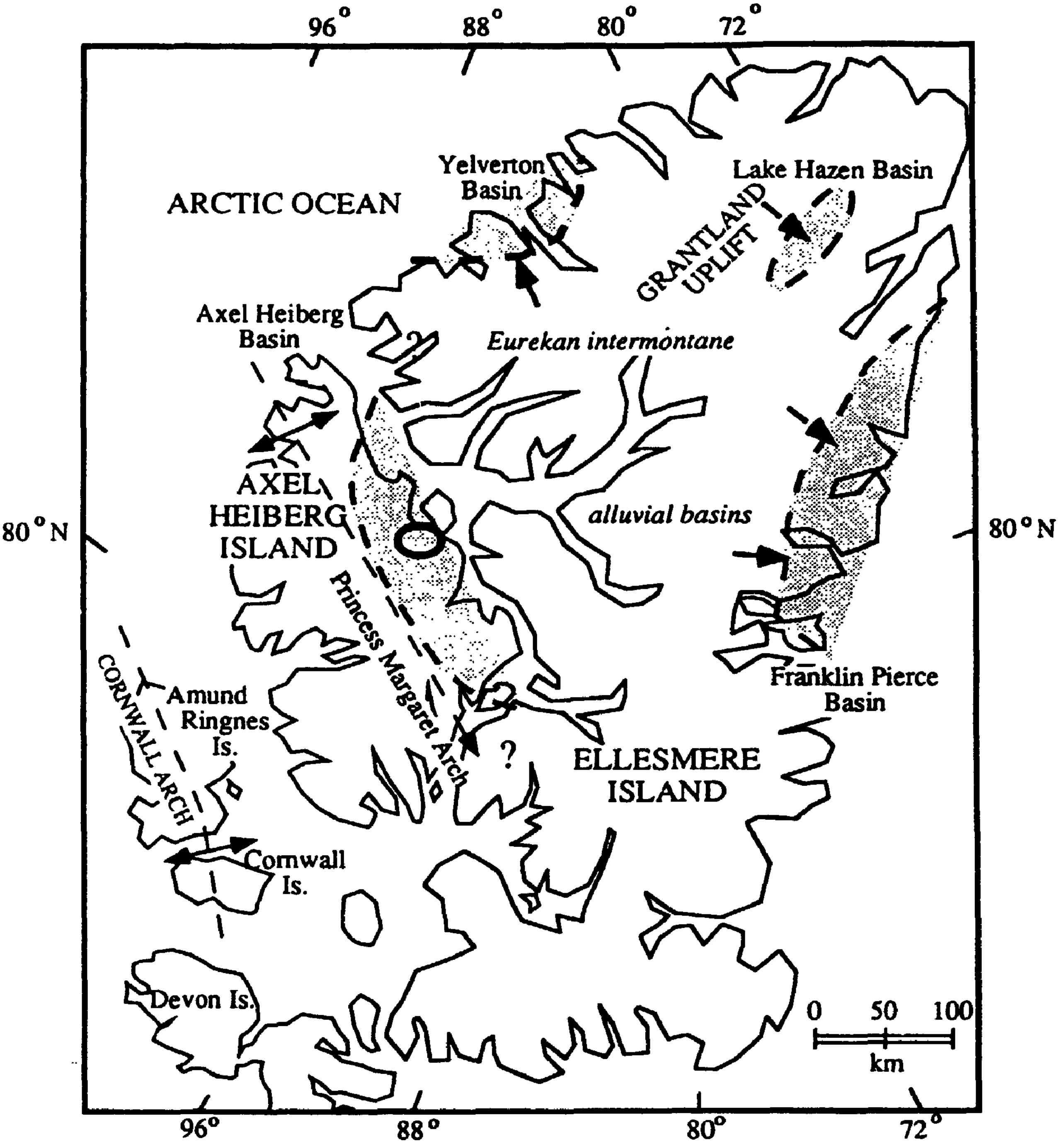


Figure 1.5. Paleogeography during the Middle Eocene (Buchanan Lake Formation). The forests (circled) within the Axel Heiberg intermontane basin, are shown in relation to other Eurekan synorogenic basins (stippled areas; from Ricketts, 1991). Arrows indicate general sediment supply-transport trends.

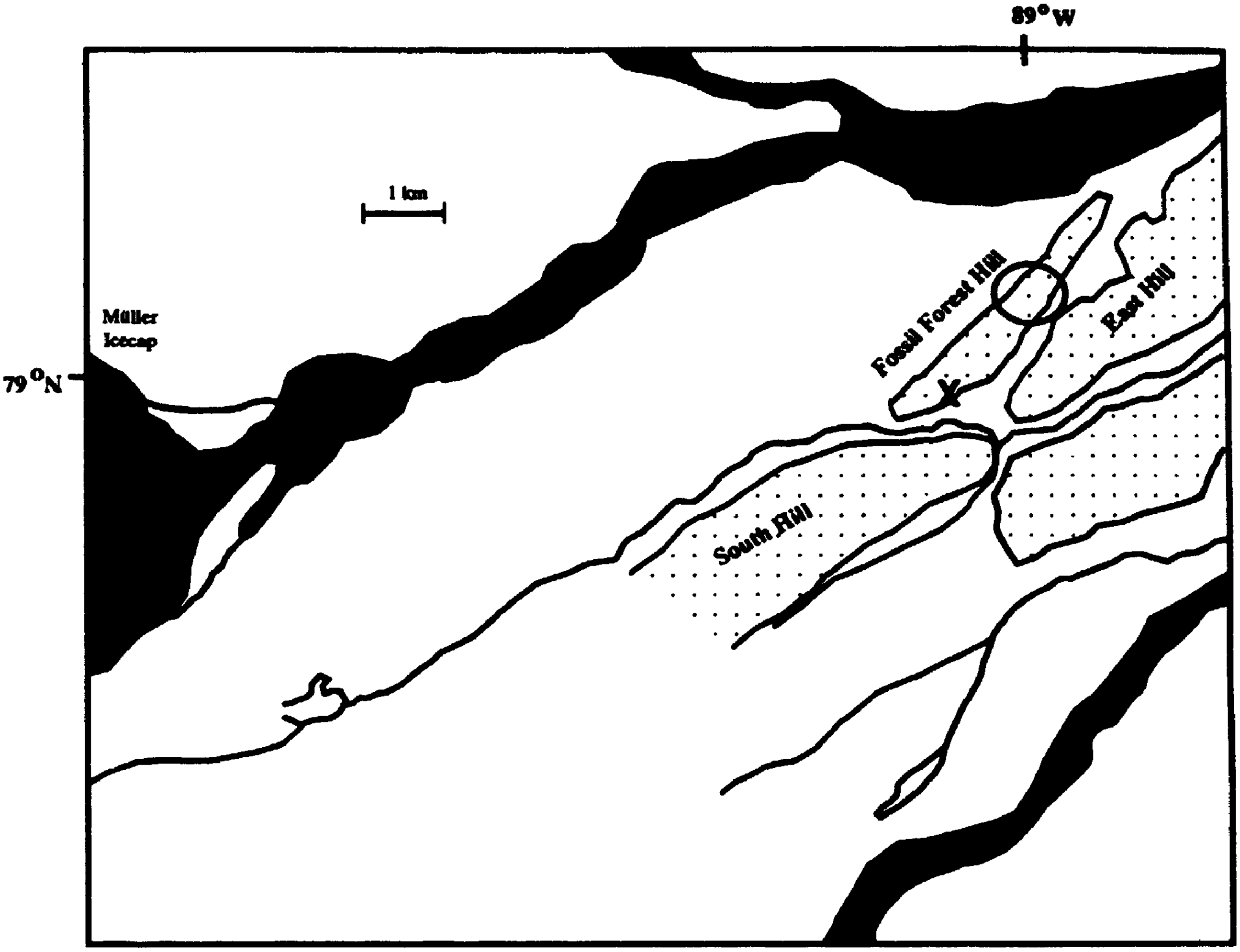


Figure 1.6. Fossil Forest Site Map. Heavy shading represents glacial melt water from the Müller Glacier to the west.

O Heart rot stumps
X Sampling

sandstones and mudstones, with minor amounts of conglomerates derived from sources within the Sverdrup Basin and around its periphery (Trettin, 1989).

Basin development occurred in four phases (Stephenson *et al.,* 1987, and Embry and Osadetz, 1988): 1) Carboniferous - Early Permian rifting, 2) Early Permian - earliest Cretaceous thermal subsidence, 3) Early Cretaceous - earliest Late Cretaceous rifting, and 4) Late Cretaceous - Eocene thermal subsidence. A tectonic break between phases two and three, which coincided with an Arctic-wide tectonic realignment, was followed by Mesozoic volcanism late Hauterivian and Campanian; Balkwill, 1978; Plauchut, 1971). Widespread sill and dyke intrusion accompanied the volcanic activity during the Late Cretaceous; the volcanism was restricted to the extreme northeast (northern Ellesmere Island; Embry and Osadetz, 1988). The volcanic succession is believed to be the southeastern limit of the Alpha Ridge, a major volcanic edifice that developed as a hot-spot track across Canada Basin during sea-floor spreading in the Late Cretaceous (Forsyth *et al.,* 1986). A major rifting period of the adjacent oceanic Canada Basin coincided with this activity. During the final phase (Late Cretaceous - Eocene), basin development had undergone thermal subsidence (Stephenson *et al.,* 1987; Embry and Osadetz, 1988) and has been further complicated by the mid-Tertiary Eurekan Orogeny (Ricketts and McIntyre, 1986). The results were uplift and compression in the eastern part of the basin, affecting Axel Heiberg and Ellesmere islands, possibly as late as the Oligocene (Miall, 1986). Miall (1986) suggests that the succession post-dated the last orogeny in the eastern Arctic Islands. The structural highs in the basin included the Princess Margaret Arch and Cornwall Arch and elsewhere the orogen is characterized by thrust faults and associated folds (Ricketts, 1986, 1987; Trettin, 1989).

The Mesozoic succession in the Sverdrup Basin consists largely of sandstone and shales. These clastic sediments were derived from source areas, possibly quite distant, to the south and west of the basin (Cornwall and Princess Margaret arches, respectively). Generally a non-marine fluvial-deltaic facies occupies the southern and eastern sides of the basin and grades northwest toward the centre of the basin into marine shales (Miall, 1986; Ricketts, 1986).

The youngest sediments in the Sverdrup Basin are dominantly continental sands and shales of Late Cretaceous to Paleogene age, assigned to the Eureka Sound Group. A rich fauna of early Cenozoic age has been found in the Eureka Sound sediments of the associated adjacent fossil forest sites in the Remus basin on Ellesmere Island. It includes mammals and reptiles indicative of a subtropical to tropical climate (West *et al.*, 1975; West and Dawson, 1977; McKenna, 1980; Estes and Hutchison, 1980). During the Middle to Late Eocene, Eurekan thrusting resulted in the deformation of the Sverdrup Basin (Ricketts and McIntyre, 1986). Volcanic rocks preserved in structural depressions (footwall of major thrusts or in thrust-plate synclinoria) of northwestern Axel Heiberg Island are interpreted to represent Cretaceous volcanism; these volcanics underwent tectonic activity (thrusting) during the Eocene. In west-central Axel Heiberg Island, the volcanics are preserved in domes and basinal structures that have structural culminations commonly cored by diapirs of Carboniferous evaporites (Fischer, 1984; Ricketts, 1987). All sampled localities are contained within detached thrust sheets. Deposition took place in predominantly fluvial and deltaic settings under unstable tectonic conditions (Miall, 1984a, 1986; Ricketts, 1986, 1991). The Cretaceous strata represent the major depocentre in the Arctic Islands from the Carboniferous to early Tertiary (Balkwill, 1978; Embry and Osadetz, 1988). Non-marine conditions prevailed in the eastern parts of the archipelago with shallow marine conditions prevailing in the north-central and southwestern parts.

On eastern Axel Heiberg Island, the uppermost and youngest unit of the Eureka Sound Group consists predominantly of diabase pebble conglomerates and lithic sandstones (Ricketts, 1986). Palynological determinations have dated the formation as Middle Eocene (Ricketts and McIntyre, 1986). Bustin (1982) reported a Miocene-Pliocene age for strata east of Geodetic Hills based on palynological evidence, but this age range has been shown to be incorrect by Ricketts and McIntyre (1986). Reworked Maastrichtian pollen and spores in the syntectonic Buchanan Lake Formation were derived from a western source (older Eureka Sound deposits), possibly located in central or western Axel Heiberg Island (Trettin, 1989). Paleocurrent determinations and facies trends indicate that sediment transport was eastward (Bustin, 1982). Consequently, Ricketts (1986, 1987) has argued against the existence of a pre-Eocene Princess Margaret Arch. Choi (1983) suggested that this major ridge existed during the Paleocene and peneplanation of this ridge during the Early to Middle Eocene caused significant clastic shedding in the region.

CHAPTER 2. SYSTEMATIC PALYNOLOGY

Anteturma Pollenites Potonie
Turma Poroses (Naumova) *emend.* Potonie
Subturma Triporines (Naumova) *emend.* Potonie

Genus *Paraalnipollenites* Hills and Wallace 1969

type species: *Paraalnipollenites confusus* (Zaklinskaya) Hills and Wallace 1969

***Paraalnipollenites* sp.**
Plate 1, figures 16, 17

Triporopollenites sp. 2 cf. *Paraalnipollenites alterniporus* Wingate, 1983, p. 117, Pl. 5, fig. 17

Description: Triporate. Oblately flattened. Subtriangular to rounded triangular outline in polar view. Sides straight to convex. Arci weakly developed in each hemisphere, extending between pore to a "false" pore in the interapertural region or swinging back without joining to the false pore, 1.5 - 2.5μm wide. Triaperturate, non-vestibulate pores, circular to subcircular, 2.5μm diameter. Number of pores half the number of arci. Exine double layered, 1.0 - 1.5μm thick, smooth to faintly granulate. Weak exinous thickening on one hemisphere, central or subcentral circular or elliptical ring (1.5 - 2.5μm diameter).

Dimensions: 26.5 - 35.0μm diameter (2 specimens)

Remarks: A similar form is illustrated by Wingate (1983) as *Triporopollenites* sp. 2 cf. *Paraalnipollenites alterniporus*. The unique arci and false pores preclude assignment to *Paraalnipollenites*, out of the generic realm of *Triporopollenites*. This form is *Paraalnipollenites* but it displays a weak development of arci and an exinal ring.

Comparison: The species is triporate but the development of the false pores gives the appearance of being multiporate (Wingate, 1983). It superficially resembles *Alnipollenites* but differs in having unique arci and only half the number of pores compared to the arcus number (Simpson, 1961). This particular feature may indicate an early evolutionary stage in *Alnipollenites*. *Trivestibulopollenites claripites* with weakly developed arci may also superficially resemble this species, but the former lacks a central ring.

Paraalnipollenites differs from *Alnipollenites* and modern *Alnus* by the false pores, unusual arci and the absence of vestibula (Jansonius and Hills, 1976). These criteria and the circumpolar ring are features diagnostic enough to differentiate this genus from other pollen types fitting in the "betuloid" complex. Wingate (1983) suggested an intergradation of *Paraalnipollenites* spp. and *Triporopollenites* spp. (rather than with *Alnus*-type forms) based on his specimens from the Eocene of Nevada. *Paraalnipollenites* has also been compared with pollen of *Casuarinidites* and the modern Casuarinaceae but the latter lack arci, polar exinal ring and false pores (Zaklinskaya, 1963).

Triatriopollenites confusus Zaklinskaya and *Paraalnipollenites confusus* (Zaklinskaya) Hills and Wallace are given in the synonomy of *Fushunpollis arcuatus* Sung and Tsao. Sung and Tsao (1976) consider the type of *T. confusus* to lack the diagnostic features to warrant its assignment to *Paraalnipollenites* (as Hills and Wallace, 1969; Bratzeva, 1969; Rouse and Srivastava, 1972 had presumed). According to Sung and Tsao (1976), *Paraalnipollenites* has no nomenclatural basis because the type species *P. confusus* does not properly fit into the generic description. Despite the poor state of preservation of the type species photographed by Zaklinskaya and the loose description of the genus *Paraalnipollenites* by Hills and

Wallace, *Fushunipollis* must be considered a junior synonym (Jansonius and Hills, 1976). Distinctiveness of the arci and exinal ring are not criteria that consistently differentiate *Fushunipollis* from *Paraalnipollenites*. The type species of *Fushunipollis*, *F. arcuatus* much resembles *Paraalnipollenites confusus*, which makes the status of the former genus dubius.

Botanical Affinities: Probably of betulaceous affinity (Simpson, 1961). Most similar to *Alnipollenites* and extant *Alnus* (Wingate, 1983).

Occurrences: This species most resembles the form found in the Eocene of Nevada (Wingate, 1983). The genus has been observed in Maastrichtian to Eocene deposits in Scotland (Srivastava, 1975; Simpson, 1961), U.S.S.R. (Zaklinskaya, 1963; Bratzeva, 1969), and North America (Hills and Wallace, 1969; Rouse and Srivastava, 1972; McIntyre, 1974; Doerenkamp *et al.*, 1976; Ioannides and McIntyre, 1980; Wingate, 1983; Choi, 1983; Frederiksen, 1988).

Genus *Carpinipites* (Wodehouse 1933) Srivastava 1966

type species: *Carpinipites ancipites*(Wodehouse 1933) Srivastava 1966

Carpinipites ancipites (Wodehouse) Srivastava 1966

Plate 1, figure 18; Plate 2, figures 4, 6

Carpinus ancipites Wodehouse, 1933, p. 510, fig. 42
Carpinipites ancipites (Wodehouse) Srivastava, 1966, p. 522, Pl. 7, fig. 1
Carpinites ancipites (Wodehouse) Srivastava, 1966, p. 530, Pl. 7, fig. 1 [misspelling]
Carpinites dilatus Agranovskaya in Pokrovskaya and Stelmak, *non* 1960, p. 369, Pl.3, figs. 17, 18 (*nomen nudum*)

Description: Triporate, occasionally tetraporate, oblate. Triangular to subtriangular outline with convex sides and angular apices. Pores equatorial, circular to meridionally elongate, 2 -3μm diameter. Slight labrum and/or tumescence may be present. Never with atrium or vestibulum. Surface psilate to indistinctly ornamented. Exine single-layered, thin, approx. 0.5 - 1.0μm thick.

Dimensions: * 21.8 (36.0) 36.0μm diameter (14 specimens)

Remarks: The size range of the Fossil Forest Hill specimens is narrower than the range, 22.7 - 44.5μm diameter, given by Wodehouse (1933). In all other features, however, the observed specimens are very similar to those originally described by Wodehouse (1933).

Srivastava (1966) instituted this genus to include all fossil pollen resembling yextant *Carpinus* Linnaeus (i.e. triporates and tetraporates with a smooth exine and a simple pore structure). *Carpinipites* is not comparable to the genus *Carpinites* Agranovskaya, the latter genus is not a junior synonym of *Carpinipites* Srivastava (Srivastava, 1966, 1972a; Jansonius and Hills, 1976). *Carpinites* is somewhat larger (36 - 39μm diameter) and has a scabrate surface sculpture. *Carpinites* is considered an invalid genus because *Carpinites dilatus* Agranovskaya was described without a separate generic diagnosis (as required by art. 42 of the Botanical Code for a monotypic genus) and, therefore, is invalid (by art. 43 of the Code). The generic name was also associated with an already described species (Srivastava, 1972a). However, the potential confusion over the similar names is evident in Srivastava's 1966 paper with the several misspellings of *Carpinipites* Srivastava as *Carpinites.*

Nagy (1969, p. 315) preferred the generic name *Carpinuspollenites* Thiergart to *Carpinipites* Srivastava because the former name appeared earlier in the literature. However, Srivastava (1972a) and Potonie (1960) argued that Thiergart never intended to formally establish *Carpinus?-pollenites* as a genus, especially with a prefix

---

* the notation represents the size range and the modal diameter, i.e. minimum (mode) maximum diameters.

Carpinus? inferring a doubtful affinity to *Carpinus*. *Carpinuspollenites* was not validly published in 1938 by Thiergart, because there was no diagnosis, simply a species description. Pflug (in Thomson and Pflug, 1953), however, proposed another genus to include species of *Carpinus* under the genus *Polyporopollenites*. *Carpinipites* Srivastava is diagnosed as having three to four pores, and Takahashi (in Takahashi and Kim, 1979) instituted a new genus, *Carpinuspollis* to accommodate all polyporate forms, (three- to seven-pored, but mostly four- to five-pored), which are comparable to *Carpinus* pollen and designated *Carpinuspollis carpinoides* (Pflug) Jansonius and Hills as the type species. *Carpinuspollis, Carpinuspollenites* and *Polyporopollenites* are considered to be junior synonyms of *Carpinipites*.

Comparison: *Carpinipites* is readily distinguished from all other genera in having a thin, single-layered grain with an unornamented surface and a simple pore pattern, i.e. club-shaped (Wodehouse, 1933). Stanley (1965) noted that the lack of a thickened region in the pore area usually permitted separation of pollen of this genus from other genera, especially in Betulaceae that produce similar pollen.

Unlike *Triporopollenites, Carpinipites* Srivastava lacks a distinct annulus or tumescence (Choi, 1983). *Carpinipites* differs from *Momipites* in lacking atria and in being generally larger (Choi, 1983). A similar form, *Carpinipites subtriangula* (Stanley) *nov. comb.* has a distinctly scabrate exine unlike this species, although, Frederiksen (1979) reassigned this species in the realm of *Triatriopollenites*.

Botanical Affinities: Morphologically similar to extant *Carpinus* (Wodehouse, 1933; Srivastava, 1966; Nagy, 1969), probably betulaceous affinity.

Occurrences: *Carpinus* was much more widespread than it is at present and appears to have been a common constituent in many of the North American Tertiary floras

(Wodehouse, 1933; Hopkins, 1969) except in those flora of the southwest United States.

Genus *Trivestibulopollenites* (Wodehouse 1933) Pflug 1953

type species: *Trivestibulopollenites betuloides* Pflug 1953

Trivestibulopollenites betuloides Pflug 1953
Plate 2, figure 3

Trivestibulopollenites betuloides Pflug in Thomson and Pflug, 1953, p. 85, Pl. 9 figs. 25-34.
Trivestibulopollenites betuloides Pflug; Norris, 1986, p. 40, Pl. 10, figs. 38-42

Description: Triporate, oblate. Subcircular to convexly triangular outline. Pores circular, 2.5μm diameter, equatorial, slightly aspidate. Small indistinct vestibula, no atria. Weak annuli and labra if present. Exine thin, 0.5 - 1.0μm thick, psilate to finely granulate.

Dimensions: 25.0 (26.5) 31.0μm diameter (8 specimens)

Remarks: This species is relatively rare as compared to the abundance of *T. claripites* in the Fossil Forest Hill section.

Trivestibulopollenites was validly published first and appears to have priority over *Betulaceoipollenites* (Jansonius and Hills, 1976). The type species *T. betuloides* is very similar to that of *Betulaceoipollenites*, therefore, the justification of the latter genus is dubius (Potonie, 1960). *Betulaceoipollenites* becomes the obligate junior synonym of *Trivestibulopollenites* (Jansonius and Hills, 1976).

Comparison: *Trivestibulopollenites claripites* is similar but it possesses a triangular outline and a thicker and faintly ornamented exine (Norris, 1986). Wodehouse (1933) referred to the pore pattern in fossil *Betula* pollen as "*broad knob*" or *Betula* pattern. The presence of a small indistinct vestibulum and subcircular outline readily separates this species from species of *Trivestibulopollenites* and other *Betula*-type pollen.

Botanical Affinities: Betulaceae. Morphologically similar to *Betula* pollen such as *B. occidentalis* Hook and *B. alleghanensis* Britton. Both species differ slightly in having a sculptured exine and a slightly different pore structure.

Occurrences: There have been few reported occurrences of this species in Tertiary sediments: Paleogene and Neogene MacKenzie Delta, Northwest Territories, Canada (Norris, 1986) and Pliocene Germany (Pflug in Thomson and Pflug, 1953).

Trivestibulopollenites claripites (Wodehouse) Choi 1983
Plate 2, figures 1, 2

Betula claripites Wodehouse, 1933, p. 509-510, fig. 41
Betula claripites Wodehouse; Wilson and Webster, 1946, p. 275, fig. 12
Betula claripites Wodehouse; Martin and Rouse, 1966, p. 197, figs. 72, 73
Betula cf. *B. claripites* Hopkins, 1969, p. 1118, figs. 84-85
Trivestibulopollenites claripites (Wodehouse) Choi, 1983, Pl. 44, fig. 333
Trivestibulopollenites claripites (Wodehouse) Norris, 1986, p. 40, Pl. 10, figs. 47-49

Description: Triporate, rounded triangular, often spheroidal to subspheroidal. Angular outline because of prominent pores. Pores circular to lolongate, 1.5 - 2.5μm diameter, equatorial, strongly aspidate. Distinct vestibulum; thickening at pore region causing the strongly aspidate character of pores. Exine thin, 0.5 - 1.0μm thick, faintly granulate. Sexine twice as thick as nexine. Poor to well-defined arci (1.5 -2.5μm wide) between pores may be present.

Dimensions: 20.3 (24.2) 36.7μm diameter (101 specimens)

Remarks: These forms are easily identifiable by their inflated rounded triangular shape and sharply protruding pores. Their frequent occurrence throughout the leaf litter zones, makes it second most abundant species after *Alnipollenites*. Wodehouse (1933) provided no specific details of the pore structure, having only a "*broad-knob*" (*Betula*) pattern. It is clear from his diagrams that the aspides (i.e. annuli) are present (Wodehouse, 1933), but Martin and Rouse (1966) claimed the pores were not annulate in their Skonun pollen grains. The vestibulate nature and aspidate pores are most characteristic of *Trivestibulopollenites claripites* (Wodehouse) Choi and are present in all specimens examined. Arci between pores are visible in some grains but often grains are folded along arci.

Erdtman (1952) and Wodehouse (1933) observed the presence of arci, distinct or faint. In this study, one figured specimen displays well-defined arci (Pl. 2, fig. 1). *T. claripites* has a tendency to fold, and as a result some grains appear less spheroidal or inflated as a result. These exinal folds do not tend to be regularly oriented and are not interpreted as arci. Similarly, Stanley (1965) remarked on the arc features included in Wodehouse's (1933) original specific description and diagnosis but he did not observe such features in his *Betula*-type grains of South Dakota.

The characteristic features of this genus are shared with many other genera in several families (Wodehouse, 1933): Myricaceae, Juglandaceae (*Engelhardtia, Pterocarya, Platycarya*), Cannabidaceae (*Cannabis*), Urticaceae (*Morus, Broussonetia*) and Haloragidaceae (*Myriophyllum*). Wodehouse (1933) suggested that grains of Betulaceae represented a form towards which the grains of many wind-pollinated species of diverse origins tend to approach, i.e. the "*Betula*"-type form. The resemblance of various genera to grains of Betulaceae may make their identification difficult and occasionally uncertain. Distinct pore patterns can distinguish similar generic forms of various families (Wodehouse, 1933).

Comparison: This species closely resembles *Betulaceoipollenites bituitus* (Potonie, 1960; Martin and Rouse, 1966), *Casuarinidites* spp. and other *Triatriopollenites* forms (Erdtman, 1952; Srivastava, 1972b; Jansonius and Hills, 1976).

Trivestibulopollenites claripites is distinguished from *T. betuloides* in possessing a triangular outline, a thicker lightly sculptured exine and small endopore (Norris, 1986). *T. infrequens* (Stanley) *nov. comb.* is similar but appears to have well-defined exinal ornamentation and distinct annuli.

Botanical Affinities: Morphologically similar to modern *Betula*-type pollen (Wodehouse, 1933). Earlier comparisons have been suggested with modern *Betula* species, including: *B. lenta* (sweet or cherry birch; Wodehouse, 1933) and *B. papyrifera* (paper birch; Martin and Rouse, 1966).

Occurrences: Reported from the Maastrichtian to Miocene from western North America, Canadian Arctic and Siberia. *Trivestibulopollenites* had a wide distribution during the Tertiary (Hopkins, 1969). Betulaceae still remains as one of the principal floral families of North America (Lewis *et al.,* 1983). The absence of the genus from the southeastern regions may be due to the too-warm climate (Wodehouse, 1933). Wodehouse (1933) proposed that the presence of fossil *Betula* and *Alnus* in the Green River flora implies a rather cool and humid climate in the Colorado and Utah area.

Among the numerous localities where it has been found are the interior of British Columbia (Martin and Rouse, 1966); Northwest Territories (Norris, 1986); Green River Oil Shales, Colorado and Utah (Wodehouse, 1933) and South Carolina (Frederiksen, 1980).

Genus *Caryapollenites* Raatz 1938 ex. Potonie 1960 *emend.* Krutzsch 1961

type species: *Caryapollenites simplex* (Potonie 1931) Raatz 1938

Caryapollenites viridifluminipites (Wodehouse) Choi 1983

Plate 3, figures 1, 2

Hicoria viridi-fluminipites Wodehouse, 1933, p. 503, fig. 29
Carya viridifluminipites (Wodehouse) Martin and Rouse, 1966, p. 196, fig. 81
Carya viridifluminipites (Wodehouse) Martin and Rouse; Piel, 1971, p. 1909, fig. 103
Caryapollenites viridifluminipites (Wodehouse) Choi, 1983, p. 333, Pl. 45, fig. 349

Description: Triporate, oblate. Subcircular to broadly elliptical outline in polar view. Pores circular to elliptical, 2.5 - 4.0μm diameter, predominantly subequatorial, heteropolar. Weak atria. Tumescence and labra absent. Exine thin, 0.5 - 1.0μm thick. Surface psilate to faintly sculptured. Tendency to develop folds.

Dimensions: 23.4 (32.0) 38.2μm diameter (18 specimens)

Remarks: Fossil Forest Hill specimens exhibit a slighter broader size range than those of the Green River Oil Shales, which measure 36 to 39μm diameter (Wodehouse, 1933), otherwise, they are morphologically identical. Previous workers have observed larger size ranges: middle to late Tertiary Skonun specimens, 35 - 45μm diameter, (Martin and Rouse, 1966); Paleogene Axel Heiberg and Ellesmere island specimens, 34 - 49μm diameter, (Choi, 1983).

C. viridifluminipites is characterized by a subcircular shape, heteropolarity of pores, the lack of a distinct polar-thinned area and by relatively large size (Choi, 1983). Nichols and Ott (1978) have interpreted incomplete heteropolarity of pore position as primitive, a feature often observed in the modern species *Carya sinensis* and the fossil ancestral species *Caryapollenites viridifluminipites*.

Comparison: This species lacks polar islands or other such polar thinned exinal modifications which are characteristic of most fossil *Carya*. The circular outline, the heteropolarity of pores and the lack of observable pore thickenings, readily distinguish this species from other species of *Caryapollenites* and *Subtriporopollenites*. Similar types of *Carya*-type pollen include the relatively larger form *Caryapollenites spackmaniana* (Traverse) Choi, (56μm diameter), and the smaller *C. simplex* (Potonie) Raatz, (25 - 38μm diameter).

Botanical Affinities: Affinity to Juglandaceae (Potonie, 1960). General resemblance to modern *Carya* Nutt, though extant forms are usually 10 to 20μm larger in diameter. Wodehouse (1933) believed that *C. viridifluminipites* is related to *myristicaeformis* group (nutmeg) of hickories (Wodehouse, 1933, p. 503). This species matched in all respects, except in its smaller size, with *Hicoria myristicaeformis* (i.e. *Carya myristicaeformis* or nutmeg hickory; Wodehouse, 1933). Wodehouse (1933) suggested that this form may represent an extinct species.

Occurrences: This species is frequent in Tertiary deposits of North America and Europe (Wodehouse, 1933; Martin and Rouse, 1966; Choi, 1983). Extant species of *Carya* are indigenous to North America and Asia (Willis, 1973; Lewis *et al.*, 1983; Mabberley, 1987).

Caryapollenites juxtaporipites (Wodehouse) Choi 1983
Plate 3, figure 3

Hicoria juxtaporipites Wodehouse, 1933, p. 504, fig. 30
Carya juxtaporipites (Wodehouse) Rouse, 1962, p. 203, Pl. 2, figs. 13-14, 16
Carya juxtaporipites (Wodehouse) Rouse; Hopkins, 1969, p. 1120, figs. 106-109
Carya juxtaporipites (Wodehouse) Rouse; Piel, 1971, p. 1909, figs. 101, 102
Caryapollenites juxtaporipites (Wodehouse) Choi, 1983, p. 332, Pl. 44, fig. 348

Description: Triporate, oblate. Subcircular to rounded triangular outline in polar view, sides convex. Pores small (2.0 - 2.5μm diameter), subequatorial, heteropolar, 2μm away from the equator. No polar thinning. Exine finely scabrate, 0.5 - 1.0μm thick. Folding common.

Dimensions: 32.8 - 35.9μm diameter (2 specimens)

Remarks: *Caryapollenites juxtaporipites* is characterized by the relatively small subequatorial pores, a distinctly scabrate sculpture and the absence of a thinned polar ring.

Comparison: *Caryapollenites juxtaporipites*, although similar to *C. viridifluminipites*, can be distinguished by ornamented surface and the strongly subequatorial pores. This species differs from *C. viridifluminipites* and *C. inelegans*, in having a rounded triangular outline in polar view, and relatively small pores (less than 1.5 - 2.0μm diameter) which are located approx. 2μm off the equator. *Caryapollenites imparalis* may also resemble this species but differs in having ambs that are not entire (Nichols, 1973, i.e. the pores break up the outline of the grain) and in having more strongly convex sides.

Botanical Affinities: Juglandaceae. Wodehouse (1933) commented on the strong resemblance of this species with modern *Carya*, differing only in size.

Occurrences: This fossil taxon occurs in the Eocene-Oligocene of British Columbia (Rouse, 1962; Hopkins, 1969; Piel, 1971), the Maastrichtian-Early Paleocene of Canadian Arctic Islands and the Eocene of Colorado and Utah (Wodehouse, 1933).

***Caryapollenites* sp. cf. *C. veripites* (Wilson and Webster) Nichols and Ott 1978**
Plate 3, figures 5, 6

Caryapollenites veripites Wilson and Webster, 1946, p. 274, fig. 14 [in part]
Caryapollenites veripites (Wilson and Webster) Nichols and Ott, 1978, p. 106, Pl. 2, figs. 12, 13 [in part]
Caryapollenites sp. A Ioannides and McIntyre, 1980, Pl. 31.4, figs. 1, 2
Caryapollenites veripites (Wilson and Webster) Nichols and Ott; Wingate, 1983, p.

117, Pl. 5, fig. 21.
Caryapollenites sp. 1 Choi, 1983, p. 335, Pl. 45, fig. 353

Description: Triporate, oblately flattened. Subcircular to rounded triangular outline in polar view. Pores 2.5 - 3.0μm diameter, circular to slightly elliptical, subequatorial, heteropolar. No thickening observed in the pore region. Atria weak, 3.9μm deep, 11.7μm wide. Exine thin, 0.5 - 1.0μm thick, psilate to faintly granular. Thinned polar area without polar island, subtriangular to subpolygonal outline, 11.7 - 15.6μm diameter. Tendency to develop folds.

Dimensions: 28.9 (28.9) 39.8μm diameter (4 specimens)

Remarks: Distinguishing features include complete heteropolarity of pores and the circumpolar ring of thinning exine. It differs from *C. veripites* by the absence of a circumpolar island of normal exinal thickness (Nichols and Ott, 1978). The polar area indicates a thinner exinal area or an area of weakness, resulting in broken or torn specimens, as if the sides of the thinned areas were pulled back. This species is very similar to forms described by Choi (1983) and by Wingate (1983), identified as *Caryapollenites* sp. 1 and *C. veripites*, respectively.

Two distinctions have been made about *Caryapollenites* and modern *Carya* (Nichols and Ott, 1978). They differ in showing polar thinning. Modern *Carya* pollen have thinned polar spots unlike polar rings as observed in the fossil *Carya* pollen. They also differ in pollen grain size. Fossil *Carya* pollen are considerably smaller than modern *Carya* pollen; modern grains may be 30 to 60μm in diameter, with an average size of 45μm. Nichols and Ott (1978) concluded that, based on these two features, *Caryapollenites veripites* was part of a morphologic continuum, with a parallel line leading from *C. wodehousei* to *C. veripites*. This lineage trended towards smaller size, but in light of the phyletic position, Nichols and Ott (1978) considered this species to be the most advanced species of the *Caryapollenites* lineage, at least, in the Paleocene of Wyoming. Despite the primitive condition of smaller size exhibited by *C. veripites*, Nichols and Ott (1978) proposed that the size increase reversal exhibited by the species was a temporary situation, and that the trend toward increased size was reasserted later in Tertiary time.

Comparison: A similar form is *Caryapollenites* sp. 1 of Choi (1983) which he describes as lacking a true polar ring and island of normal exinal thickness. *Caryapollenites veripites* illustrated by Wingate (1983) appears very similar with the notable absence of a polar island.

This species differs from *C. veripites* only in having a psilate exine, and a weakly developed polar thinning modification, unlike the well-developed polar thinning as a circumpolar ring surrounding a polar island of normal thickness, typical of *C. veripites* (Nichols and Ott, 1978).

Unlike *C. viridifluminipites*, this species is rare in the Fossil Forest Hill assemblages. The larger size and the lack of exinal modifications is very characteristic of the former and can easy distinguish it from this species.

Botanical Affinities: Affinity to the Juglandaceae (Potonie, 1960). There is a general resemblance to modern *Carya*, but extant forms are usually 10 to 20μm larger in diameter (Whitehead, 1963, 1965; Nichols and Ott, 1978). This species is closest to the modern species, *Carya sinensis* Dode (Chinese hickory), a "primitive" living species, in most characters (Nichols, 1973; Nichols and Ott, 1978).

The author has observed two modern species, *Carya texana* (average 48.4μm diameter) and *Carya pecan* (average 50.8μm diameter) that closely resemble this species in having a polar thinned area without a polar island.

Occurrences: This species is rare throughout the leaf litter section. It is considered one of the important fossils in the Tertiary flora of North America (Wilson and Webster, 1946; Hopkins, 1969).

***Caryapollenites* sp. cf. *C. inelegans* Nichols and Ott 1978**
Plate 3, figure 4

Carya viridifluminipites Wodehouse; Wilson and Webster, 1946, p. 274, fig. 13
Carya viridifluminipites Wodehouse; Leffingwell, 1971, p. 1909, Pl. 6, fig. 4
Caryapollenites inelegans Nichols and Ott, 1978, p. 105, Pl. 2, figs. 7,8

Description: Triporate, oblate. Rounded triangular outline in polar view; sides convex. Pores located almost entirely in one hemisphere, circular to lolongate, 1.5 - 2.5μm diameter. Atria small, 2.0μm deep, 3.9μm wide, faint. Exine thin, 0.5 - 2.0μm thick, finely granulate.

Dimensions: 28.1 (28.1) 35.9μm diameter (6 specimens)

Remarks: According to the species diagnosis, forms may express weakly structural modifications of polar exine, but nothing truly distinctive as, for example, the polar islands characterizing *Caryapollenites veripites* and *C. wodehousei*. The author did not observe a ring structure in this form, but in all other respects, this species is similar to *C. inelegans*. Nichols and Ott (1978) questioned the assignment of specimens of *C. viridifluminipites* by Leffingwell (1971) and Wilson and Webster (1946) and considered that the forms belonged to *C. inelegans* based on the presence of the weak circumpolar ring and the smaller size.

Comparison: The lack of a true polar ring or other structural modifications readily distinguishes this species from other *Carya*-type pollen with polar exinal structures such as a circumpolar ring and polar island (*Caryapollenites wodehousei* and *C.*

veripites). *Caryapollenites inelegans* differs from *C. imparalis* in having all pores completely subequatorial, and from all other species of *Caryapollenites* in lacking the polar thinning typical of most species of the genus (Nichols and Ott, 1978). Unlike *C. viridifluminipites*, this species is slightly smaller by 5 - 10μm.

Botanical Affinities: Probably belongs to Juglandaceae, similar to extant *Carya*.

Occurrences: This species has been reported from the early Tertiary of North America (Nichols and Ott, 1978) and a single occurrence in the Oligocene of British Columbia (Piel, 1971).

***Caryapollenites* sp. A**

Plate 3, figures 9, 10

Description: Triporate, oblate. Circular to subcircular in outline in polar view. Pores circular to slightly lolongate, 2.5 - 3.0μm diameter, equatorial. Slight labrum and tumescence. Atriate, 3 - 4μm deep, 5.5 - 9.5μm wide, weak and indistinct. Surface sculpture psilate to finely granulate, coarse granules in region of pore. Exine thin, 0.5 - 1.0μm thick, double-layered.

Dimensions: 30.4 (32.8) 39.0μm diameter (12 specimens)

Remarks: The author has chosen to leave this form as *Caryapollenites* rather than assign it to *Triatriopollenites*. Pflug (in Thomson and Pflug, 1953) intended only *Triatriopollenites* to include triporate pollen with triangular ambs and corners more or less rounded, never circular. It is a tentative assignment because the slight tumescence and predominantly equatorial pores in these forms are uncharacteristic of *Caryapollenites* grains.

Comparison: The specimens are closest in description to that of *Caryapollenites paleocenica* (Stanley) Norris and *C. juxtaporipites* (Wodehouse) Choi. The heteropolarity of pores and the juglandaceous nature of the wall at the pore region is diagnostic of *Carya*-type species (species of *Caryapollenites* and *Subtriporopollenites*). *C. paleocenica* resembles this species by having a scabrate surface sculpture, large pores, approximately 3μm diameter, and a circular shape in polar view. Some specimens also closely resemble *C. juxtaporipites* in shape, size (31.2 - 39.0μm diameter) and exine sculpture and possibly similar thick exine thickness but the latter does not have small and subequatorial pores.

Botanical Affinities: Probable botanical affinities to Juglandaceae based on the large circular grain, near complete heteropolarity of the pores and the juglandaceous nature of the pore pattern.

Genus *Platycaryapollenites* Nagy 1969 *emend.* Frederiksen and Christopher 1978

type species: *Platycaryapollenites miocaenicus* Nagy 1969

Platycaryapollenites sp. cf. *P. platycaryoides* (Roche) Choi 1983

Plate 3, figures 7, 8

Triatriopollenites platycaryoides Roche, 1969, p. 135, textfigs. 6-7, Pl. 1, fig. 19
Platycarya sp. Hopkins, 1969, p. 1120, Pl. 8, figs. 114-116
Platycarya platycaryoides Frederiksen and Christopher, 1978, p. 138, Pl. 3, figs. 3-6
Platycarya sp. Nichols and Ott, 1978, p. 101, Pl. 2, fig. 14
Platycarya platycaryoides Frederiksen, 1979, p. 149, Pl. 1, fig. 39
Platycaryapollenites sp. cf. *P. platycaryoides* (Roche) Choi, 1983, p. 330, Pl. 44, fig. 345

Description: Small triporate oblate. Slightly rounded triangular shape with gently convex sides. Pores equatorial lolongate, 1.0 - 1.5μm diameter. Atria present; annuli and labra absent. Exine thin, approx. 0.5 - 1.0μm thick. Sexine thicker than nexine: no distinct columellae. Psilate or finely scabrate. Two or three pseudocolpi on each hemisphere, pseudocolpi 1.0 - 1.5μm wide. Secondary folding may also occur in some specimens.

Dimensions: 18.7 - 21.0μm diameter (2 specimens)

Remarks: The characteristic pseudocolpi distinguish the genus from the pollen of similar size of *Triatriopollenites* and *Momipites* species and other *Engelhardtia*-type pollen. Some grains (may) also exhibit some secondary folding (Nagy, 1969).

Pseudocolpi (Faegri and Iversen, 1964) have been termed "arcoid" streaks (Erdtman, 1972), slit openings in the exine (Whitehead, 1965); slit-like thinning, actual furrows (colpi) or "grooves" (Wodehouse, 1933, 1935); arcoid bands (Nagy, 1969); crossfolds or splits [?] (Hopkins, 1969); and crease-like thinnings of exine (Manchester, 1987). The exact nature of these interwoven bands, as a result of thinnings or exinal thickenings, is uncertain (Nichols, 1973). In modern grains, the troughs of the pseudocolpi are formed partly by invaginations but primarily by thinning of the ectosexine and endosexine (Stone and Broome, 1975).

The pores are reported to have a *Corylus* pattern (Wodehouse, 1933; Thiergart, 1940) and are slightly offset from the equator (i.e. juglandaceous in nature; Hopkins, 1969; Nichols and Ott, 1978).

Comparison: There may be little distinction between pollen grains of fossil *Platycarya* and *Engelhardtia* and certain members of Betulaceae, however, the small size and the characteristic pseudocolpi are diagnostic of *Platycarya*-type pollen (Hopkins, 1969).

Frederiksen and Christopher (1978) imply polyphyletic origins for *Platycaryapollenites-Momipites-Plicatopollis* complex based on the complexities of intergradations between species of *Platycarya, Platycaryapollenites, Momipites* and *Plicatopollis*. In their comprehensive study of triatriate forms from the Cretaceous and Paleogene of South Carolina, Frederiksen and Christopher (1978) regarded the definition of microcoryphaeus group of *Momipites* (*M. coryloides, M. inaequalis*, Nichols, 1973) as similar to their definition of the genus *Platycaryapollenites*, the latter in having pseudocolpi. Nichols (1973) also remarked on the similarities of the microcoryphaeus group and *Platycarya*-types.

Botanical Affinities: Similar in form to extant *Engelhardtia* but smaller and in having pseudocolpi (Wodehouse, 1933, 1935). Nichols (1973) also commented on the similarity of this genus to *Engelhardtia-Alfaroa* group, the former differing only in having pseudocolpi. *Platycarya* is the closest modern comparison to *Platycaryapollenites*, sharing similarities in structural modifications of the exine (pseudocolpi) and size range (Manchester, 1987). The thin areas and/or long folds of *Platycaryapollenites* distinguish the species from modern *Platycarya* pollen (Frederiksen and Christopher, 1978). The orientation and the number of arcoidal bands are arranged differently than those in *Platycarya* (Frederiksen and Christopher, 1978). A single modern species occurs in Japan, *Platycarya strobilacea* Sieb. and Zucc. (Willis, 1973; Mabberley, 1987). Fossil grains are larger than modern ones (Frederiksen and Christopher, 1978). Frederiksen (1988) assigned all *Platycarya*-type specimens to *Platycarya platycaryoides*-type that have similar pseudocolpi to modern pollen of this genus. Those specimens that are different from those of the modern genus, Frederiksen (1988) assigned to the form genus *Platycaryapollenites*. Wing and Hickey (1984) also proposed the practice of assigning Eocene pollen to the modern genus *Platycarya* based on the Eocene leaves and fruits of *Platycarya*-type.

Occurrences: Although *Platycarya* is a monotypic genus today, it was more diverse in the Paleogene (Manchester, 1987). The range of *Platycarya*-type pollen in North America (Hopkins, 1969; Rouse *et al.*, 1971; Choi, 1983; Frederiksen, 1988), Europe (Zaklinskaya, 1963; Roche, 1969; Bratzeva, 1969) is from Upper Paleocene to

Eocene. This genus appears to be restricted to Eocene rocks (and older) in the New World (Hail and Leopold, 1960; Hopkins, 1969; Wing and Hickey, 1984; Frederiksen, 1988). Although relatively abundant in Early and Middle Eocene, *Platycarya*-like pollen is unknown in North America beyond the Early Oligocene (Manchester, 1987).

Frederiksen and Christopher (1978) suggested a southern origin and northward migration of *Platycaryapollenites* based on the rare occurrence in the Paleocene of the southern United States. *Platycaryapollenites* appeared suddenly in the midwest and eastern United States in the lowermost Eocene (Leopold and MacGinitie, 1972; Nichols and Ott, 1978).

Genus *Momipites* Wodehouse 1933 *emend.* Frederiksen and Christopher 1978

type species: *Momipites coryloides* Wodehouse 1933

Momipites coryloides Wodehouse 1933

Plate 3, figures 11, 12

Momipites coryloides Wodehouse, 1933, p. 511, fig. 43
Momipites coryloides Wodehouse; Wilson and Webster, 1946, p. 274, fig. 15
Momipites coryloides Wodehouse; Frederiksen and Christopher, 1978, p. 119, Pl. 1, fig. 1

Description: Triporate, suboblate to oblate. Triangular to rounded triangular in polar view. Sides strongly convex. Pores equatorial, circular to meridionally elongate, 1.5 - 2.5μm diameter. Distinct atria, 2.5 - 3.0μm deep, 8.5μm wide. Pore pattern is club-shaped (according to Wodehouse, 1933). Presence or absence of annuli or tumescence, slight tumescence if present. No prominent labrum. Lacks polar islands or triradiate folds or thickenings. Exine 1.0 - 1.5μm thick. Sexine is much thicker than nexine.

Dimensions: 20 (21.0) 25.7μm diameter (33 specimens)

Remarks: Frederiksen and Christopher (1978) considered this species a Middle Eocene form in Late Cretaceous-Paleogene South Carolina. They generally categorized species of *Momipites* by size. *M. microfoveolatus* was placed in the *inequalis* Group, size range 15 -24µm diameter and *M. coryloides* was placed in *coryloides* Group, size range 21 -33µm diameter. Nichols (1973) lumped them together as simply the *coryloides* group (size class 15 - 40µm diameter) for fossil taxa that were essentially the same as modern species of *Engelhardtia* and *Alfaroa*.

Comparison: This species is a relatively rare form and somewhat larger (21 - 33µm diameter) than *Momipites microfoveolatus* (15 - 22µm diameter). The small overlap in their size ranges and the slightly to more convex sides of this species often makes speciating these two forms difficult. The latter species can be recognized by the lack of any tumescence, annulus or labrum; *M. coryloides* typically show slight tumescence and/or annuli (Frederiksen and Christopher, 1978).

Botanical Affinities: Juglandaceous affinity (Potonie, 1931). Pollen morphology is similar in all respects to pollen of the *Engelhardtia-Alfaroa* group, however, this group of pollen exhibits a greater size range (Nichols, 1973; Frederiksen and Christopher, 1978).

This pollen type might share affinities with the Betulaceae, especially *Corylus* Linnaeus, and closely approaches the form of *Ostrya* and *Myrica* (Kirchheimer, 1932; Wodehouse, 1933; Simpson, 1936, 1961). Previously, this species was assigned to several families including the Ulmaceae (Wodehouse, 1933; Hopkins, 1969), Urticaceae (nettle family, Wodehouse, 1933; Wilson and Webster, 1946), and Juglandaceae (Nichols, 1973). *Momipites coryloides* is of problematic status according to Wodehouse (1933) who considered identification of this pollen difficult, since this species also closely resembles *Corylus* Linnaeus (Betulaceae), *Engelhardtia* Leschen (Juglandaceae) and *Celtis* Linnaeus (Ulmaceae). He suggested affinity with *Momisia (=Celtis) iguanacea* and *Celtis debequensis* (both of Ulmaceae), *Engelhardtia spicata* (Juglandaceae) and species of *Corylus* and *Carpinus* Linnaeus (Betulaceae). A northern connection of the Green River flora is suggested if the form was *Corylus*, or a southern connection if it was *Celtis (=Momisia)* or *Engelhardtia* (Wodehouse, 1933).

"Engelhardioid" pollen has gone under various names, *Momipites, Engelhardtia, Engelhardtioidites, Engelhardtioipollenites, Triatriopollenites, Triporopollenites* and *Myricipites* (Potonie, 1960; Nichols, 1973; Manchester, 1987). Manchester (1987) preferred the fossil generic name *Momipites* for dispersed juglandaceous pollen that is triatriate, isopolar like that of Engelhardiaceae.

Occurrences: *Momipites coryloides* is common and widespread in early Tertiary deposits (Wodehouse, 1933; Wilson and Webster, 1946; Nichols, 1973; Frederiksen and Christopher, 1978). The "*coryloides*" group of *Momipites* (Nichols, 1973) is reportedly present as early as Maastrichtian in North America and common in the Paleocene of North America and western Europe (Manchester, 1987).

Momipites microfoveolatus **(Stanley) Nichols 1973**
Plate 3, figure 13

Engelhardtia microfoveolata Stanley, 1965, p. 300-301, Pl. 45, figs. 8-13
Momipites microfoveolatus (Stanley) Nichols, 1973, p. 107
Momipites microfoveolatus Stanley) Nichols; Frederiksen and Christopher, 1978, p. 130, Pl. 1, figs. 7-10
Momipites microfoveolatus (Stanley) Nichols; Frederiksen, 1980, p. 39, Pl. 7, figs. 15, 16
Momipites microfoveolatus (Stanley) Nichols; Choi, 1983, p. 329, Pl. 44, fig. 329

Description: Small triporate, suboblate to oblate. Triangular to subtriangular in polar view. Pores lolongate, 0.5 - 1.5μm diameter, equatorial, non-aspidate, distinctly atriate (atrium 2μm deep, 6.2μm wide). Tumescence absent. Lacks polar-thinning or other structural modifications (such as pseudocolpi, folds or thickenings). Exine thin, 1.0 - 1.5μm thick, microfoveolate.

Dimensions: 14.0 (20) 21.8μm diameter (63 specimens)

Remarks: In this study, *M. microfoveolatus* is a frequent pollen taxa, typically in good to excellent condition and is an ubiquitous form in the Fossil Forest Hill leaf litter horizons.

Comparison: Grains of *Carpinipites* may look similar to certain species of *Momipites* but the smaller size and the atriate nature of the pores of the latter genus, readily separates the two genera. *M. coryloides* may look very similar to *M. microfoveolatus*, but the main differences between the two are the size, slight pore modifications, and the convexity of the sides of the grains. The latter species is smaller, typically less than 20μm diameter and has slightly concave to slightly convex sides. *M. coryloides* is a larger form (about 21 - 28μm diameter), with more convex sides and slightly annulate and slightly tumescent pores.

Botanical Affinities: Affinities with the Juglandaceae (Nichols, 1973). The morphology of species of *Momipites* has been interpreted as characteristic of Juglandaceae and closely related to modern representatives of the family, *Engelhardtia, Alfaroa* (Whitehead, 1965; Nichols, 1973; Crepet *et al.*, 1975; Nichols and Ott, 1978; Frederiksen and Christopher, 1978; Crepet *et al.*, 1980). Other *Momipites* species exhibit further juglandaceous features characteristic in species of *Carya* and *Platycarya*, such as triradiate folds and polar islands (Nichols and Ott, 1978; Frederiksen, 1979; 1980).

Similar juglandaceous triporate pollen has been recorded as *Engelhardia* (or *Engelhardtia*) and *Engelhardtiopollenites* (Traverse, 1988). *Momipites* pollen, resembling *M. microfoveolatus*, has been recovered from *Eokachyra* (Crepet *et al.*, 1975) and *Eoengelhardia* (Crepet *et al.*, 1980), form genera for Eocene juglandaceous catkins. Elsik (1969) suggested that ancestral *Engelhardtia*-types evolved from the Normapolles group of pollen in the late Cretaceous. The distinctive Paleocene forms existing in the Gulf Coast may be representatives of extinct genera of the Juglandaceae (Elsik, 1969).

Occurrences: The species is widespread and common in Late Cretaceous to early to late Tertiary sediments (e.g. Elsik, 1969; Nichols, 1973; Nichols and Ott, 1978; Choi, 1983; Demchuk, 1988).

Genus *Plicatopollis* Krutzsch 1962 *emend.* Frederiksen and Christopher 1978

type species: *Plicatopollis plicata* (Potonie 1934) Krutzsch 1962

***Plicatopollis* sp. of the *P. plicata*-type (Potonie) Krutzsch; Frederiksen and Christopher 1978** Plate 3, figures 14, 15, 17, 18

Pollenites plicatus Potonie, 1934, p. 55, pl. 2, fig. 19
Plicatopollis plicatus (Potonie) *auct. non* Krutzsch, 1962, p. 277, text-fig. 6
Plicatopollis spp. of the *P. plicata* type (Potonie) Krutzsch; Frederiksen and Christopher, 1978, p. 121, pl. 2, figs. 5-8
Plicatopollis plicatus (Potonie) Krutzsch; Nagy, 1969, p. 475, Pl. 53, fig. 24
Plicatopollis plicata (Potonie) Krutzsch; Frederiksen, 1979, p. 141, Pl. 1, figs. 33-37
Plicapollis sp. 1 Choi, 1983, p. 539, Pl. 45, fig. 360

Description: Triporate oblate. Triangular outline with convex sides. Pores circular or lolongate, 2.0 - 2.5μm diameter; atriate (atria 2.5 - 4.0μm deep; 6.2 - 7.3μm wide). Coarse granules in pore region. Small annulus or slight tumescence may be present; with or without a weak labra. Exine thin, 0.5 - 1.0μm thick, psilate to faintly granulate, with strongly triradiate structures on one or both hemispheres. Plicae extend to atria and sometimes to the equator. Wall multilayered, possibly three layers (possibly folds?). Sexine much thicker than nexine.

Dimensions: 25.0 (27.3) 31.2μm diameter (3 specimens)

Remarks: Specimens found in this study show no distinctive thinned spots or "solution fields" adjacent to the endoplicae. Interradial pillows, so distinctive in Krutzsch's diagram (1962, p. 277), appear to be very weak or absent. In one specimen, the plicae appear as rolls of folds towards the polar direction.

Frederiksen and Christopher (1978) comprehensively studied *Plicatopollis* and related *Momipites* groups. They proposed that the *triradiatus* and *triorbicularis* Groups of *Momipites* are morphologically related to each other and to *Plicatopollis*; and that *Plicatopollis* cannot be distinguished consistently from the *triorbicularis* Group of *Momipites.*

Comparison: Similar genera include *Momipites* and *Platycaryapollenites*. Frederiksen and Christopher (1978) emended the original diagnosis, proposing that the main characteristics of *Plicatopollis* are the presence of only thin spots and/or the triradiate structure. *Momipites triorbicularis* and *triradiatus* groups (Nichols, 1973) are included in this genus (Frederiksen, 1979). *Plicatopollis* differs from other similar forms, such as the *microcoryphaeus*-group, in the symmetrical distribution with regard to the equatorial plane of the solution fields (Jansonius and Hills, 1979). *Momipites triradiatus* Nichols resembles *P. plicata* but is much smaller, 19 - 25μm diameter and closer to *Engelhardtia*-type pollen rather than *Plicatopollis* and other plicatoid pollen (Nichols, 1973). Frederiksen and Christopher (1978) considered *Momipites triradiatus* in the realm of *Plicatopollis*, hence, *P. triradiatus* (Nichols 1973) Frederiksen and

Christopher.

Botanical Affinities: Probably juglandaceous affinity, commonly associated with members of Juglandaceae family: *Platycaryapollenites* and *Momipites* (Frederiksen and Christopher, 1978). Frederiksen and Christopher (1978) discuss pollen of the general *Carya-Platycarya* type of morphology, including *Plicatopollis*. Krutzsch (1962) supposed that this form was a late juglandaceous one, a Poltavian element, however, Nichols (1973) suggested that plicatoid pollen does not appear to belong to the Juglandaceae. Otherwise, very little has been written in the palynological literature about the affinities of this fossil genus.

Occurrences: This fossil pollen taxon has been reported from numerous localities in North America (Tschudy, 1973; Frederiksen and Christopher, 1978; Frederiksen, 1979), Canadian Arctic (Choi, 1983) and Europe (Potonie, 1934; Krutzsch, 1962). Several forms also occur in the Miocene (Nagy, 1969) but rarely in Oligocene sediments (Jansonius and Hills, 1976).

***Plicatopollis* sp. A**
Plate 3, figure 16

Momipites triaradiatus Nichols, 1973, p. 108, Pl. 1, figs. 10-15
Plicatopollis triradiata (Nichols) Frederiksen and Christopher, 1978, p. 123
Plicatopollis cretacea Frederiksen and Christopher, 1978, p. 121, Pl. 2, figs. 17-22 [in part]

Description: Triporate, oblate. Rounded triangular outline with convex sides. Pores equatorial to slightly subequatorial, circular or lalongate, 1.56 - 2.34μm diameter. Atria weak, 1.56 - 2.34μm deep, 6.24 - 7.80μm wide. Slight tumescence. Exine two-layered, 1.0μm thick. Sexine slightly thicker than nexine. Wall layers tightly appressed except in pore area. Surface psilate to finely granulate. Endoplicae, 2.0 -

4.0μm thick, slightly curved and irregular; terminate gradually at the atria. Lack of exinal thinnings adjacent to the triradiate structures.

Dimensions: 28.86 (30.42) 30.42μm diameter (3 specimens)

Remarks: This species is morphologically similar to *Plicatopollis triradiata (=Momipites triradiatus)* but is larger by about 5 - 9μm and lack thin spots that Nichols (1973) and Frederiksen and Christopher observed (1978) in their southeastern U.S. material. Frederiksen and Christopher (1978) regarded the *triradiatus* and *triorbicularis* Groups of *Momipites* of Nichols (1973), (in which *P. triradiata* was originally placed in the former group), as morphologically related to each other and to *Plicatopollis* and, therefore, reassigned both groups to the latter genus. If one accepts the redefinition of *Plicatopollis* (i.e. with triradiate structures and thin spots on one or both poles) by Frederiksen and Christopher, then this species falls into the realm of *Plicatopollis*, rather than *Momipites* (i.e. no pseudocolpi, triradiate structures, or thin spots).

Observed specimens are slightly larger than the similar species *P. cretacea* by nearly 2 - 7μm diameter (Frederiksen and Christopher, 1978) and have more convex sides. Similarities include the lack of polar thinnings adjacent to the triradiate structures and the slightly curved endoplicae.

Comparison: The lack of thin spots and distinct triradiate polar thickening in this form, are most characteristic of *Plicatopollis triradiata* (Nichols) Frederiksen and Christopher *(=Momipites triradiatus)*. The triradiate structure of this form appears to be of normal exinal thickness. Another similar form, *Plicatopollis plicata*, has a more irregular triradiate structure. This species looks like *Caryapollenites* in part but the former has a triradiate structure, possibly on both hemispheres. The convexity of the sides and the slightly curved endoplicae of this species differs from the triangular outline and straight-sided endoplicae of *P. cretacea* which it also closely resembles. The absence of thin spots also distinguishes this species from other species of *Plicatopollis* (Frederiksen and Christopher, 1978).

Botanical Affinities: Juglandaceae (Nichols, 1973). Similar triradiate structures are not found among modern species of the Juglandaceae, but the pollen morphology is otherwise similar in all other respects to the *Engelhardtia-Alfaroa* group (Nichols, 1973). Morphologically related to other members of Juglandaceae (*Plicatopollis, Caryapollenites, Platycaryapollenites*) in part or in whole, with structural exinal modification such as thickenings, folds and polar thinnings.

Occurrences: *Plicatopollis triradiatus* is observed in the Late Paleocene of Texas (Nichols, 1973). Frederiksen and Christopher (1978) noted that many uppermost Cretaceous-Lower Eocene assemblages include specimens having triradiate structures, whereas most Middle Eocene-Middle (?) Oligocene assemblages do not.

P. cretacea has not been observed in any Tertiary deposits, and is reported only from Upper Cretaceous (?Campanian-?upper Maastrichtian) from the middle Atlantic States (Sohl and Mello, 1970; Wolfe, 1976; Frederiksen and Christopher, 1978).

Genus *Triatriopollenites* Pflug 1953

type species: *Triatriopollenites rurensis* Pflug and Thomson in Thomson and Pflug 1953

Triatriopollenites subtriangulus (Stanley) Frederiksen 1979
Plate 4, figure 4

Carpinus subtriangula Stanley. 1965, p. 291-292, Pl. 43, figs. 12-16
Triatriopollenites subtriangulus (Stanley) Frederiksen, 1979, p. 151, Pl. 2, figs. 19-21,

(non Pl. 2, fig. 22)

Description: Triporate, oblate. Rounded triangular outline in polar view with strongly convex sides. Pores circular to slightly lolongate, 2.5 - 3.0μm diameter, predominantly equatorial, some slightly subequatorial; tarsus pattern. Atria small, 3.5μm deep, 4.0 - 6.0μm wide, distinct. Exine thin, 0.5 - 1.0μm thick, two-layered, tightly appressed except at the pores. Surface sculpture psilate to faintly granulate. Slight labrum and tumescence may be present. Tendency to fold.

Dimensions: 24.2 (24.2) 28.0μm diameter (9 specimens)

Remarks: The close similarity of this form to species of *Carpinipites* is apparent, however, this species is clearly *Triatriopollenites* by the atriate condition of the pores. Frederiksen (1979) observed atria in the pores in the specimens of Stanley and placed *Carpinus subtriangula* into the realm of the genus *Triatriopollenites* as *T. subtriangulus*. However, Choi (1983) assigned both species of Stanley and Frederiksen to *Triporopollenites mullensis* (Simpson) Rouse and Srivastava. It is apparent that the wall structure and pore pattern are sometimes difficult to ascertain. Many workers recognized these problems when identifying and distinguishing between species of *Triatriopollenites* and *Extratriporopollenites* (Skarby, 1968), and between the form genera *Triatriopollenites, Triporopollenites* and *Carpinipites* (Wingate, 1983). The author also encountered difficulties in differentiating the form genera, *Triatriopollenites, Triporopollenites; Carpinipites, Trivestibulopollenites* and *Myricipites* with certainty (e.g. *Carpinipites* sp. on Pl. 2, fig. 5 that verges into the generic realm of *Triporopollenites*).

Takahashi and Kim (1979) published a new species, *Triatriopollenites subtriangularis* in the same year that Frederiksen (1979) reassigned *Carpinus* *subtriangula* Stanley to the genus *Triatriopollenites*, as *Triatriopollenites subtriangulus*. The form by Takahashi and Kim (1979) morphologically resembles that of Frederiksen (1979) and Stanley (1965). Even though the existing form by Stanley was first considered under a different generic name and based on the morphologically similarity of the two species, by the priority of the earliest publication of the valid species (Art. 11.3 of the Botanical Code), the author rejects *T. subtriangularis* Takahashi and Kim as a *nomen nudum* and places it in the synonomy of *Triatriopollenites subtriangulus* (Stanley) Frederiksen.

Comparison: This species compares to similar species of fossil *Carpinus* (Betulaceae; Stanley, 1965) and fossil *Comptonia* (Myricaceae; Frederiksen, 1979). The former lacks atria and a double-wall structure, and the latter has strongly aspidate pores.

Botanical Affinities: Definite botanicial affinities to *Betula*-type pollen, such as *Comptonia* and *Myrica*, both of Myricaceae (Frederiksen, 1979), *Carpinus* (Stanley, 1965). *Corylus* and *Ostrya*, both of Betulaceae, also appear very similar. This species has been suggested to be closer in resemblance to *Comptonia* than to *Myrica* (Frederiksen, 1979), although Takahashi and Kim (1979) considered their form and other *Triatriopollenites* spp. of Korea to have a botanical affinity to the Myricaceae.

Occurrence: *Triatriopollenites subtriangulus* has been found to occur in the early Tertiary U.S. Midwest (Stanley, 1965; Frederiksen, 1979, 1988) but has not been reported in the southeastern United States (e.g. Frederiksen, 1979).

***Triatriopollenites* sp. A**
Plate 4, figures 1-3

Triatriopollenites triangulus Frederiksen, 1979, p. 151, Pl. 2, figs. 23-26

Description: Triporate, oblate, rarely spheroidal. Rounded triangular to subtriangular outline with strongly convex sides. Tendency to fold along ambs. Pores circular, 1.5 - 2.0μm diameter, equatorial, protruding. Atria small, 1.5 - 2.5μm deep, 3.9 - 4.7μm wide, distinct. Surface psilate to faintly granulate. Slight annuli and tumescence, 1.0 - 1.5μm thick. Exine two-layered, thin, 0.5 - 1.0μm thick.

Dimensions: 21.8 (23.4) 28.0μm diameter (10 specimens)

Remarks: This rare to infrequent species is identified as *Triatriopollenites* sp. based on the presence of small atria. The solution fields are considerably weaker and smaller than *Triatriopollenites subtriangularus*. The author declined to assign this form to *T. triangulus* because observed specimens had strongly convex sides and, therefore, appeared less triangular in outline.

Comparison: This form is closer in most respects to *T. triangulus* but the sides are more convex than those figured in Frederiksen (1979). His specimens have a stronger triangular outline and small solution fields unlike the similar species *T. subtriangularus*, and has a tarsus pore pattern unlike this species.

Triatriopollenites sp. A may be difficult to distinguish from species of *Myricipites*, but the latter has distinct pore thickenings and strongly protruding pores (Wodehouse, 1933; Martin and Rouse, 1966). In her comprehensive study of fossil Myricaceae, Gladkova (1965) studied many triatriate forms and considered them to be *Myrica*-types. The most similar species are *Myrica eocenica* Kulkova, which is larger; *M. paradoxa* Gladkova (= *Triatriopollenites paradoxus* (Gladkova) Frederiksen), which is smaller and has arcoid folds; and *M. diversa* Gladkova, which has a deeper atrium (Frederiksen, 1979). *Triporopollenites bituitus* (Potonie, 1931) Thomson and Pflug and *Carpinipites* species may also resemble this species but it has no tarsus pore pattern or atria.

Botanical Affinities: Probably *Betula*-type pollen. Frederiksen (1979) suggested that *Triatriopollenites triangulus* is of the *Myrica*-type pollen. Frederiksen (1988) transferred fossil form species of *Myrica* and *Comptonia* in the Gulf Coast material to *Triatriopollenites*, contending that fossil pollen grains can not convincingly be assigned to individual modern genera of Myricaceae.

Occurrences: Similar forms reported from southeastern United States, Claibornian Virginia and upper Sabinian (or lower Claibornian) Georgia (Frederiksen, 1979), Gulf Coast (Frederiksen, 1988) and western Siberia (Gladkova, 1965).

Triatriopollenites sp. B

Plate 4, figures 7, 8

Description: Triporate, oblate. Subtriangular to rounded triangular outline; sides convex. Pores equatorial, circular, 1.5 - 2.0μm diameter, slightly protruding. Distinct tumescence present, labrum slight or absent. Atrium small, weak to distinct, 2.0 - 3.0μm deep, 5.5 - 6.0μm wide. Weak polar exinal ring of normal thickness present, 11.7μm diameter. Large areas of thinning around ring. Weakly developed arci (1.5 - 2.5μm thick) extending to atria but not to equator. Exine thin, 0.5 - 1.0μm thick, surface psilate to faintly granulate.

Dimensions: 30.4μm diameter (2 specimens)

Remarks: Only two specimens have been observed in the Fossil Forest Hill samples; neither Choi (1983) nor McIntyre (1991) have reported similar forms. Based on the presence of the atria, the author has assigned this form to *Triatriopollenites*.

Polar thinning and/or exinal rings are typically present in *Triporopollenites*, *Plicatopollis*, *Momipites* and *Caryapollenites*. Therefore, such features are atypical in *Triatriopollenites* and discriminate this species from all other species of

Triatriopollenites. This form also has arci characteristically observed in genera such as *Trivestibulopollenites*, *Paraalnipollenites* and *Alnipollenites*. It is only in *Paraalnipollenites* that arci and a polar exinal ring occur but this genus lacks thinned areas.

Comparison: *Caryapollenites* species commonly display polar thinning and structural modifications. Similarly, *Triporopollenites* species commonly have a exinal ring of normal thickness as seen in this species.

Botanical Affinities: May be related to the juglandaceous family, sharing similar features such as polar thinning, exinal ring; or betulaceous family with arci and a "*betuloid*" form.

***Triatriopollenites* spp. cf. *T. arboratus* Pflug 1953**
Plate 4, figures 9-11

Triatriopollenites arboratus Pflug in Thomson and Pflug, 1953, p. 80, Pl. 7, figs. 144-146
Triatriopollenites giganteus Pflug in Thomson and Pflug, 1953, p. 83, Pl. 8, fig. 181
Triatriopollenites robustus Pflug, 1953, p. 126, Pl. 22, figs. 21-32
Triatriopollenites arboratus Pflug, 1953, Pl. 20, figs. 50-55, Pl. 21, fig. 9
Corylus granilabrata Stanley, 1965, p. 293, Pl. 43, figs. 17-28
Casuarina pulchra Simpson, 1961, p. 433, Pl. 10, figs. 2, 4 and 7
Casuarina verrucosa Simpson, 1961, p. 434, Pl. 10, fig. 6
Triatriopollenites convexus Groot and Groot, 1962, p. 166, Pl. 30, figs. 6-10
Triatriopollenites convexus Groot and Groot, 1962, p. 160, Pl. 30, figs. 6-10
Triatriopollenites arboratus Pflug; Elsik, 1968b, p. 612, Pl. 18, figs. 10-13, Pl. 19, figs. 1-7
Triporopollenites bituitus (Potonie) Elsik, 1968b, p. 610,612; *auct. non.* Pl. 18, fig. 6-8
Triporopollenites bituitus (Potonie) Elsik, 1968b, p. 610, Pl. 17, figs. 9-14, *(non figs. 15,16)*; Pl. 18, figs. 4-5, 9 *(non figs. 1-3, 6-8)*
Triatriopollenites granilabratus (Stanley) Norton and Hall, 1969, p. 40, Pl. 5, fig. 18
Casuarinidites granilabratus (Stanley) Srivastava, 1972b, p. 243, Pl. 9, figs. 1-12; Pl. 10, figs. 1-4.
Casuarinidites pulcher (Simpson) Srivastava, 1972b, p. 244, 246, Pl. 10, figs. 5-8; Pl. 11, figs. 1-6
Triatriopollenites spp. of the *T. arboratus* type Tschudy, 1973, p. 1313, Pl. 2, figs. 7, 8
Casuarinidites convexus (Groot and Groot) Frederiksen and Christopher, 1978, p.

140, Pl. 3, figs. 22-23

Casuarinidites cf. *C. granilabratus* (Stanley) Srivastava; Frederiksen, 1980, p. 40, Pl. 7, figs. 25-27

Casuarinidites convexus (Groot and Groot) Frederiksen and Christopher; Choi, 1983, p. 326, Pl. 44, fig. 341

Description: Triporate, oblate. Subtriangular to subcircular outline in polar view. Sides convex, angulaperturate. Pores small, circular to lolongate, 2.5 - 3.0μm diameter, slightly to strongly thickened around pores. Slightly aspidate in some specimens; weakly developed to distinct labrum. Triatriate but the thinness of the nexine may obscure the atria. Exine 1.0 -1.5μm thick, double-layered, faintly and indistinctly patterned. Sexine thicker than nexine.

Dimensions: 25.7 (31.2) 35.9μm diameter (14 specimens)

Remarks: *Triatriopollenites* spp. cf. *T. arboratus* is a problematic form. In the literature, many workers have identified this form as *Triatriopollenites arboratus* (Pflug in Thomson and Pflug, 1953; Tschudy, 1973) and other *Triatriopollenites* spp. (Pflug, 1953; Groot and Groot, 1962), *Triporopollenites bituitus* (Elsik, 1968b), *Corylus granilabratus* (Stanley, 1965) and *Casuarinidites* spp. (Srivastava, 1972b; Frederiksen and Christopher, 1978; Frederiksen, 1979, 1980; Choi, 1983; Barnett, 1989). It is unlikely this species is a *Casuarina*-type (*Casuarinidites*) based on its southern connection (McIntyre, *pers. comm.*, 1991; Basinger, *pers. comm.*, 1991). *Casuarina*, its modern equivalent, is found only in the southern hemisphere (Willis, 1973; Lewis *et al.*, 1983; Mabberley, 1987). North American occurrences of *Casuarinidites* during the Tertiary have been reported by Barnett (1989), Choi (1983), Frederiksen (1979, 1980), Frederiksen and Christopher (1978) and Srivastava (1972b). This North American form in the Tertiary probably represents a form morphologically similar to *Casuarina* but is likely to be a *Betula*-type form.

Srivastava (1972b) revised the original generic diagnosis of *Casuarinidites* by Cookson and Pike (1954) based on his specimens from the Paleocene of Alabama. He observed definite differences between his North American species and their Australian counterparts, the former differing in having a thicker sexine than nexine, distinctly columellate wall structure and weakly aspidate pores with a triatriate condition. Although *Casuarinidites* does not have an interloculum, both Srivastava (1972b) and Elsik (1968b) observed the tendency of the nexine to pull away from the sexine. The author has not observed this condition. The atrium is often obscured where the nexine and sexine are closely appressed (Srivastava, 1972b), however, Elsik (1968b) considered these forms to be *Triporopollenites mullensis*.

Comparison: *Betulaceoipollenites* is very similar, also with sexine thicker than the nexine but it may be more so than in *Casuarinidites* (Srivastava, 1972b). This species is morphologically similar to many betuloid-type pollen of the families Betulaceae and Myricaceae. Similarities of this species with *Subtriporopollenites anulatus* Pflug and Thomson *emend.* Krutzsch were suggested by Frederiksen and Christopher (1978), particularly where grains were obliquely flattened and the pores appeared subequatorial. Frederiksen and Christopher (1978) attempted to compare their specimens with those of Simpson (1961), however, Simpson's specimens were badly corroded, so that comparisons were difficult.

Botanical Affinities: Affinity is suggested with the Betulaceae or Casuarinaceae (Srivastava, 1972b). Morphologically similar to grains of living species of *Casuarina* (Srivastava, 1972b) but probably belongs to the following families having similar types of "betuloid" form: Betulaceae, Juglandaceae, Loganiaceae and Myricaceae (Erdtman, 1952).

Occurrences: Present in the Paleogene of North America (Groot and Groot, 1962; Stanley, 1965; Elsik, 1968b; Norton and Hall, 1969; Srivastava, 1972b; Frederiksen and Christopher, 1978; Frederiksen, 1979, 1980; Barnett, 1989) and the Canadian Arctic (Choi, 1983).

Genus *Triporopollenites* Pflug and Thomson in Thomson and Pflug 1953

type species: *Triporopollenites coryloides* Pflug in Thomson and Pflug 1953

Triporopollenites mullensis (Simpson) Rouse and Srivastava 1972

Plate 4, figures 12, 16

Corylus mullensis Simpson, 1961, p. 444, Pl. 13, figs. 13-16
Triporopollenites mullensis (Simpson) Rouse and Srivastava, 1972, p. 1179, fig.61
Triporopollenites mullensis (Simpson) Rouse and Srivastava; Srivastava, 1975, p. 144, Pl. 13, figs. 3-10; Pl. 14, figs. 1-6

Description: Triporate, oblate. Convexly triangular in polar view, never circular. Pores circular to lolongate, 2.0 - 2.5μm diameter, equatorial, less often slightly subequatorial. Slight labrum or tumescence (1.0 - 2.0μm thick) usually present. Without a true annulus and never with an atrium or vestibulum. Exine 1.0 - 1.5μm thick, two-layered, layers tightly appressed except in pore region; grains frequently folded. Surface psilate to finely scabrate. Circumpolar ring on one hemisphere may be present.

Dimensions: 22.6 (25.0) 37.3μm diameter (42 specimens)

Remarks: A wide range of morphological variations among the 42 specimens has been observed. Features include: 1) folding, 2) a ring-shaped exinal thickening on one pole, and 3) presence or absence of the labrum. Choi (1983) considers these morphological features to be intraspecific variations.

Comparison: Upon comparison of species of *Triporopollenites* with those of

Triatriopollenites and *Carpinipites*, there are similar superficial features between the genera which leads to difficulties in species identification and differentiation. *Triporopollenites* may or may not have distinct tumescence or annuli (Simpson, 1961; Rouse and Srivastava, 1972; Choi, 1983). As with many *Triporopollenites* grains approaching a *Carpinus*-type form, identification becomes uncertain and dubious, particularly where a double-layered exine is so tightly appressed that the exine appears as a single layer (see Pl. 2, figure 5, *Carpinipites* sp.).

Botanical Affinities: Morphologically similar to *Betula*-type pollen. Some genera of the Betulaceae, e.g. *Corylus* (hazelnut, Simpson, 1961; Rouse and Srivastava, 1972) and *Ostrya* (ironwood, Rouse and Srivastava, 1972) are comparable. Simpson (1961, p. 444) suggested that this fossil form resembles extant *Corylus coluna* Linnaeus in pore character; its distribution extends from Spain to China. A western North American species, *Corylus californica* is also similar (Simpson, 1961). The pollen morphology of *Triporopollenites mullensis* is very similar to that of *Corylus conuta* Marsh (beaked hazelnut), distributed in eastern North America. Others (Stanley, 1965; Takahashi and Kim, 1979) also have suggested species of *Triporopollenites* were botanically related to the Betulaceae. However, Edwards (1981) has demonstrated the difficulty in distinguishing pollen of *Corylus* (Betulaceae) and *Myrica* (Myricaceae) in modern and fossil samples using light microscopy, therefore, comparisons to these modern genera may not be all that certain (Edwards, 1981; Frederiksen, 1988). Although, many workers (Gladkova, 1965; Takahashi and Kim, 1979; Frederiksen, 1979, 1988) consider that species of *Triatriopollenites* have botanical affinities to the Myricaceae.

Occurrence: Examples of this species have been recorded in the Paleogene of North

America (Potonie, 1931; Wodehouse, 1935; Rouse and Srivastava, 1972); the Maastrichtian to Lower Eocene of the Canadian Arctic (Choi, 1983) and the Maastrichtian of Scotland (Simpson, 1961; Srivastava, 1975).

***Triporopollenites* sp. A**
Plate 4, figures 13-15

Triporopollenites sp. 1 Wingate, 1983, p. 117, Pl. 5, fig. 15
Triporopollenites n. sp. A Choi, 1983, p. 322, Pl. 44, fig. 336

Description: Triporate, spheroidal. Rounded triangular to subcircular in polar view. Sides strongly convex. Pores circular, 1.5 - 2.5μm diameter, slightly subequatorial to subequatorial. Slight labrum and tumescence (1.5 - 2.0μm thick) usually present. Without a true annulus, atrium or vestibulum. Exine thin, 1.0μm thick, psilate to faintly sculptured. Arci 0.5 - 1.5μm wide, straight to gently convex, distinct, extend from pore to pore. Arci encircles pore, making pores appear almost annulate.

Dimensions: 22.6 (25.0) 27.3μm diameter (11 specimens)

Remarks: A form rarely observed in the forest succession. A spheroidal specimen (possibly as in nature) and oblately flattened specimens are figured (Pl. 4, figs. 13-15).

Comparison: *Triporopollenites* sp. A has very strong and distinct arci, strongly convex sides and subequatorial pores unlike *Triporopollenites mullensis*. This species is unlike any form reported by McIntyre (1991). A similar form is illustrated and described by Choi (1983) as *Triporopollenites* n. sp. A.

Triporopollenites sp. A closely resembles *Triporopollenites* sp. 1 of Wingate's (1983) study of Eocene sediments of Nevada, U.S.A. These two forms are probably of betulaceous affinity, especially *Corylus*-type and *Carpinus*-type forms. The absence of atria precludes assignment to *Triatriopollenites* Pflug; similarly, the lack of vestibula precludes assignment to *Trivestibulopollenites* Pflug. No description was given by Wingate (1983), however, his species displays distinct arci (not folds). He also diagnosed a second species of *Triporopollenites* (*T.* sp. 2), which he has proposed as a possible transitional form. The author does not agree that the distinctiveness of the arci should define or speciate two similar forms and concludes that they are the same form. Forms illustrated by Wingate (1983) appear similar.

Botanical Affinities: Possibly Betulaceae or Myricaceae.

Occurrences: This form has been observed in the Eocene of Nevada (Wingate, 1983) and in Late Cretaceous to Paleocene of Arctic Canada (Choi, 1983).

Genus *Subtriporopollenites* Pflug and Thomson 1953

type species: *Subtriporopollenites anulatus* Pflug and Thomson in Thomson and Pflug 1953

Subtriporopollenites anulatus Pflug and Thomson 1953

Plate 4, figure 17, 18

Subtriporopollenites anulatus ssp. *anulatus* Pflug and Thomson in Thomson and Pflug, 1953, p. 85, Pl. 9, figs. 42-46, 48-49 only
Subtriporopollenites anulatus ssp. *notus* Pflug and Thomson in Thomson and Pflug, 1953, p. 122, Pl. 24, fig. 52-54, figs. 56-59
Subtriporopollenites anulatus Pflug and Thomson *emend.* Krutzsch, 1961, p. 310
Carya anulatus (Pflug and Thomson) Elsik, 1968b, p. 604, Pl. 19, figs. 8-10, Pl. 20, figs. 1-2
Subtriporopollenites anulatus Pflug and Thomson; Frederiksen and Christopher, 1978, p. 139, Pl. 3, fig. 11

Description: Triporate, oblate. Circular to subcircular in polar view. Pores circular to lolongate, 1.0 - 1.5μm diameter, predominantly subequatorial. Exine 1.5 - 2.0μm thick, psilate to faintly granulate, multi-layered wall distinctly delineated. Slight exinal thickening at the pore region.

Dimensions: 28.9 (32.0) 33.4μm diameter (6 specimens)

Remarks: This species is rare throughout the fossil leaf layer section.

Krutzsch (1961) restricted *Subtriporopollenites anulatus* to include triporate pollen having subequatorial pores, a thick exine, distinct columellae and surface ornamentation but lacking polar areas of thinned exine. Polar thinned areas are typical of *Caryapollenites* species. Pollen taxa closely resembling modern *Carya* , including *Caryapollenites simplex*, were excluded from *Subtriporopollenites* (Krutzsch, 1961). An important distinguishing feature, the very thick multi-layered exine is emphasized by Thomson and Pflug (1953) and Krutzsch (1961). Other features that separate species of *Subtriporopollenites* and *Caryapollenites* (Nichols, 1973) include: 1) subequatorial pores, 2) the lack of juglandaceous atrium sculpture, and 3) polar thinning. Frederiksen and Christopher (1978) rejected Krutzsch's emendation because they preferred assigning fossil *Carya*-type genera that do not differ significantly from modern *Carya* into *Caryapollenites*.

According to Thomson and Pflug (1953), *Subtriporopollenites* is a senior synonym of *Caryapollenites* and is therefore invalid. However, Potonie (1960) recognized the junior status of *Caryapollenites*, because of the close resemblance of *C. simplex* to the type species of *Subtriporopollenites, S. anulatus.*

Comparison: Morphology similar more or less to *Caryapollenites* pollen (Krutzsch, 1961; Nagy, 1969; Nichols, 1973; Nichols and Ott, 1978; Frederiksen and Christopher, 1978; Frederiksen, 1979), but *Subtriporopollenites* species differ in having a multi-layered exine, exclusively subequatorial apertures and in lacking of polar thinned areas, all of which Nagy (1969) terms as "caryoid" elements of the family Juglandaceae.

Botanical Affinities: Morphology is more or less similar to *Carya* (Krutzsch, 1961;

Nichols, 1973, etc.). Probably belong to *Carya*-type pollen (Nagy, 1969; Takahashi and Kim, 1979).

Occurrence: This species is observed mainly in early Tertiary deposits of southern United States (Texas, Elsik, 1968b; South Carolina, Frederiksen and Christopher, 1978; Virginia, Frederiksen, 1979), Canadian Arctic (Choi, 1983), central Europe (Thomson and Pflug, 1953) and late Tertiary of Korea (Takahashi and Kim, 1979).

Subtriporopollenites nanus **(Pflug and Thomson) Frederiksen 1980**
Plate 4, figures 19, 20

Subtriporopollenites anulatus ssp. *nanus* Pflug and Thomson in Thomson and Pflug, 1953, p. 86, Pl. 9, figs. 54-55
Subtriporopollenites anulatus ssp. *nanus* Pflug, 1953, p. 163, Pl. 24, fig. 51
Subtriporopollenites anulatus ssp. *nanus* Pflug and Thomson; Gruas-Cavagnetto, 1968, Pl. 5, figs. 2-4
Carya? spp. Frederiksen and Christopher, 1978, p. 137, 1978, Pl. 3, figs. 16, 17 only, *non figs. 19-21*
Subtriporopollenites nanus (Pflug and Thomson) Frederiksen, 1980, p. 149, Pl. 1, figs. 18-20
Subtriporopollenites nanus (Pflug and Thomson) Frederiksen; Frederiksen, 1988, p. 51, Pl. 3, figs. 5, 6

Description: Triporate. Circular in polar view. Pores small subequatorial, 0.5 - 1.0μm diameter. Annuli, atria, and vestibula are lacking. Exine psilate to weakly granulate. Exine 1.5 - 2.0μm thick, multi-layered (three layers) wall distinctly delineated. Sexine usually twice as thick as nexine.

Dimensions: 25.0 (29.6) 35.1μm diameter (17 specimens)

Remarks: This species occurs infrequently at the top of the leaf layer section (A horizon). Specimens attributed to this species are morphologically similar to *S. anulatus* ssp. *nanus* Pflug and Thomson (17 - 25μm diameter) but are generally larger by 1 to 10μm.

Frederiksen (1980) raised *S. anulatus* ssp. *nanus* to species level, *S. nanus*. He regarded differences in size and the exine structure of the *S. anulatus* ssp. *nanus* to be significant in differentiating it from *S. anulatus* ssp. *nanus* Pflug and Thomson. *S. anulatus* ssp. *notus* is regarded as synonomous with *S. anulatus* ssp. *anulatus* Pflug and Thomson (Frederiksen, 1980).

Comparison: Unlike *Subtriporopollenites anulatus*, this species has a circular outline and subequatorial pores. *S. anulatus* appears to be morphologically more similar and closer to the *Carya sensu stricto* while *S. nanus* is smaller and has a much less structured exine than *S. anulatus* ssp. *notus* (Thomson and Pflug, 1953).

Botanical Affinities: Probable affinity to *Carya*-type pollen. Morphology similar more or less to *Caryapollenites* pollen (Krutzsch, 1961; Nichols, 1973; Nichols and Ott, 1978; Frederiksen and Christopher, 1978; Frederiksen, 1979, 1988).

Occurrence: This species occurs in Tertiary sediments from southeastern North America (Carolina, Frederiksen and Christopher, 1978; Frederiksen, 1980, 1988) and central Europe (France, Gruas-Cavagnetto, 1968).

Genus *Annutriporites* Gonzalez Guzman 1967

type species: *Annutriporites iversenii* (van der Hammen) ex. Gonzalez Guzman 1967

Annutriporites sp.

Plate 4, figure 5, 6

Description: Triporate, oblate. Rounded triangular outline. Sides convex. Pores circular, 2.5 - 3.0μm diameter, equatorial, slightly protruding. Slight to distinct tumescence present, labrum slight or absent. Atrium small, distinct, basal margins uneven and irregular, appears as ektexinal thickenings like a dark ring. Surface psilate to faintly granulate. Exine approx. 0.5 - 1.0μm thick. Wall two-layered.

Dimensions: 25.7 (28.2) 29.6μm diameter (8 specimens)

Remarks: *Annutriporites* sp. has an unique ektexinous thickening outlining the irregular and uneven margin of what is possibly the atrium, appearing as a dark ring. The atrium is small but distinct. The pores are protruding somewhat (i.e. aspidate), and the dark ring may correspond to an annulus, hence, these forms may be a species of *Annutriporites*.

Comparison: This species appears morphologically similar to *Annutriporites* but it has a larger size range and atriate pores. The ektexinal thickenings (possibly annuli) appear like those of *Annutriporites*.

Botanical Affinities: Probable affinity to *Betula*-type pollen.

Occurrences: The genus has been reported from the high Arctic (Ricketts and McIntyre, 1986; Norris, 1986), and western Canada (Martin and Rouse, 1966) in the early Tertiary.

Genus *Thomsonipollis* Krutzsch 1960

type species: *Thomsonipollis magnificus* (Thomson and Pflug 1953) Krutzsch 1960

Thomsonipollis sp.

Plate 5, figures 1, 2

Description: Tetraporate, oblate. Subcircular outline. Pores 4.0 - 5.5μm diameter, subcircular, equatorial. Slight pore (nexinous) thickenings. Exine 0.5 - 1.0μm thick, psilate to faintly sculptured. Exine stratification obscure.

Dimensions: 32.0 - 32.8μm diameter (2 specimens)

Remarks: This species has been observed only in sample A4. Though species of *Thomsonipollis* have been known to occur as diporates, triporates and tetraporates, the author has observed only tetraporates for this species. The large pores and slight pore thickenings are characteristic of *Thomsonipollis*. The slight pore thickenings have been referred to as endannuli by Frederiksen (1979), a nexinous ring by Jansonius and Hills (1976) and Elsik (1968b, 1974), or nexinous invaginations by Krutzsch (1960).

Comparison: *Thomsonipollis* sp. appears similar to specimens illustrated by Frederiksen (1979; Pl. 2, figs. 36-39) as *Thomsonipollis* cf. *T. expolitas*. However, his specimens are smaller (18 - 19μm diameter), and have a punctate sculpture. The author observed only poorly developed nexinous invaginations in this species; such invaginations are characteristic of the genus. The lack of surface ornamentation and very thick nexinous ring and wall structure, differentiates the type species *Thomsonipollis magnificus* Thomson and Pflug) Krutzsch from this species. Maastrichtian *Complexipollis* has been found with a similar invagination in the pore region (Jansonius and Hills, 1976). There are nexine invaginations around apertures in *Proteacidites* Cookson ex. Couper and *Triorites* Erdtman ex. Cookson, both Southern Hemisphere forms, but *Thomsonipollis* never has the triangular concave invaginations as in these *Normapolles* genera (Tschudy, 1975; Jansonius and Hills, 1976).

Botanical Affinities: Elsik (1968b) suggested that *Thomsonipollis* evolved from a proteaceous-type grain. Contemporary forms with similar invaginate pores include: *Duroia*, *Randia malabarica* and *Gnettardia speciosa* (the latter two of the Rubiaceae; Elsik, 1968b; Srivastava, 1972b). All have different surface sculptures.

Occurrences: The genus is known only from the Lower Eocene from eastern to mid-Europe and North America, not in east Europe or Asia (Elsik, 1968b, 1974;

Srivastava, 1972a; Jansonius and Hills, 1976; Frederiksen, 1988).

Genus *Santalacites* Stelmak 1960

type species: *Santalacites santaloides* Stelmak 1960

Santalacites sp. cf. *S. santaloides* Stelmak 1960

Plate 5, figures 3, 4

Santalacites santaloides Stelmak in Pokrovskaya and Stelmak, 1960, p. 226, Pl. 10, fig. 16

Gothanipollis santaloides (Stelmak) Zaklinskaya, 1963, p. 152, Pl. 1, figs. 10-12

Santalacites sp. cf. *S. santaloides* Stelmak; Choi, 1983, p. 340, Pl. 45, fig. 361

Description: Triporate. Triangular with straight, slightly convex or slightly concave sides in polar view. Pores equatorial, isopolar, meridionally elongate, indistinct, 1.5 - 2.0μm diameter Lack of annuli, tumescence, or labra. Exine thin, 0.5μm thick, single layer. Sculpture psilate to scabrate. Pores interconnected by arcuate folds, about 2 - 3μm wide.

Dimensions: 14.0 (20.3) 28.0μm diameter (52 specimens)

Remarks: The specimens observed by Stelmak (in Pokrovskaya and Stelmak, 1960) displayed a wider size range, 18 - 27μm diameter, than those of Choi (1983), 26 (29.0) 31μm diameter. The author found specimens well within both their size ranges, but generally in the middle range of that of Stelmak (1960).

The relatively simple pore structure and the characteristic folding of the exine along the sides of the grain are the distinguishing features of this species. There have been many terms to describe the exinal folds: ridge-like foldings (Choi, 1983); arcuate exinal folds (Christopher, 1979); ridge-like dilatations (Stelmak, 1960) and endoplicae of exine connecting pores (Jansonius and Hills, 1976). Species of *Santalacites* may also have arci which are commonly observed.

Comparison: *Santalacites minor* Christopher is similar but differs in having a thin, microgranulate exine and a smaller size than *S. santaloides* (Christopher, 1979). Another similar form *Complexiopollis* sp. V has no distinct ridge-like thickenings but folds along the sides may resemble arci (Christopher, 1979).

Botanical Affinities: Probably Santalaceae. Certain species of *Thesium*-type pollen have very similar pores (Jansonius and Hills, 1976). The nearest modern comparison is *Thesium* with a tricolpate condition. However, *Thesites* Agranovskaya is the fossil pollen taxon that accomodates forms referable to *Thesium*. *Santalacites* also resembles contemporary *Fusanus* (or *Eucarya* of the family Santalaceae; Jansonius and Hills, 1976). Members of the family Rhamnaceae (buckthorn) are comparable but *Santalacites* do not have colpi or a tricolporate condition which is characteristic of grains in this family (Jansonius and Hills, 1976).

Occurrence: This species is not well represented in early Tertiary sediments, reported only in the Northern Hemisphere, Ellesmere Island (Choi, 1983); Siberia (Stelmak, 1960) and U.S.S.R (Zaklinskaya, 1963), and an upper Cretaceous occurrence in New Jersey, United States (Christopher, 1979).

Genus *Myricipites* Wodehouse 1933

type species: *Myricipites dubius* Wodehouse 1933

Myricipites annulites (Martin and Rouse) Norris 1986

Plate 5, figures 5, 6

Myricipites dubius Wodehouse, 1933, p. 504, fig. 31
Myrica annulites Martin and Rouse, 1966, p. 195, Pl. 9, figs. 91, 92
Myricipites dubius Wodehouse; Srivastava, 1966, p. 528, Pl. 7, figs. 4-6
Myrica annulites Martin and Rouse; Hopkins, 1969, p. 1124, Pl. 10, figs 153, 154
Myricipites annulites (Martin and Rouse) Norris, 1986, p. 39, Pl. 10, figs. 30, 34

Description: Triporate, spheroidal. Rounded triangular grain with slightly protruding pores. Pores 1.5 - 3.0μm diameter, circular to slightly lolongate, equatorial, atriate (tarsus pattern; Wodehouse, 1933). Atria small, 2.5 - 4.0μm deep, 5.5 - 6.0μm wide. Slight to strong tumescence, ave. 1.5μm thick at pores, and slight labra may be present. Sculpturing finely scabrate. Exine thin, 0.5 -1.0μm thick, tectate,

Dimensions: 22.6 (25.0) 28.0μm diameter (6 specimens)

Remarks: The Fossil Forest Hill specimens of this species are rare and of good to very good condition, unlike the "*shrunken*" or folded appearance of the single specimen of *Myricipites dubius* described by Wodehouse (1933) in the Green River shales. Both the generic diagnosis and the type species description by Wodehouse (1933) are simple and vague. Although the diagram of *M. dubius* by Wodehouse (1933) clearly illustrates the atriate condition of the pores, he did not elaborate on the tarsus pore pattern or the nature of the atria. Srivastava (1966) redescribed the type species but suggested that the pores were vestibulate. Specimens observed in this study have atriate pores and a tarsus pore pattern.

The apparent similarity of this species to *Myricipites annulites* is evident but Martin and Rouse (1966) declined to equate them and considered their new species as justified based on the scabrate surface texture and the weakly aspidate pores. The author suspects, as Martin and Rouse (1966) mentioned, that there is a close resemblance between the two species. The character of the pores and pore thickenings are displayed in both species and were the primary reasons Wodehouse (1933) originally assigned his form to *Myrica*. The author has not seen the specimen of Wodehouse, but based upon the figured specimens of Martin and Rouse (1966) and both specific descriptions, Fossil Forest Hill forms are most similar to *Myricipites* *annulites* (Martin and Rouse) Norris.

Comparison: According to the specific description, *Myricipites dubius* has greatly protruding pores and a smooth texture unlike *M. annulites*. The observed finely sculptured grains with slightly protruding pores are more like those of *M. annulites*. It may be that the optics in 1933 were not able to resolve a finely sculptured ektexine, and if *M. dubius* has a sculptured surface it would suggest that the two species are one and the same. Martin and Rouse (1966) did not examine *M. dubius*, and therefore, could not compare the two species.

The characters of this grain also fit closely with those of *Triatriopollenites triangulus* Frederiksen and *T. subtriangulus* Frederiksen, but both these species are characterized by medium size, shallow atrium and only slightly developed labrum and slight tumescence and annulus, or the latter may be lacking (Frederiksen, 1979). In practice, these criteria are not reliable (i.e. the weak development of the labrum, annulus and tumescence in these two species of *Triatriopollenites*, in comparison to the strong development of these same features in *Myricipites*) and can not guarantee accurate species identification. Frederiksen (1979) suggested that *T. triangulus* is of the *Myrica*-type form and *T. subtriangulus* of the *Comptonia*-type; whether his intentions meant botanical affinities or simply morphologic similarity is not entirely certain. Frederiksen (1979, 1988) may have intended these form species to accommodate fossil form species of *Myrica* and *Comptonia* because fossil pollen grains could not be assigned to individual modern genera of Myricaceae.

It is difficult to distinguish pollen of *Myricipites* from those of probable betulaceous affinity, especially *Trivestibulopollenites claripites* (Wodehouse, 1933) and *Carpinipites ancipites* (Srivastava, 1966). Distinct atria and tarsus pore pattern of

Myricipites differ from different pore patterns and the absence of atria of *Trivestibulopollenites* and of *Carpinipites*.

Botanical Affinities: Possible affinity to Myricaceae or Betulaceae. Very similar to *Myrica gale* (sweet gale) except for size (Martin and Rouse, 1966; Wodehouse, 1933). Previous SEM analyses show that grains of *M. gale* are similar to those of *Betula papyrifera* (white birch or paper birch; Bassett *et al.*, 1978). *Myrica pennsylvanica* differs from this species by its smaller size and extremely aspidate pores. Pollen of *Ostrya virginiana* also agree very closely with *Myricipites annulites* but may lack the strong tumescence of the latter genus. Contemporary pollen also very similar to those of *Betula*-type forms include *Comptonia, Myrica, Betula,* (e.g. *B. papyrifera*) and *Carpinus* (Frederiksen, 1979).

Occurrences: *Myricipites* is one of the most abundant and widely distributed genera of the Tertiary and is also present in the Upper Cretaceous but in greatly reduced numbers (Wodehouse, 1933; Hopkins, 1969). The known North American range of *Myricipites annulites* is possibly Eocene to Oligocene (Martin and Rouse, 1966; Hopkins, 1969; Rouse and Srivastava, 1972; Norris, 1986). Srivastava (1966) reported a Maastrichtian age for *M. dubius*.

Genus *Diervillapollenites* Nagy and Rakosi 1964

type species: *Diervillapollenites hungaricus* Nagy and Rakosi 1964

***Diervillapollenites* sp.**
Plate 5, figure 7

Diervilla sp. McIntyre, 1991, p. 19, Pl. 4, figs. 1,2

Description: Large, triporate, oblate. Subtriangular with strongly convex sides. Large prominent pores, 5.5μm diameter, equatorial, circular, strongly annulate. Atria distinct (9.4μm deep, 15.6μm wide) and strong labra. Exine 1.0μm thick, multi-layered, tegillate; ornamented with spines (approximately 1.5 - 2.5μm long, 1.0μm thick, 5 - 8μm apart). Sexine about as thick as nexine.

Dimensions: 46.8μm diameter (1 specimen)

Remarks: The single specimen found in **Nb** horizon is covered with many long and slightly tapering processes. Abundant reduced spinules in the pore region obscure the intrabaculate structure.

Comparison: Jansonius and Hills (1976, 1983) remarked on its similarity to *Lonicerapollenites* (Krutzsch) Nagy. The main differences are the size of the spines and the presence of the colpi. *Diervillapollenites* has larger and thinner spines, more prominent pores, and lacks plicae (Krutzsch, 1962). *Weigelapollis* Takashashi is similar but differs in being a smaller grain (32 - 36μm diameter) with larger annulate pores, variable ornamentation (verrucae, baculae and echinae) and the lack of atria (Takashashi and Kim, 1979; Jansonius and Hills, 1982).

Botanical Affinities: Probably belonging to the family Caprifoliaceae. The closest modern comparison is *Diervilla* Linnaeus (McIntyre, 1991), or the Asian counterpart *Weigela*. *Diervilla* is well-represented in eastern North America, but is apparently absent only in the extreme southwest (Grimm, 1957; Mabberley, 1987). The introduction of many modern forms of eastern North America derive from Eurasia or Asia, (China and Japan; Lewis *et al.,* 1983). Other similar pollen are *Lonicera* Linnaeus and *Linnaea*, also of the Caprifoliaceae.

Occurrence: Fossil *Diervilla* has an eastern Europe occurrence from Oligocene to Miocene (Pokrovskaya, 1956; Nagy and Rakosi, 1964), except for the recent discovery of this fossil genus in the Middle Eocene of Arctic Canada (McIntyre, 1991; this study).

Genus *Pistillipollenites* Rouse 1962

type species: *Pistillipollenites macgregorii* Rouse 1962

Pistillipollenites macgregorii Rouse 1962

Plate 5, figures 9-12

P. mcgregorii Rouse, 1962, p. 206, Pl. 1, figs. 8-12
P. mcgregorii Rouse; Hedlund, 1966, p. 31, Pl. 9, fig. 6
P. macgregorii Rouse *emend.* Elsik, 1968b, p. 638, Pl. 34, fig. 9; Pl. 35, figs. 1-3
P. Mcgregorii Rouse; Kulkova, 1968, p. 1411, Pl. 1, figs. 1-3, Pl. 2, figs. 1-3
P. mcgregorii Rouse; Hopkins, 1969, p. 1123, Pl. 10, figs. 139-142
P. macgregorii Rouse; Rouse and Srivastava, 1970, p. 88, Pl. 10, figs. 1-25
P. mcgregorii Rouse; Wilson, 1978, p. 145, Pl. 10, figs. 6-7
P. macgregorii Rouse; Frederiksen, 1980, p. 145, Pl. 3, fig. 5
P. mcgregorii Rouse; Choi, 1983, Pl. 45, fig. 357-359
P. mcgregorii Rouse; Wingate, 1983, p. 121, Pl. 6, figs. 1-3, *non fig. 4*
P. sp. Wingate, 1983, p. 121, Pl. 6, fig. 5, *non fig. 6*
P. mcgregorii Rouse; McIntyre, 1991, p. 21, Pl. 3, figs. 28-31

Description: Triporate. Circular to broadly subtriangular, triatriate or triaperturate pollen grain. Pores equatorial, meridionally elongate, usually bordered by two gemmae, 2 -4μm diameter. Gemmate exinal protrusions may obscure details of the aperture. Slight tumescence and annuli may be present. Exine dense (1.0 - 2.5μm diameter), distinctly stratified. Surface sculpture psilate to faintly sculptured. Sparse to dense ornamentation, 1 - 2μm diameter, 1 - 3μm long, arranged in a random orientation. Reduced gemmae (less than 1μm diameter) present at germinals. Gemmae shape variable, baculate, clavate to gemmate.

Dimensions: 15.7 (25.0) 31.0μm diameter (117 specimens)

Remarks: Fossil Forest Hill specimens commonly displayed baculate pistil ornaments, rarely gemmate ones. Few grains were observed to have reduced ornamentation or none at all. The size range is also different, with a slightly wider size range than that of Rouse (1962), 20 - 30μm diameter. The pollen grains often tend to clump 20 - 30 specimens together.

Kulkova (1968) observed a finely punctate-reticulate surface at x 1000 magnification. Rouse and Srivastava (1970) determined, on the basis of SEM studies, that *P. macgregorii* is distinctly stratified into three layers and as a result of this differentiated wall complex, the resultant surface pattern is variable: gemmate to nannoverrucate and may also appear negative reticulate. The surface sculpture of Fossil Forest Hill specimens appears psilate to faintly sculptured under light microscopy.

There has been some speculation as to the triporate condition of the fossil genus. Elsik (1968b) emended the original diagnosis by Rouse (1962) so as to also include "tricolpoidorate" and "tricolpoidate" grains but these conditions have never been demonstrated by him or others. Crepet and Daghlian (1981) resurrected this theory, that perhaps the mid-Cretaceous forms were possibly tricolpate, but they did not equate these older forms with those of the Late Cretaceous to Early Tertiary with a triporate condition. Rouse and Srivastava (1970) rejected the emendation proposed by Elsik (1968b). Their detailed SEM studies of the species reveal that they have a triporate condition not tricolpoidorate or tricolpoidate condition.

The spelling of this species has been curiously inconsistent since its introduction by the original author (Rouse, 1962). Note the variation in spelling of the species in the synonomy, even by Rouse. *P. macgregorii* with an "a" is acceptable (Frederiksen, 1979; Jansonius and Hills, 1976; Rouse and Srivastava, 1970; Elsik, 1968b), according to Recommendation 73C, 4a) of the International Code of Botanical Nomenclature (1988). Its intention was to standardize the formal naming of taxa, particularly on a generic and specific level. Complying with the recommendation, the author has followed Jansonius and Hills (1976) and others in the spelling of the species with an "a".

Comparison: No comparable fossil pollen taxa.

Botanical Affinities: *P. macgregorii* is definitely an angiosperm pollen but its botanical affinity remains uncertain. Its exact generic and familial affinities are unknown (Rouse and Srivastava, 1970). Some workers suggest Gentianaceae affinities (Rouse, 1962; Crepet and Daghlian, 1981; Daghlian and Crepet, 1986; Wing and Daghlian, 1989) or Euphorbiaceae (spurge family, Wing and Daghlian, 1989) or Caesalpiniaceae (senna family, Fasbender, 1959; Elsik, 1968b). It has been suggested that Paleogene *Pistillipollenites* pollen was probably produced by early successional rosids (i.e. Order Rosales) of uncertain familial affinity (Wing and Daghlian, 1989). Rouse (1962) suggested that this genus is similar to the description of an extant Bolivian genus *Rusbyanthus* Gilg (Gentianaceae) and included the species description of *Rusbyanthus cinchonifolius* originally given by Erdtman (1952). In his study of modern species of *Macrocarpaea* (Gentianaceae), Nilsson (1968) suggested a possible relationship between *Rusbyanthus* and *Rusbyanthus cinchonifolius* of the *Macrocarpaea corymbosa*-type and a possible affinity to *Lisianthus*. He proposed that *Rusbyanthus cinchonifolius* and *Macrocarpaea pachystyla* are of the *Macrocarpaea corymbosa*-type. *Rusbyanthus* and *Macrocarpaea* has since been synonymized, the latter is the senior synonym (Crepet and Daghlian, 1981).

Previously, this species had not been assigned to an extant family due to the lack of an exact modern analogue. It wasn't until recently that Crepet and Daghlian (1981) noted that a few species of four extant families have similar gemmate ornamentation for comparison: 1) *Tournefortia* spp., Boraginaceae (borage family), but they are associated with large gemmae, the large processes supported by raised platforms of exine and pores covered by ornamented ektexine layers and no columellae; 2) *Zimmermannia* spp., Euphorbiaceae, but they have a tricolpate condition; 3) *Herpyza*, Papilionoideae, but they have apertures that are independent of the gemmae, and 4) *Macrocarpaea* spp., Gentianaceae, but they are densely ornamented. Four gentian species of extant South American *Macrocarpaea* have more gemmae but the apertures are similar to those of the fossil *Pistillipollenites*, either surrounded by separate gemmate processes as in *Macrocarpaea pachystyla* or flanked by elongate processes as in *M. corymbosa* (Crepet and Daghlian, 1981). Variation in ornament morphology was first observed and studied by Rouse and Srivastava (1970) in their exhaustive SEM study of this fossil genus and species.

Flowers shown to have *in situ* pollen of *Pistillipollenites macgregorii* have been demonstrated by Stockey and Manchester (1988) and Crepet and Daghlian (1981) from British Columbia and of Texas respectively. The flowers are believed to have affinities to the Gentianaceae and have an Eocene age (Crepet and Daghlian, 1981; Stockey and Manchester, 1988).

Occurrence: *Pistillipollenites macgregorii* was widely distributed in the Paleogene of the Northern Hemisphere (e.g. Daghlian and Crepet, 1986; Wing and Daghlian, 1989, etc.). It has been reported from rocks as old as Cenomanian, Oklahoma, U.S.A. (Hedlund, 1966) and as young as Eocene, Vancouver, B.C., Canada (Rouse, 1962; Martin and Rouse, 1966; Hopkins, 1969) but it is almost exclusively a Paleogene form; the acme of these grains was during the Eocene (Kedves, 1988). Kedves (1988) systematically mapped out the paleophytogeography of *Pistillipollenites* pollen during the Upper Cretaceous and the Tertiary, and also reported Oligocene occurrences from the Far East of Asia and from the *Aquilapollenites* province. An Eocene age has been supported by radiometric dating of fossil mammal bones reported by Rouse and Mathews (1961) and Hills (1965).

***Pistillipollenites* sp. A**
Plate 5, figures 13-16

Pistillipollenites sp. Wingate, 1983, p. 121, Pl. 6, fig. 6 only (*non fig. 5*)
Pistillipollenites macgregorii Wingate, 1983, p. 121, Pl. 6, fig. 4 only (*non figs. 1-3*)

Description: Triporate, oblate. Subcircular to broadly subtriangular triatriate or triaperturate pollen grain. Sides strongly convex. Pores equatorial, circular to lolongate, 2.5 - 5.0µm diameter. Pores usually bordered by two or more large baculate (or rarely gemmate) pistils. Slight to moderate tumescence and slight annuli may be present. Reduced gemmate exinal protrusions may obscure details of the aperture. Exine thin, 1µm thick, appears single-layered, smooth to faintly sculptured. Weak to strong endoexinal triradiate scar present. Sparse to dense ornamentation, confined to ektexine directly above triradiate structure. Reduced ornaments present or absent along margin of triradiate structure, interapertural areas and pore openings.

Dimension: 16.3 (24.2) 29.6µm diameter (61 specimens)

Remarks: *Pistillipollenites* sp. A has been observed only in basal Nb layer where *P. macgregorii* is very abundant.

This species is very distinctive but may represent an intermediate form with an unique structural modification, between a psilate and a highly ornamented form of *Pistillipollenites macgregorii*. Wingate (1983), however, did not differentiate this unique form (he did not even mention it), but divided his species of *Pistillipollenites* on the basis of size rather than this triradiate feature. This triradiate structure is too even and regular in about five dozen specimens to [illegible] fact. Perhaps, this structure is representative of the pollen described by Elsik (1968b) having a "tricolpoidorate" or "tricolpoidate" condition, however, he did not illustrate these conditions.

Future TEM and SEM work may confirm if this structure is indeed real and if this form is a new species of *Pistillipollenites.*

Comparison: This species is considered different from *P. macgregorii* based upon the presence of the triradiate structure. The ornamentation is typically confined to the triradiate region and it appears that the nexine has pulled away from the sexine along the ambs of the grains. The interapertural regions are generally devoid of ornamentation or finely ornamented with reduced gemmae/baculae. A similar form is figured in Rouse and Mathews (1988) as *Pistillipollenites* n. sp. (Pl. 2, fig. 7), however, the lack of a description/diagnosis prevents any adequate comparison.

Certain palm species (Jarzen, *pers. comm.*, 1991) and *Ilexpollenites* species in polar view may appear similar but the presence of the colpi differentiate these species from *Pistillipollenites* sp. A.

Botanical Affinities: Definitely angiospermous dicotyledon; probably Gentianaceae like *Pistillipollenites macgregorii.*

Occurrence: The author believes this form may be associated with *Pistillipollenites macgregorii* and therefore may also be an exclusively early Tertiary occurrence in the fossil forest layers.

Subturma Polyporines Naumova *emend.* Potonie 1960

Infraturma Stephonoporiti van der Hammen

Genus *Alnipollenites* Potonie 1931

type species: *Alnipollenites verus* (Potonie) ex. Potonie 1931

Alnipollenites verus (Potonie) ex. Potonie 1931

Plate 1, figures 1-3, 5-10

Pollenites verus Potonie, *non 1931a*, p. 332, Pl. 2, fig. 40 *(nomen nudum)*
Alni-pollenites verus Potonie, 1931b, p. 4, Pl. 14, figs. 12, 16
Alnus speciipites Wodehouse, 1933, p. 508, fig. 40
Alni-pollenites verus Potonie, holotype, 1934, p. 58, Pl. 2
Polyvestibulopollenites verus (Potonie) Thomson and Pflug, 1953, p. 90
Alnus pre-cordata Simpson, 1961, p. 442, Pl. 13, figs. 1, 2, 6
Alnus pre-japonica Simpson, 1961, p. 442, Pl. 13, figs. 3, 4
Alnus rubriformis Simpson, 1961, p. 442, Pl. 13, figs. 7, 8
Alnus quadrapollenites Rouse, 1962, p. 202, Pl. 2, figs. 9, 36
Alnus quinquepollenites Rouse, 1962, p. 202, Pl. 2, figs. 7, 8
Alnus verus (Potonie) Martin and Rouse, 1966, p. 196, figs. 69-71
Anipollenites quadrapollenites (Rouse) Srivastava, 1966, p. 530, Pl. 7, fig. 3
Alnus vera (Potonie) Martin and Rouse; Frederiksen, 1980, p. 154

Description: Stephanoporate oblate. Subtriangular to polygonal outline in polar view, depending on the number of pores. Angular to subangular. Pores three to seven, typically 4 or 5-pored, less commonly 3 or 6. Pores equatorially situated, circular to elliptical, 1 - 2μm diameter. Thickened annuli, distinct vestibula. Weakly to strongly developed arcs, 2μm thick, extending between pores, one set on each hemisphere. Exine psilate to very faintly granulate, 1μm thick. Sexine thicker than nexine.

Dimensions: 18.7 (24.2) 28.0μm diameter (100 specimens)

Remarks: This species is the most abundant triporate pollen taxon in the layers and it is ubiquitous throughout the section. A few samples from **Ka** comprise almost exclusively triporate *Alnus*-type grains, rarely tetraporate. This species usually exhibits 4 or 5 pores in all other horizons. In the middle of the section, horizons I, J, K, M has been designated the *Alnus*-layers, so named based on the high abundance of the genus in these layers.

Alnipollenites was validly published in combination with the type species by monotypy (Art. 42 of the Botanical Code). *Alnipollenites* Potonie is senior to *Polyvestibulopollenites* Thomson and Pflug and the latter genus becomes an obligate junior synonym of *Alnipollenites*.

Rouse (1962) and Stanley (1965) have attempted to speciate certain forms of fossil *Alnus*-type grains on the basis of the number of pores. Such a practice is not without basis. Apparently, many extant species of *Alnus* Hill show relative abundances of exclusively certain number of pored forms (Whitehead, 1963). It is not always reliable but it may be applied to fossil *Alnus* as a general rule for species identification. For example, in modern *Alnus crispa* and *A. tennufolia*, about two-thirds of the specimens have 5-pored forms (one-third is 6-pored in the former and one-third is 4-pored in the latter; Whitehead, 1963). *Alnus alnobetula* and *A. rugosa* (hazel alder) are exclusively 4-pored and 5-pored forms, respectively. In fossil grains, *Alnipollenites verus* is commonly stephanoporate and *A. trina* is triporate.

The distinctiveness of the arci and vestibula are very characteristic of the genus. In modern *Alnus* grains, certain species display varying degrees of distinctiveness of arci and vestibula which can be distinguishing features between species (Whitehead, 1963, 1965). Similarly in the fossil grains, *Alnipollenites verus* has distinct vestibula and curved arci, unlike *Alnipollenites trina* which has weak or absent vestibula and straight arci.

The author has observed a few specimens with four or five pores, well-developed arci and a distinct polar exinal ring. The form morphologically resembles *A. venus* (both of which have the number of pores equal to the number of arci), except for the presence of the exinal ring, typical of *Paraalnipollenites* species. Similar 4- and 5-pored *Alnus*-type forms with a polar exinal ring of normal thickness, *Alnipollenites scotica* Simpson and *A. bremanoirensis* Simpson, respectively, have been reported by Simpson (1961). Simpson (1961) observed that certain modern Japanese species, *Alnus sieboldiana* Matsum and *Alnus firma*, are very similar. It is unknown if this is simply a form modification of *A. venus* or *Paraalnipollenites* species or an intermediate form between the two genera.

Comparison: Stanley (1965) recognized a 3-pored form as *Alnus trina* and a 4-pored form as *Alnus quaternaria* from his Paleocene samples of South Dakota. Some workers consider *Alnus quaternaria* to be a junior synonym of *Alnipollenites venus* (Frederiksen, 1980; Choi, 1983). The Fossil Forest Hill specimens are clearly *A. venus*. Grains of *Alnipollenites trina* (Stanley) *nov. comb.* can be easily distinguished from *A. venus* by the straight arci and indistinct vestibula. *Alnipollenites quadrapollenites* (Rouse) *nov. comb.* and *Alnipollenites quinquepollenites* (Rouse) *nov. comb.*, 4- and 5-pored forms respectively proposed by Rouse (1962), are generally accepted as basionyms of *A. venus*.

Botanical Affinities: Morphologically similar to living *Alnus*. The American species *Alnus rubra* (red alder; Simpson, 1961; Martin and Rouse, 1966), *Alnus maritima (=A. japonica, =A. formosana)* found on the North American and Asian Pacific coasts (Simpson, 1961; Rouse, 1962), and the Western Mediterranean species *A. chordata* (Simpson, 1961), are almost identical to this fossil species.

Occurrences: *Alnipollenites verus* has been found in numerous Tertiary floras in North America (Wodehouse, 1933; Rouse, 1962; Stanley, 1965; Martin and Rouse, 1966; Hopkins, 1969; Choi, 1983; Frederiksen, 1980, 1988).

Alnipollenites trina (Stanley) *nov. comb.*

Plate 1, figure 4

Alnus trina Stanley, 1965, p. 289, Pl. 43, figs. 4-6
Alnus trina Stanley; Frederiksen, 1980, p. 149, Pl. 1, fig. 21-22
Jarzenipollenites trinus (Stanley) Kedves, *non 1980*, p. 289, Pl. 43, fig. 4 *(nomen nudum)*
Jarzenipollis trina (Stanley) Kedves; Jansonius and Hills, *non 1982*, card # 4106 [misspelling]
Polyvestibulopollenites trina (Stanley) Thomson and Pflug; Norris, 1986, p. 41, Pl. 10, figs. 4-6

Description: Triporate, less commonly tetraporate, oblate. Triangular (or squarish) outline in polar view, depending on the number of pores; with sides straight to slightly convex. Pores equatorially situated, circular to meridionally elongate, 1 - 2μm diameter. Poorly developed or absent vestibulum. Arcs more or less parallel sides of grain, extending between pores, one set on each hemisphere. Arci 0.5 - 1.5μm thick. Exine psilate to slightly granulate, 1.0 - 1.5μm thick. Sexine thicker than nexine. Annulus, 2μm thick, slight labrum present.

Dimensions: 16.3 (21.0) 25μm diameter (44 specimens)

Remarks: This species is readily separated from *Alnipollenites verus* by having characteristically 3 pores and arci more or less parallel the sides of the grain. This species is so named after the three pores which are most typical of the species.

Alnipollenites trina occurs in the middle of the section, referred to by many as the *Alnus*-layers (Basinger, 1986; Francis and McMillan, 1987; Day, 1991). This species occurs infrequently with *Alnipollenites verus*.

Jarzenipollenites trinus (=Jarzenipollis trina) Kedves is considered a *nomen nudum* by many because its diagnosis falls under the circumscription of *Alnipollenites trina*. Since *Alnipollenites trina* was validly published first by Stanley as *Alnus trina* and later recombined with the form genus *Alnipollenites* by the author, *Jarzenipollenites trinus* becomes an obligate junior synonym. It is not known why the generic name *Jarzenipollenites* was instituted. If one considers *Alnipollenites* as invalid, the next oldest valid generic name would be *Polyvestibulopollenites* Thomson and Pflug.

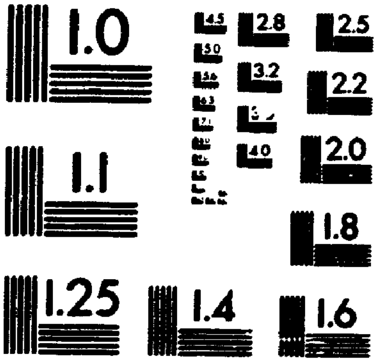
Comparison: Closely resembles *Alnipollenites verus* and *Paraalnipollenites* spp., with which it consistently occurs. The amb of the former is subcircular with curved arci extending between vestibulate pores, while the polar ring of the latter species indisputably distinguish it from *A. trina*. Both species commonly occur as polyporates (three to six pores or more). The small size, and vestibulate apertures are distinguishing features of *A. trina*.

Botanical Affinities: Definite botanicial affinities to modern *Alnus*. Stanley (1965) demonstrated in a comparison study with seven extant forms of *Alnus*, that *Alnipollenites trina* and *Alnipollenites quaternaria* lacked exine stratification but in all other respects were morphologically similar to modern *Alnus* grains. The arcs extending between pores are diagnostic of extant and fossil grains of *Alnus*.

Occurrences: Previously reported from the Paleogene of North America (North Dakota, Stanley, 1965; South Carolina, Frederiksen, 1980, 1988; N.W.T., Norris, 1986).

2

PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT



PRECISION℠ RESOLUTION TARGETS

PIONEERS IN METHYLENE BLUE TESTING SINCE 1974

MICRO D

Alnipollenites sp. A
Plate 1, figures 11-15

Description: Stephanoporate, rarely triporate, oblate. Subpolygonal or subtriangular grain with slightly convex sides. Pores equatorially situated; circular to meridionally elongate, 1.5μm diameter. Weak or absent vestibula; slight labra and tumescence. Outline of arcs irregular, wavy. Arci extend between pores, one set of arci on each hemisphere. Exine thin psilate to faintly granulate, 0.5 - 1.0μm thick.

Dimensions: 17.2 (21.0) 24.2μm diameter (34 specimens)

Remarks: Specimens in the Fossil Forest Hill assemblage exhibit 3 to 5 pores and distinct wavy arci. Tetraporates are more commonly observed. The vestibula are absent or weakly developed, possibly because of the thinness of the nexine.

Alnipollenites sp. A appears to be associated with *Alnipollenites verus* and *A. trina* with which it frequently occurs in the "*Alnus*" layers.

Comparison: This species is distinguished from *Alnipollenites verus* by having unusual arci with an irregular and wavy outline. It does not have straight smooth arci or a triangular outline in polar view as in *Alnipollenites trina*. The unique arci have not been observed in any *Alnus*-type grains (modern or fossil), either in the literature or through an examination of eight different species of *Alnus* in the pollen reference collection of the CMN, and may justify instituting a new species of *Alnipollenites*. The pore structure is often obscured by arci and the (weakly) vestibulate nature is not clearly evident.

Botanical Affinities: Botanicial affinities to modern *Alnus* based on the presence of the arci.

Genus *Ulmipollenites* Wolff 1934 *emend.* Srivastava 1969

type species: *Ulmipollenites undulosus* Wolff 1934

***Ulmipollenites undulosus* Wolff 1934**

Plate 2, figures 7-11

Ulmipollenites undulosus Wolff, 1934, p. 75, Pl. 5, fig. 25
Ulmus sp. Fairchild and Elsik, 1969, p. 84, Pl. 37, fig. 12
Ulmus or *Zelkova* Hopkins, 1969, p. 1122, Pl. 9, figs. 128, 129
Ulmipollenites sp. Tschudy and Van Loenen, 1970, Pl. 3, fig. 22
Ulmipollenites undulosus Wolff; Takahashi and Kim, 1979, p. 57, Pl. 20, figs. 18, 20; Pl. 21, figs. 3, 7, 8
Zelkovaepollenites potoniei Nagy; Takahashi and Kim, 1979, p. 57, Pl. 20, fig. 19, Pl. 21, figs. 1, 2, 4, 6

Description: Four- to five-pored, rarely three-pored. Oblate. Rounded polygonal outline in polar view. Pores equatorial, circular to lolongate, 2.5 - 3.5μm diameter. Weakly to distinctly annulate, slightly aspidate. Arci weak or absent. Sculpture variable, verrucate to brevirugulate to rugulate, sometimes reticulate. Exine thin, 0.5 - 1.0μm thick.

Dimension: 21.8 (29.6) 39.0μm diameter (49 specimens)

Remarks: Specimens of this species display variable ornamentation. Srivastava (1969) emended the generic description *Ulmipollenites* to include only pollen having a slightly undulate to rugulate sculpture. He and Frederiksen (1980) proposed that *Ulmipollenites* be senior to *Ulmoideipites*. The author agrees with Srivastava's emendation and considers *Ulmoideipites* to be an obligate junior synonym. The generic description of *Ulmipollenites* included all ulmaceous forms with slightly undulate to brevirugulate to rugulate sculpture (Srivastava, 1969). Thomson and Pflug (1953) broadened the description so as to include forms having distinctly rugulate to irregularly reticulate surface in this species. As in living *Ulmus* grains, *Ulmipollenites* grains display various surface ornamentation, number of pores and arci within and between species and genera. Both generic descriptions for *Ulmus*-type grains (Wolff, 1934; Thomson and Pflug, 1953; Anderson, 1960; Srivastava, 1969; Frederiksen, 1980) rely mainly on the presence (or absence) of indistinct arci and the shape and outline of the grains to differentiate species.

Comparison: *Ulmipollenites krempii* is different in that it possesses an ulmoid sculpture, very distinct arci, poorly developed annuli and three or four equatorial or slightly subequatorial pores. Frederiksen (1980) noted the close similarity of *Planera thompsoniana* Traverse and *U. undulosus*. The main difference is the very distinct arci in *P. thompsoniana*, however, this distinction may be difficult to recognize (Frederiksen, 1980) because *U. krempii* grains also have distinct arci.

Nagy (1969) established the genus *Zelkovaepollenites* for polyangulate grains with rugulate surfaces and distinct annuli, which essentially falls under the circumscription of *Ulmipollenites undulosus*, which shows variable surface sculpture. Criteria such as a slightly thinner, less coarsely rugulate, and smoother exine in *Ulmipollenites* (Nagy, 1969; Takahashi and Kim, 1979), are not definitive and will not consistently differentiate between *Ulmipollenites* from *Zelkovaepollenites*. The author considers *Zelkovaepollenites* to be a junior synonym of *Ulmipollenites*.

Botanical affinities: Definite affinity to the family Ulmaceae. Morphologically similar to living *Ulmus* (Wodehouse, 1935; Hopkins, 1969; Nagy, 1969), *Zelkova* (Hopkins, 1969; Nagy, 1969; Takahashi and Kim, 1979) and *Planera* (Frederiksen, 1980, 1988). This species is a closer relative to extant ulmaceous pollen than to *Ulmipollenites krempii* (Frederiksen, 1980). *Ulmus* is slightly larger (ave. 37μm diameter; *Ulmipollenites undulosus* is *ca.* 35μm diameter), mostly has 5 pores, less commonly 4 or 6 pores with a convoluted or rugulate surface, however, arci are weak or absent. This species is a generally four- to five-pored grain with convex sides and indistinct arci and is distinctly rugulate.

The author has ooserved the following extant species that closely resemble *U. undulosus*: *Ulmus mexicana*, *Zelkova servata* (Japanese zelkova), *Ulmus rubra* (red elm) and *Ulmus americana* (American elm or white elm).

Ulmipollenites undulosus looks morphologically similar to modern *Phyllostylon rhamnoides* and *Ulmus americana* but has more distinct arci (Wodehouse, 1935). According to Wodehouse (1935), fossil *Ulmus* grains look much like the modern *Ulmus americana* but the modern species characteristically has five pores.

Hopkins (1969) commented on the striking resemblance of fossil pollen of *Ulmus* and *Zelkova*, even modern pollen grains. However, he did not detail further discussion on their resemblance, leaving phylogeny and botanical affinities for speculation by others (e.g. Takahashi and Kim, 1979).

Occurrences: Frequent constituent in the Tertiary of North America, especially southeastern North America (Anderson, 1960; Elsik, 1968b; Hopkins, 1969; Frederiksen, 1979, 1980, 1988). Arctic occurrences have also been reported (Choi, 1983; Norris, 1986; McIntyre, 1991).

***Ulmipollenites tricostatus* (Anderson) Frederiksen 1980**
Plate 2, figure 18

Ulmoideipites tricostatus Anderson, 1960, p. 20-21, Pl. 4, figs. 9-11, Pl. 6, figs. 4, 5, Pl. 7, fig. 8, Pl. 8, figs. 8, 9
Ulmipollenites tricostatus (Anderson) Frederiksen, 1980, p. 149, Pl. 1, fig. 41
Ulmipollenites tricostatus (Anderson) Frederiksen; Choi, 1983, p. 539, Pl. 45, fig. 356
Ulmoideipites tricostatus Anderson; Norris, 1986, p. 83, Pl. 11, figs. 1, 2

Description: Triporate oblate. Triangular to subtriangular outline in polar view.

Straight to slightly convex sides. Pores equatorial; subcircular to elliptical, 1.5 - 3.0μm diameter, with slight annuli. Sculpture brevirugulate. Distinct arci, 3.0 - 4.5μm thick, nearly parallel to sides of grains. Exine thin, 0.5 - 1.0μm thick.

Dimensions: 28.9 - 29.6μm diameter (2 specimens)

Remarks: Anderson (1960) observed smaller grains (17 - 23μm diameter) with variable surface sculpture (irregularly verrucate to brevirugulate) from deposits of New Mexico.

Comparison: *Ulmipollenites tricostatus* is distinguished from other ulmaceous species by being triporate with straight sides, distinct arci and a verrucate to brevirugulate exinal ornamentation.

Botanical Affinities: Possible affinity to Ulmaceae.

Occurrences: This species has been reported in rare numbers by several authors from Upper Cretaceous to Oligocene deposits in North America (Anderson, 1960; Frederiksen, 1980, 1988) and the Arctic (Bratzeva, 1965; Choi, 1983).

***Ulmipollenites krempii* (Anderson) Frederiksen 1979**
Plate 2, figures 12-17

Ulmoideipites krempi Anderson, 1960, p. 20, Pl. 4, fig. 12, Pl. 6, figs. 2,3, Pl. 10, fig. 8
Ulmoideipites planeraeformis Anderson, 1960, p. 20, Pl. 4, fig. 13
Planera hebridica Simpson, 1961, p. 447, Pl. 14, figs, 8,9
Planera mullensis Simpson, 1961, p. 447, Pl. 14, figs, 10,11
Ulmoideipites krempii Anderson *emend.* Elsik, 1968b, p. 608, Pl. 17, figs. 4-7
Planera sp. Hopkins, 1969, p. 1122, Pl.9, fig. 130
Ulmoideipites krempii Anderson; Srivastava, 1972b, p. 280, Pl. 25, fig. 19
Ulmus sp. Elsik, 1974, Pl. 2, fig. 41 only
Ulmipollenites krempii (Anderson) Frederiksen, 1979, p. 145, Pl. 3, figs. 6-8
Ulmipollenites tricostatus (Anderson) Frederiksen 1980; Wingate, 1983, p. 121, Pl. 6, fig. 18

Description: Triporate or tetraporate. Slightly peroblate to slightly oblate.

Subcircular to subpolygonal outline in polar view with slightly to strongly convex sides. Pores equatorial or slightly subequatorial, circular to subcircular outline, 2.5 - 3.0μm diameter. Slight annuli continuous with distinct arci. Sculpture variable, irregularly verrucate (ulmoid) to brevirugulate to rugulate to reticulate. Exine thin, 0.5 - 1.0μm thick.

Dimension: 23.4 (24.2) 32.0μm diameter (10 specimens)

Remarks: *Ulmipollenites krempii* occurs as commonly 4- and rarely 3-pored forms sporadically throughout the forest succession in low frequencies.

Although Srivastava (1972b) intended to formally combine Anderson's species, *Ulmoideipites krempii* with the generic name *Ulmipollenites*, it was wrongly cited as *Ulmoideipites krempii nov. comb.* rather than *Ulmipollenites krempii nov. comb.* Since, the newly combined name was not formally in print in Srivastava (1972b) due to the error, the author has declined to credit Frederiksen (1979).

The original diagnosis of *Ulmoideipites* was intended to accommodate certain ulmaceous pollen that cannot be related to extant genera with certainty (Anderson, 1960). Species of *Ulmoideipites* possess an (often indistinct) ulmoid sculpture (i.e. verrucate) but may or may not have arci; Anderson (1960) included forms similar to *Planera, Ulmus, Zelkova,* and *Hemiptelia*, excluding genera *Celtis* and *Celtoidanthus* Weyland, Pflug and Jahnichen. The intentions of Anderson (1960) are uncertain because the new species he established both have very distinct arci. Modern forms can display incredible range of exinal morphology (verrucate to brevirugulate-rugulate to reticulate surface sculpture), and absent or weak to distinct arci within genera and species. *Ulmipollenites* has indistinct arci but a rugulate to irregularly reticulate sculpture (according to Wolff, 1934). In practise, distinguishing between the two genera is difficult at times.

Elsik (1968b) emended the species diagnosis to include forms with weak to distinct arci, however, this author has observed typically distinct arci in the Fossil Forest Hill specimens. Many workers (Srivastava, 1969; Frederiksen, 1980) have reassigned this species under *Ulmipollenites*, a genus to include all fossil ulmaceous forms, identified as *U. krempii*. Choi (1983) observed a wide range of morphological variability in ulmaceous pollen grains of Axel Heiberg and Ellesmere Islands in terms of: 1) overall shape; 2) heteropolarity of pores and 3) distinctiveness of arci. He, however, recognized only two forms: *Ulmipollenites krempii*, *U. tricostatus*. The author reports a third species, *U. undulosus*, typically polygonal forms that lack arci.

Ulmipollenites krempii grains are interpreted as having a verrucate to brevirugulate surface (Anderson, 1960; Frederiksen, 1980) and being slightly larger, and tetraporate (or five-pored) compared to *U. undulosus* (Anderson, 1960). Elsik (1968b) refers to the sculpture as *verracoid* in nature, however, the author is uncertain what surface sculpture type is meant. The emendation by Elsik (1968b) excluded ulmaceous form-genera intended for the other ulmoid ornamentation types. In the Fossil Forest Forest Hill specimens, the observed surface ornamentation was variable: irregularly reticulate, verrucate, brevirugulate or rugulate.

The spelling of this species has changed since its introduction by Anderson (1960) who spelled *krempi* with a single "*i*". According to Recommendation 73C 1a), International Code of Botanical Nomenclature, when naming a species after a person whose name ends with *i*; a second *i* should be added. Since the common spelling of the species is with the second *i*, the author is conforming to the recommendation and following others in the spelling of *krempii*.

Comparison: A similar form, *Ulmipollenites undulosus* Wolff, is slightly smaller, generally tetraporate or pentaporate, rarely triporate and lacks distinct arci (Anderson, 1960). Triangular-shaped *Ulmus*-type grains with well-developed arci are clearly *U. tricostatus*. *Planera thomsoniania* Traverse (=*Ulmipollenites thompsonius* (Traverse) Frederiksen) also has distinct arci (Frederiksen, 1980) which could have been produced by *Planera*, *Zelkova* or some other genus of the Ulmaceae that existed during the Eocene (Frederiksen, 1988).

This species is very similar to *U. tricostatus* which is distinguished by being triporate and having straight to slightly convex sides, very distinct arci and an ornamentation that is verrucate to brevirugulate (Anderson, 1960).

Simpson (1961) compared his two fossil species, *Planera hebridica* Simpson, *P. mullensis* Simpson, with the pollen of contemporary *P. aquatica*. Elsik (1968b), however, considered these two species of Simpson as basionyms of *U. krempii*.

Botanical affinities: Definite affinity to the family Ulmaceae, however extant ulmaceous pollen are larger (average 37μm diameter), mostly with 5 pores, less commonly with 4 or 6, with a convoluted or rugulate surface. Arci vary in distinctiveness within and between species. Anderson (1960) established *Ulmoideipites* to accommodate ulmaceous type grains that could not be related to extant genera with certainty.

Some workers have noted similarities of this species with species of *Planera*, (Simpson, 1961; Elsik, 1968b; Hopkins, 1969; Frederiksen, 1980, 1988), *Ulmus*

(Simpson, 1961), *Zelkova* (Simpson, 1961) and *Celtis (=Momisia)* (Wodehouse, 1933; Simpson, 1961). Simpson (1961) compared his ulmaceous species with the modern species *Planera aquatica* (water elm), also a circular triporate form with distinct arci. Simpson (1936) had originally suggested that *Celtis (=Momisia)* was the closest modern relative to *U. krempii*.

Occurrences: *U. krempii* has been reported from various localities in the Paleogene of North America (Anderson, 1960; Elsik, 1968b, 1974; Srivastava, 1972b; Frederiksen, 1980, 1988) and the Arctic (Bratzeva, 1965; Choi, 1983) and Europe (Simpson, 1936, 1961).

Genus *Polyatriopollenites* Pflug 1953

type species: *Polyatriopollenites stellatus* (Potonie) Pflug 1953

Polyatriopollenites sp.

Plate 5, figure 17

Dimension: 35.5μm diameter

Results: *Polyatriopollenites* is a persistant polyporate form (never with a triporate condition) throughout the section is more numerous at the top of the section. Commonly with six pores or more.

Comparisons: This species closely resembles *P. stellatus* but the author cannot determine to the species level at this time.

Botanical Affinities: Juglandaceae. This form most resembles modern *Pterocarya*.

Turma Aletes Ibrahim

Subturma Azonaletes Luber *emend.* Potonie and Kremp

Genus *Taxodiaceaepollenites* Kremp 1949 ex. Potonie 1958

type species: *Taxodiaceaepollenites hiatus* Potonie 1931 ex. Potonie 1958

Taxodiaceaepollenites sp. A

Plate 5, figure 19

Dimensions: 28.9μm diameter

Remarks: Common in the top and bottom of the section, less common to rare in the middle *Alnus*-layers.

Botanical Affinites: Taxodiaceae. This species most resembles modern *Taxodium*, such as *T. distichum* (Martin and Rouse, 1966).

Taxodiaceaepollenites sp. B

Plate 5, figure 18

Dimensions: 29.64μm diameter; papilla approximately 4.7μm long.

Remarks: Probably more common in the fossil forest assemblages but unless the papilla is fully extended, it is not always recognizable. This form appears as another inaperturate taxodiaceous grain such as a *Taxodium* type or *Sequoia* type (Martin and Rouse, 1966).

The figured papillate palynomorph has a coarser exine than *Taxodium*-type and *Sequioa*-type pollens and a shorter papilla by about 2 - 4μm.

Botanical Affinities: Taxodiaceae; closely resembling modern *Metasequoia* (Rouse, 1962).

Turma Plicates Nauvmova *emend.* Potonie

Subturma Ptychotriporines Nauvmova

Genus *Tiliaepollenites* Potonie 1931

type species: *Tiliaepollenites indubitabilis* Potonie 1931

Tiliaepollenites sp.

Plate 5, figure 8

Dimensions: 35.5μm diameter

Remarks: Many taxonomic problems plague tiliaceous genera. *Tiliaepollenites* was instituted as a form genus to include all forms comparable to modern *Tilia*, however some workers believe that this genus is invalid (Krutzsch, 1961; Norris, 1986) because the type species was based on a grain of Recent *Tilia chordata*.

This form has been included under the group of tricolporate pollen based on the same pore condition as modern species. However, fossil tiliaceous species are included under triporate groups (*Intratriporopollenites*, *Tiliaceapollenites*) and tricolporate groups (*Bombacidites*).

Botanical Affinities: Tiliaceae. Similar modern forms include *Tilia americana* and *T. chordata*.

Anteturma Sporites Potonie

Genus *Ctenosporites* Elsik and Jansonius 1974

type species: *Ctenosporites wolfei* Elsik and Jansonius 1974

Ctenosporites sp.

Plate 5, figure 20

Dimensions: 35.5 x 43.3μm

Remarks: Very common fungal element at the top of the section and sporadic in the lower part of the section. This melanis palynomorph is considered to be a good age indicator of Eocene (Elsik and Jansonius, 1974).

Comparison: Morphologically similar to *Ctenosporites eskerensis*.

Botanical Affinities: Unknown fungal affinity. This multicellular structure is of fungal origins (Elsik and Jansonius, 1974).

Occurrence: This genus is a very common fungal element, included in many early Tertiary Arctic assemblages (Alaska, Elsik and Jansonius, 1974; Axel Heiberg and Ellesmere Island, Ricketts and McIntyre, 1986; McIntyre, 1991; MacKenzie Delta, N.W.T., Norris, 1986).

CHAPTER 3. RESULTS

3.1 DEFINITION OF TRIPORATE POLLEN

Triporate pollen represent one morphological group of terrestrial palynomorphs of the Fossil Forest Hill assemblages. Triporates are three-pored angiospermous pollen lacking furrows, having all pores equidistantly placed, either equatorially or subequatorially or both in one hemisphere (modified after Faegri and Iverson, 1964; Kremp, 1965; Erdtman, 1972; Traverse, 1988).

Many variants are known on the triporate theme (Fig. 3.1). An example is the tricolpate form which has three furrow-like germinal apertures (colpi) arranged 120° apart (Kremp, 1965). This arises from simultaneous meiosis of the pollen-mother-cell (tetrad) and is the precursor of triporate pollen (Fig. 3.2). The reduction of the furrows to small pores results in the triporate apertures. The intermediate form between tricolpate and triporate is tricolporate, which has pores situated within the colpi. With the onset of angiosperm differentiation, a trend towards apertural elaboration is apparent (Brazier, 1980), leading to the development of polycol(po)rates, polyporates (stephanoporates and periporates; Traverse, 1988). Variations in pore structure of triporate pollen are illustrated in Fig. 3.3.

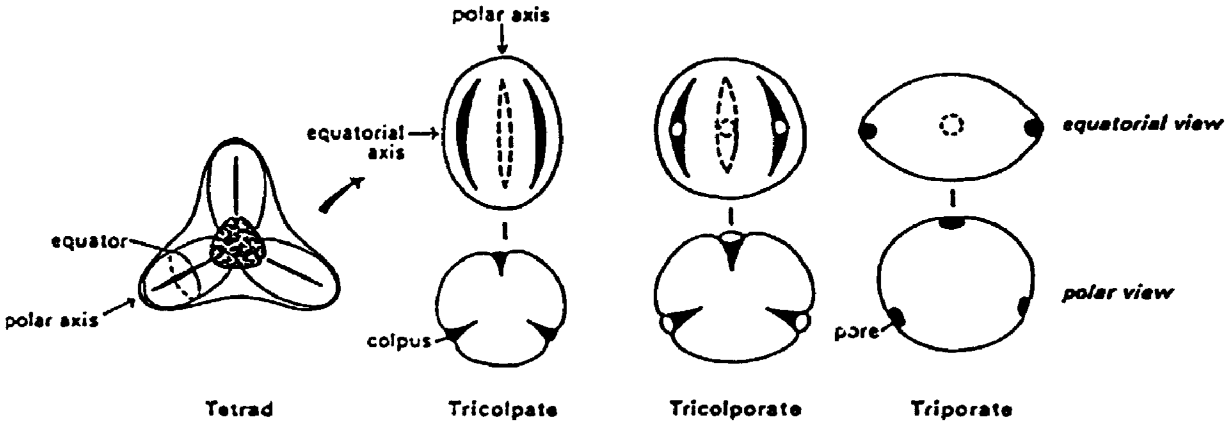


Figure 3.1. Pollen Morphogroups (from Brazier, 1980).

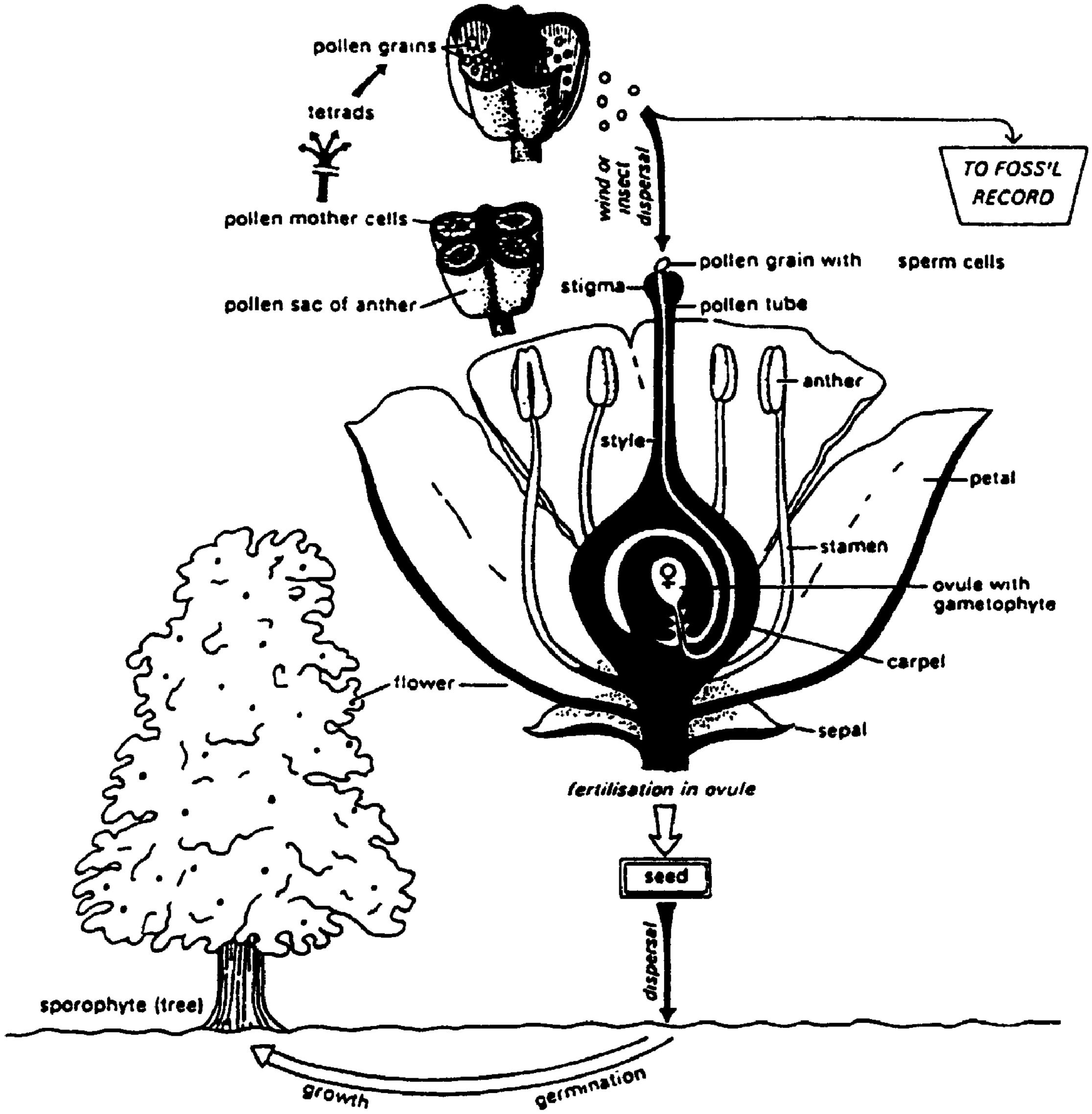


Figure 3.2. Angiosperm Life Cycle (from Brazier, 1980).

Atrium

Vestibulum

Annulus

Tumescence

Labrum

Figure 3.3. Pore Structures of Triporate Pollen (from Kremp, 1965)

3.2 ANALYSIS OF TRIPORATE ASSEMBLAGES

An examination of the overall triporate pollen reveals that 36 species from 18 genera occur over 7 (sub)horizons (Table 3.1). The overall preservation of the triporates is fair to excellent, but generally is good to very good. Triporate pollen comprise only a small component of the palynomorph assemblages, on average 9.5% of the total palynomorphs (Table 3.2); a minimum of less than 0.5% to a maximum of 42.5% (Fig. 3.4). It is significant that the triporate pollen taxa rarely dominate in any one palynomorph assemblage, except in **Ka** and **Nb** where *Alnipollenites verus* and *Pistillipollenites macgregorii*, respectively dominate.

A relatively modest triporate taxa diversity was observed, with an average of four triporate taxa per horizon (Table 3.3). The **A** horizon contains the highest species diversity per (sub)horizon, with an average of 8.8 species. This relatively high species diversity is consistent with the occurrence of abundant and varied plant macrofossils observed in the same horizon (Basinger *pers. comm.*, 1991). **Nb** and **Ka** record moderately high species diversity, averaging 6.2 and 5.2 triporate species per (sub)horizon, respectively, while **I**, **J** and **Kb** have the lowest triporate species diversity with averages of 2.8, 2.6 and 3.0 species, respectively.

The most common triporates are *A. verus* (maximum 13% of an assemblage) and *Trivestibulopollenites claripites* (maximum 6% of an assemblage), occurring in every (sub)horizon of the partial section under study. Secondary forms (about 3% of the total palynomorphs in any given (sub)horizon include: *Momipites microfoveolatus, A. trina, Triatriopollenites* spp. (where *T. subtriangularus* and

Table 3.1A. STRATIGRAPHIC OCCURRENCE OF TRIPORATE POLLEN SPECIES THROUGHOUT THE LEAF LITTER SECTION.

LEAF HORIZONS

TRIPORATE SPECIES	top **A**	**I**	**J**	**Ka**	**Kb**	**M**	base **Nb**
Alnipollenites trina				X	X	X	
Alnipollenites verus	X	X	X	X	X	X	X
Alnipollenites sp. A				X	X		
Annutriporites sp.	X						
Carpinipites ancipites	X		X	X		X	
Caryapollenites juxtaporipites	X						
Caryapollenites viridifluminipites	X				X	X	X
Caryapollenites sp. cf. *C. inelegans*	X					X	
Caryapollenites sp. cf. *C. veripites*	X			X			
Caryapollenites sp. A	X		X	X		X	
Diervillapollenites sp.							X
Momipites coryloides	X					X	
Momipites microfoveolatus	X	X		X	X	X	X
Momipites ?tenuipolis			X				
Myricipites annulites	X			X		X	
Paraalnipollenites sp.			X			X	
Pistillipollenites macgregorii	X			X	X	X	X
Pistillipollenites sp. A							X
Platycaryapollenites sp. cf. *P. platycaryoides*	X						X

Table 3.1B. STRATIGRAPHIC OCCURRENCE OF TRIPORATE POLLEN SPECIES THROUGHOUT THE LEAF LITTER SECTION.

	LEAF HORIZONS						
TRIPORATE SPECIES	top A	I	J	Ka	Kb	M	base Nb
Plicatopollis sp. of the *P. plicata*-type		X					X
Plicatopollis sp. A	X						X
Santalacites sp. cf. *S. santaloides*	X	X		X	X	X	X
Subtriporopollenites anulatus	X		X	X		X	
Subtriporopollenites nanus	X				X	X	
Thomsonipollis sp.	X						
Triatriopollenites subtriangulus	X			X		X	
Triatriopollenites spp. cf. *T. arboratus*	X	X				X	
Triatriopollenites sp. A	X			X	X	X	
Triatriopollenites sp. B	X						
Triporopollenites mullensis	X	X	X	X	X	X	X
Triporopollenites sp. A	X		X			X	X
Trivestibulopollenites betuloides	X					X	
Trivestibulopollenites claripites	X	X	X	X	X	X	X
Ulmipollenites krempii	X		X		X	X	X
Ulmipollenites tricostatus				X		X	
Ulmipollenites undulosus	X	X	X	X	X	X	X

Table 3.2. TAXA ABUNDANCE

Average relative abundances (as a %) of various palynomorph groups within each assemblage representing each horizon. 350 or more palynomorphs were counted.

LEAF LITTER HORIZONS

PALYNOMORPH GROUP	top **A**	**I**	**J**	**Ka**	**Kb**	**M**	base **Nb**
polycol(po)rates	0.74%	0.06%	0.54%	0.00%	0.05%	0.74%	0.21%
tetrads	0.03%	0.03%	0.03%	0.05%	0.00%	0.28%	0.44%
tricolpates	15.26%	1.00%	2.70%	2.19%	0.97%	5.23%	2.00%
tricolporates	3.70%	0.61%	7.06%	0.35%	0.11%	3.07%	2.06%
Taxodiaceae	21.58%	27.02%	28.49%	4.33%	3.86%	41.21%	19.08%
triporates	**4.88%**	**2.26%**	**0.58%**	**13.26%**	**6.64%**	**2.71%**	**35.90%**
spores	17.80%	3.28%	3.46%	19.22%	29.64%	4.36%	3.79%
bisaccates	4.65%	0.47%	4.36%	1.10%	0.97%	2.31%	1.76%
monosulcates	0.83%	0.78%	1.38%	2.60%	1.21%	1.02%	0.56%
fungal elements	22.85%	45.78%	43.67%	8.27%	30.12%	21.23%	16.43%
polyporates	4.79%	18.70%	7.73%	48.63%	26.43%	17.85%	17.77%

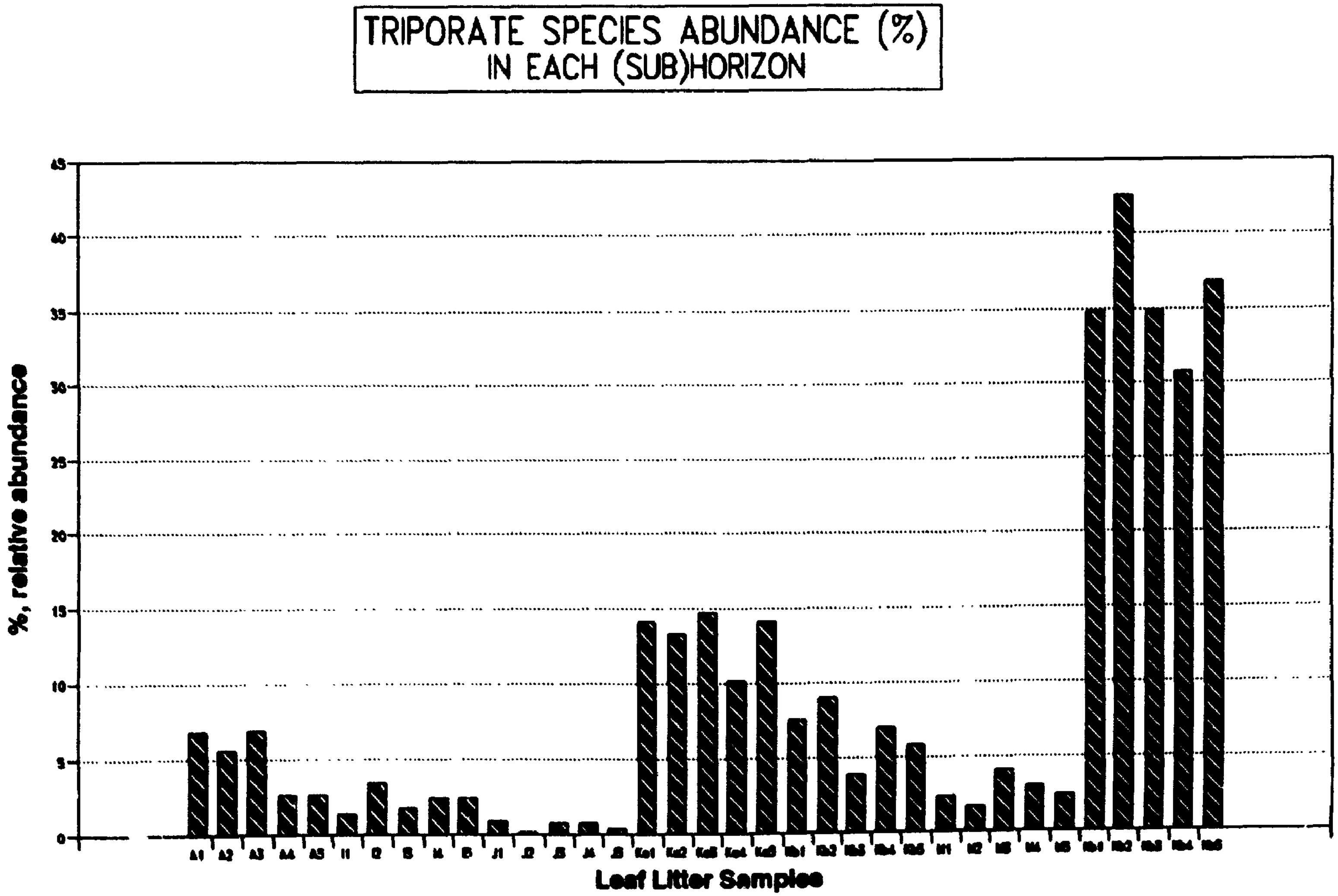


Figure 3.4. Triporate Species Abundance.

Table 3.3. TRIPORATE SPECIES DIVERSITY.
The number of triporate species observed in each leaf horizon after counts of 350 palynomorphs or more. X represents a sample within a (sub)horizon.

LEAF LAYERS

LEAF HORIZON	X_1 top	X_2	X_3	X_4	X_5 base	**Average # species per sample**
A top	9	12	8	7	8	**8.8**
I	3	2	2	4	3	**2.8**
J	4	1	3	3	2	**2.6**
Ka	7	5	4	5	5	**5.2**
Kb	4	3	3	2	3	**3.0**
M	4	4	5	4	3	**4.0**
Nb base	7	5	6	8	5	**6.2**

Triatriopollenites spp. cf. *T. arboratus* are the principal forms), *Triporopollenites* spp. (of which *T. mullensis* is occasionally abundant). Minor forms, constituting about 1% or less of the total palynomorphs present are: *Caryapollenites viridifluminipites, Myricipites annulites, Momipites coryloides* and rare triporates, typically represented by a single occurrence, that include *Ulmipollenites* spp. (*U. tricostatus, U. undulosus* and *U. krempii*), *Platycaryapollenites* sp. cf. *P. platycaryoides, Plicatopollis* sp. of the *P. plicata*-type and other *Caryapollenites* spp. (*Caryapollenites* sp. cf. *C. veripites, C. juxtaporipites, Caryapollenites* sp. cf. *C. inelegans*). *Pistillipollenites macgregorii* typically records a single or few occurrences in virtually all the (sub)horizons, except in the basal horizon, Nb.

The important families in the Fossil Forest Hill assemblages are Betulaceae and Juglandaceae with less common ?Gentianaceae, Myricaceae, Ulmaceae, Santalaceae and rare Caprifoliaceae. Many taxa are assignable to living families or genera, although some extinct triporate pollen taxa are also present such as: *Pistillipollenites macgregorii, Pistillipollenites* sp. A, *Plicatopollis* sp. of the *P. plicata*-type, *Momipites* spp. (see Table 3.4 for fossil triporate genera and their modern counterparts and common names). Look to Appendix IIIB for exact statistical figures.

Betulaceae and *Betula*-type pollen

Betulaceae (birch) is the predominant family in the fossil assemblages with betulaceous genera occurring throughout the section. Only in Nb is this family second in abundance. *T. claripites* and *A. verus* are ubiquitous. Other species of

Table 3.4.
Fossil Triporate Genera and their modern counterparts and common names.

FOSSIL	MODERN	COMMON
Alnipollenites	*Alnus*	alder
Carpinipites	*Carpinus*	hopbeam
Caryapollenites	*Carya*	hickory
Diervillapollenites	*Diervilla*	bush honeysuckle
Myricipites	*Myrica*	wax myrtle
Platycaryapollenites	*Platycarya*	-
Plicatopollis	Juglandaceae	-
Santalacites	cf. *Thesium*	toadflax
Trivestibulopollenites	*Betula*	birch
Ulmipollenites *(Ulmoideipites)*	*Ulmus* *Planera* *Zelkova* *Phyllostylon* cf. *Celtis*	elm water elm water elm hackberry
Momipites	*Engelhardtia* *Alfaroa*	-
Pistillipollenites	?Gentianaceae	-
Subtriporopollenites	cf. *Carya*	hickory
Triatriopollenites	cf. *Engelhardtia* cf. *Ostrya* cf. *Myrica* cf. *Comptonia*	- ironwood wax myrtle sweet fern
Triporopollenites	cf. *Corylus* cf. *Ostrya*	hazel, filbert ironwood

Alnipollenites, *A. trina*, *A.* sp. A are infrequent to occasionally abundant in the middle of the section. A second species of *Trivestibulopollenites*, *T. betuloides*, is very rare in the top half of the section. Other typical fossil *Betula*-type pollen include *Myricipites annulites*, *Carpinipites ancipites*, form genera: *Triatriopollenites* spp. and *Triporopollenites* spp.

By far, *Alnipollenites* is the most abundant betulaceous triporate genus in the section, reaching high concentrations in **Ka** and **Kb**, especially *A. verus*. *Alnipollenites* spp. predominantly occur with four- and five-pores, less commonly to rarely with three or six pores or more. *Alnipollenites trina* and *A.* sp. A occur in very low frequencies (<0.5% and <1.5% of the total palynomorphs, respectively) and are confined to the *Alnus*-layers (**I**, **J**, **K**, **M**, **Nb** horizons). A few occurrences of *Paraalnipollenites* sp. were observed in the **J** and **M** horizons, part of the *Alnus*-layers.

Juglandaceae

Low frequencies of juglandaceous pollen (hickory-walnut family occur in all (sub)horizons, typically comprising 3% or less of the total palynomorphs. *Caryapollenites* spp., of which *C. viridifluminipites* is the most common fossil hickory pollen, generally constitutes less than 1% of the total palynomorphs. *Subtriporopollenites anulatus* and *S. nanus* may appear morphologically similar to *Carya* pollen, and similarly have low abundances. *Momipites microfoveolatus*, always less than 1.5% of the total palynomorphs in any sample, is a recurring form. Other species of *Momipites* are uncommon to rare, including *M. coryloides* and *M. ?tenuipolis* (a single observed specimen, figured but not described, Pl. 3, fig. 19).

Platycaryapollenites sp. cf. *P. platycaryoides* was observed twice in the fossil forest succession. McIntyre (1991) did not observe this genus in his study, although, species of *Platycaryapollenites* have been reported rarely in Eureka Sound deposits of west-central Axel Heiberg and Ellesmere Islands (Choi, 1983). Frequent juglandaceous polyporates include *Juglanspollenites* sp. and *Polyatriopollenites* spp., which are closely related to the modern genera *Juglans* (walnut) and *Pterocarya* (Asian juglandaceous shrub), respectively.

***Pistillipollenites* species**

This genus is interesting in that it occurs rarely throughout the partial section, typically a single occurrence in any sample, but emerges as the dominant triporate pollen taxon (principally *P. macgregorii*) in the lowermost horizon, Nb. A second form of this genus, *P.* sp. A has been observed in Nb only and may represent a new species of this monotypic genus. The triradiate structure of this species is unique, resulting from the nexine pulling away from the sexine. This structural modification is not mentioned either in the original diagnosis (Rouse, 1962) or in the intensive study of *P. macgregorii* by Rouse and Srivastava (1970).

Ulmaceae

Fossil elm grains are persistent but infrequent forms throughout the section. All of the ulmaceous grains observed within this study have been predominantly tetraporates and pentaporates, rarely triporates and hexaporates. Three species of *Ulmipollenites* have been recorded: *U. tricostatus*, *U. undulosus* and *U. krempii*.

Other triporates

Other triporates were recovered in very low numbers. *Santalacites* sp. cf. *santaloides* is an infrequent species in the *Alnus*-layers. Its nearest modern relative, *Thesium*, has a tricolpate pollen. It is uncertain if the species is a precursor to the tricolpate condition of members of Santalaceae or if *Santalacites* is a form modification of *Alnus*-type pollen. This species appears to be associated with *Alnipollenites*, particularly where the latter is abundant.

Many other pollen taxa occur as rare or single occurrence(s) such as *Thomsonipollis* sp., *Diervillapollenites* sp., *Plicatopollis* sp. of the *P. plicata*-type, *Platycaryapollenites* sp. cf. *P. platycaryoides*, *Subtriporopollenites nanus*, etc.

3.3 OTHER PALYNOMORPHS

In general, the samples contain rich, diverse and well-preserved palynomorph assemblages. Palynological analyses of the samples indicate that the microflora was composed predominantly of angiosperm pollen, with lesser amounts of spores, fungal elements and gymnosperm pollen. Rare reworked Cretaceous pollen, spores and dynoflagellate cysts also occur very rarely in some samples (A1 - A5).

The dicotyledonous plant taxa comprise two groups, angiosperm and gymnosperm pollen. The conifers are represented by the gymnosperm pollen as bisaccate or inaperturate grains. Abundant bisaccates (Pinaceae) and inaperturate coniferous pollen (principally Taxodiaceae pollen referrable to extant *Metasequoia, Glyptostrobus, Sequoia* and *Taxodium*) and possibly *?Larix*, Pinaceae, commonly occur throughout the fossil forest succession. Large proportions of bisaccates derive from a species of *Piceapollenites* (spruces) and lesser *Pinuspollenites* (pine). Very rare forms include *Podocarpidites* (podocarp) and *Abiespollenites* (fir).

Taxodiaceous pollen form an important part of the samples studied, comprising about 41% of the observed palynomorphs in the **M** horizon, but on average, account for 27% of the grains in the fossil assemblages. The (sub)horizons with least taxodiaceous pollen are **Ka** and **Kb** (4.3% and 3.8% respectively) which are dominated by *Alnus*-type pollen grains. There is an apparent relationship between the taxa abundance of taxodiaceous pollen, and fungal elements with the triporates. Samples with high abundances of Taxodiaceae and fungal elements have low abundances of triporates and vice versa (Table 3.2). Bisaccates are consistently rare in all (sub)horizons, showing no relationship with other palynomorph groups.

The angiosperm pollen represent diverse deciduous and hardwood forest elements. The persistent occurrence of tricolpates and tricolporates (various form-genera *Tricolpites* and *Tricolporopollenites*, and genera that are referable to modern related genera: *Quercus, Salix, Acer, Nyssa, Fagus, Tilia* and fossil forms, e.g. *Tricolporopollenites kruschii*) are never observed in large quantities, characteristically less than 15% of the total number of palynomorphs. In the **A** horizon, the most abundant tricolporates are morphologically similar to *Quercus* (oak) and *Fagus* (beech). *Castanea*-type pollen in the **J** horizon record a maximum of 7% of the total palynomorphs in assemblages.

The polycolpates and polycolporates are rare throughout the section, never totalling more than 2.5% in any (sub)horizon, a maximum of 2.4% in **A5** sample.

Fraxinuspollenites (ash) is the only polycolpate genus that can be identified with certainty.

Spores of the families Osmundaceae, Lycopodiaceae and Polypodiaceae and various fungal elements (of which the multisporites type are most abundant; e.g. *Ctenosporites, Striadiporites*) are also very common at the top of the forest succession (A horizon). Other spores common to occasionally abundant include species of *Triplanosporites, Cyathidites, Deltoidea, Stereisporites, Laevigatosporites ovatus* and *L. hardtii.*

CHAPTER 4. STATISTICAL ANALYSIS

4.1 Q-MODE CLUSTER ANALYSIS

Q-mode cluster analyses grouped together samples (horizons or subhorizons) with similar species/taxa composition, therefore, palynofloral assemblages would indicate vegetational types and the prevailing environments in the area at the time of deposition.

The cluster analysis defined four distinct palynofloral zones among a total of 30 samples taken from seven (sub)horizons of the partial fossil forest sequence (Fig. 4.1). Each zone or distinct cluster of samples was characterized by a unique palynomorph composition, indicating a particular vegetational type. The palynofloral zones are identified by the most characteristic species or palynomorph group of the (sub)horizon (Table 4.1). They represent: 1) Betulaceae-Juglandaceae deciduous-hardwood forest, 2) taxodiaceous swamp forest, 3) *Alnus*-type forest, and 4) gentian-type association. Seven subzones are recognized at a Euclidean distance very close to zero, suggesting that each (sub)horizon is unique. Subtle vegetational differences separate these subzones at this fine scale but at a Euclidean distance of 0.5, similar (sub)horizons combine to form a larger palynofloral zone, such as Ka and Kb; A and M; I and J. Although these (sub)horizons probably represent similar climates, they maintained slightly different vegetation, i.e. the palynofloral zones overlapped to some degree. Two general types of palynofloral zones through the section indicate a continually changing environment that saw a repeated replacement of 1) an early successional vegetation (*Alnus* or *Pistillipollenites*) by 2) a climax

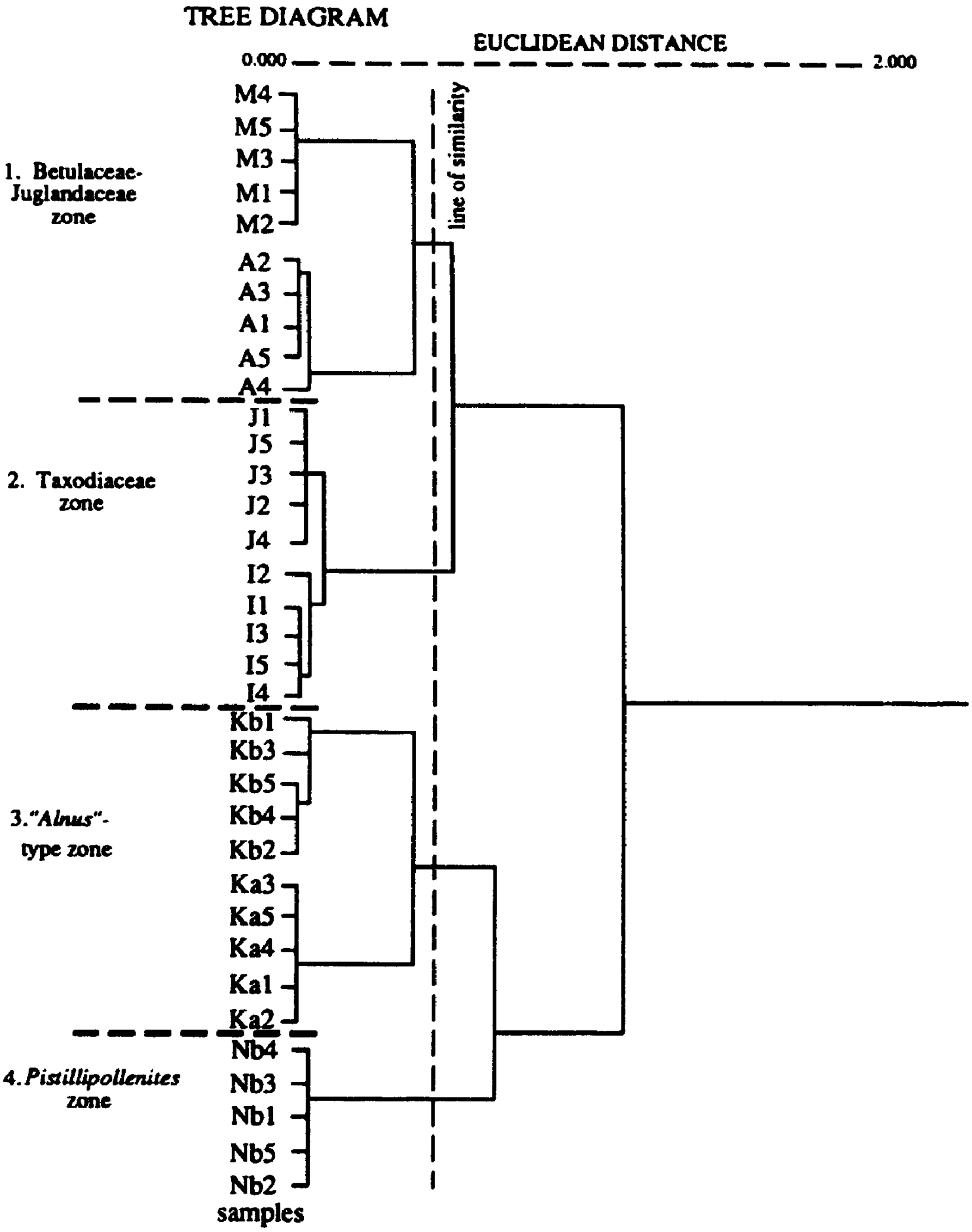


Figure 4.1. Group Q-mode dendrogram utilizing relative frequencies of nine palynomorph groups of the fossil assemblages. [Ward minimum variance method is used].

Table 4.1 Palynofloral zones and their interpreted vegetational types based on Q-mode cluster analyses.

(Sub)Horizons	**Characteristic taxa/family**	**Vegetational Type**	**early/late stage forest**
A	Betulaceae - Juglandaceae	deciduous and hardwood forest	late
I	Taxodiaceae	"*Metasequoia*" wetland forest	late
J	Taxodiaceae	"*Metasequoia*" wetland forest	late
Ka and Kb	*Alnipollenites verus*	*Alnus* (alder) forest	early
M	Betulaceae - Juglandaceae	deciduous and hardwood forest	late
Nb	*Pistillipollenites macgregorii*	gentian-type association	early

forest dominated by tall mature trees (deciduous forests of predominantly Betulaceae-Juglandaceae or Taxodiaceae members), then by an early successional forest again. A physical disturbance annihilated the late-stage forest, probably altering both the floral and physical landscape, and allowed the growth of a new early-stage forest. The successional nature of the forests suggests periods of uninterrupted growth. Although horizons A and I represent two different types of late-stage forests, the unstudied horizons between them may have represented at least one cycle followed by a disruptive event that resulted in the difference in palynofloral composition of the forests of I (Taxodiaceae) and A (Betulaceae-Juglandaceae). Such an alternation in forests is consistent with that of a floodplain or more generally, a large, active fluvial environment that regularly opened up early successional sites in the forests for pioneer plants and other precursors to a tree community.

Similar clusters are shown in the dendrograms utilizing relative frequencies of families with triporate members and of triporate species (Figs. 4.2, 4.3), although three not four palynofloral zones are resolved. The familial data represents a more reduced data set that includes only families with triporate members and does not embody all the palynomorphs nor represent the entire vegetation. Similarly, the triporate species data focuses solely on the triporates and is only a small constituent of the palynomorph assemblages. As a result, looser or larger clusters are defined. Nevertheless, the same cyclical pattern is shown in both dendrograms. Similar environments occur and vegetation types alternate regularly between young and mature forests.

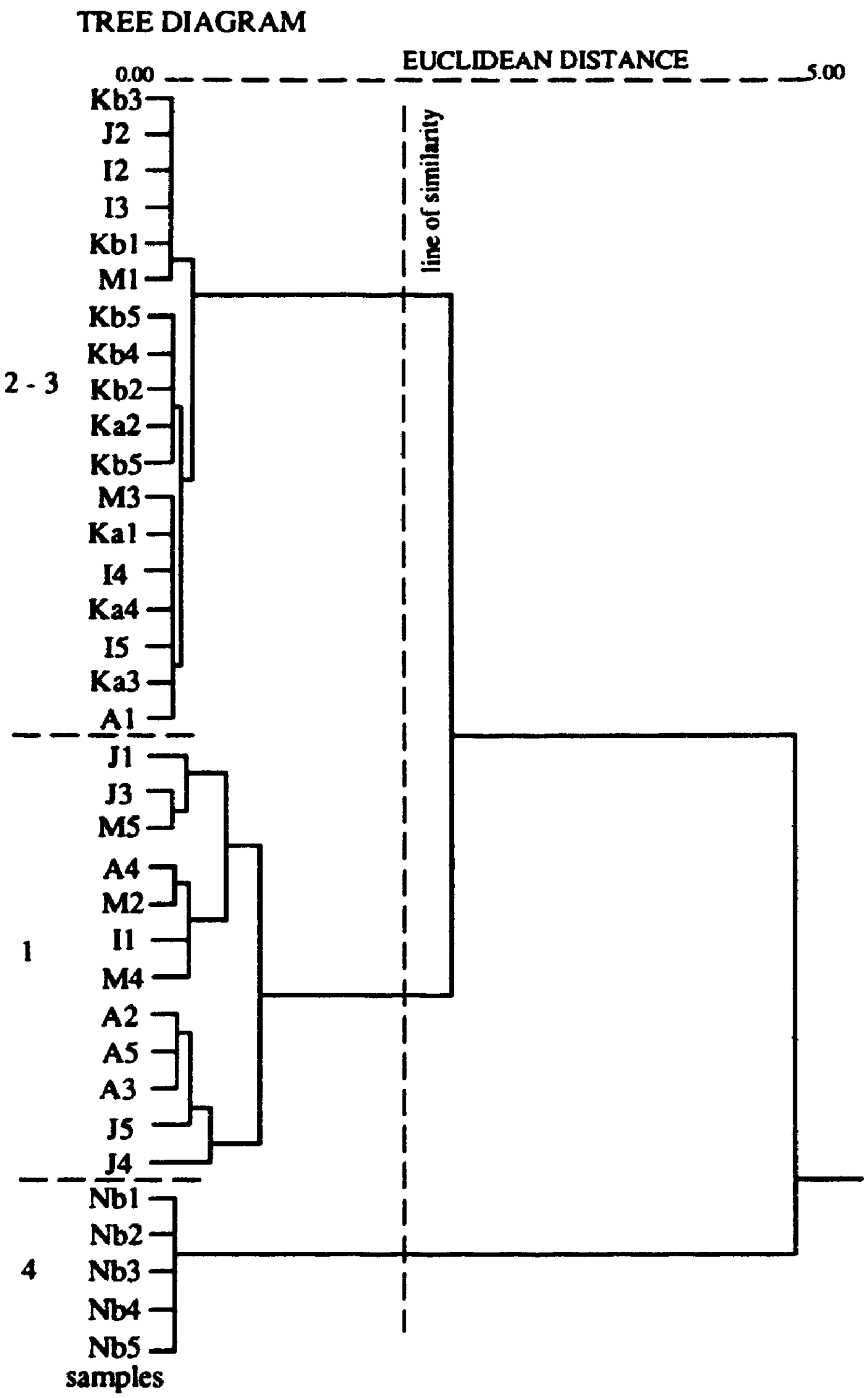


Figure 4.2. Family Q-mode dendrogram utilizing relative frequencies of four families with triporate members. [Ward minimum variance method is used].

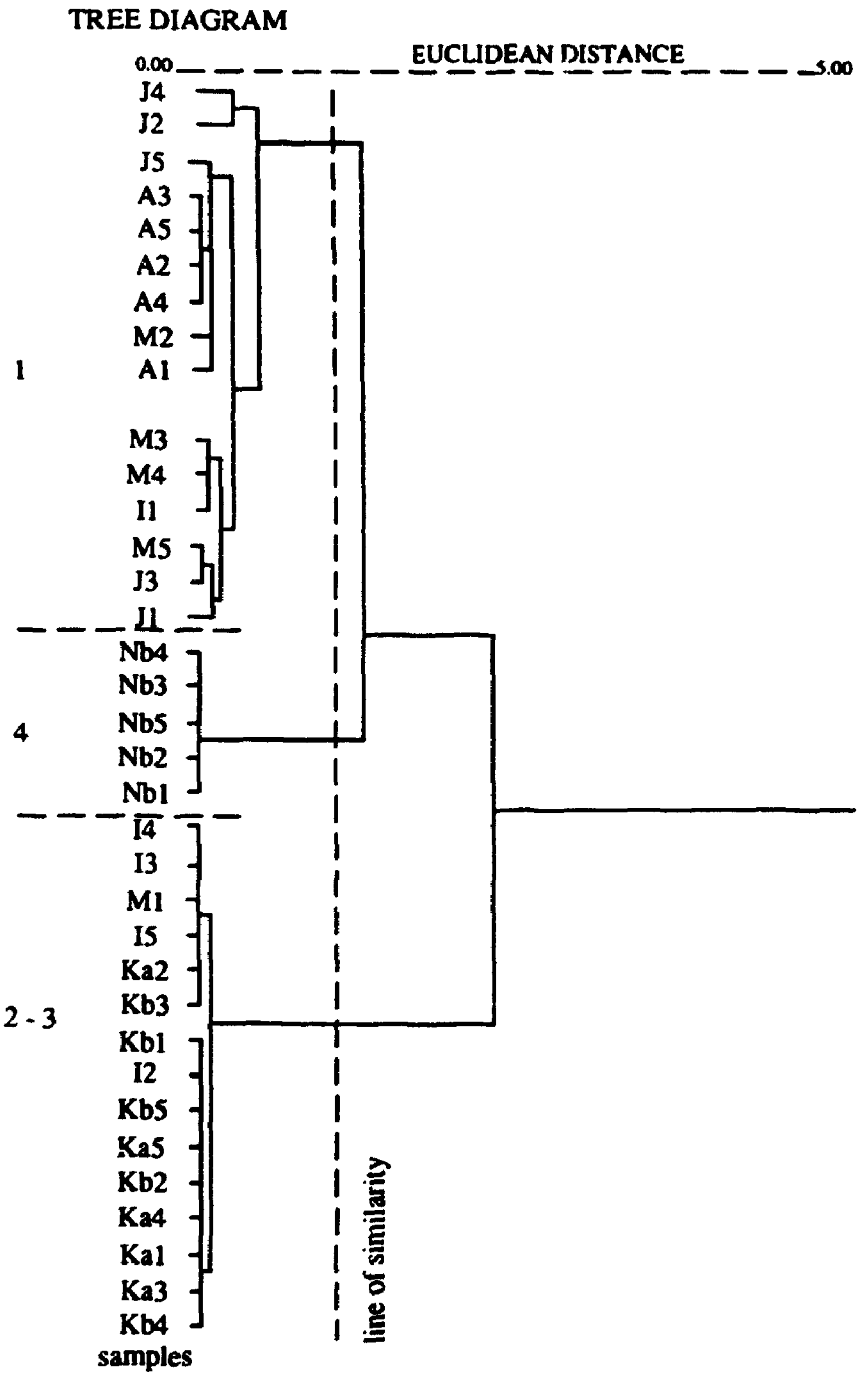


Figure 4.3. Species Q-mode dendrogram utilizing relative freqencies of triporate species from four families. [Ward minimum variance method is used].

4.2 R-MODE CLUSTER ANALYSIS

R-mode cluster analyses compared taxa in any sample, clustering those with similar relative frequencies. Distinct clusters suggested palynofloral associations, inferring palynomorph descriptions of the vegetational patterns of the Q-mode cluster analyses.

Like the Q-mode, R-mode cluster analysis demonstrated tighter and more distinct clusters on a palynomorph group level, i.e. all palynomorphs in the assemblage are included in the data set (Fig. 4.4). Four palynomorph associations were observed: 1) bisaccates ("upland taxa"), 2) taxodiaceous pollen and fungal elements ("wetland" taxa), 3) triporates, polyporates and spores, 4) tetrads, polycol(po)rates, monosulcates, tricolp(or)ates (the latter two, representing "tree" taxa).

The consistently low frequencies of the bisaccates throughout the section (never more than 6% of the total palynomorphs in any one sample) is ecologically significant. Bisaccate pollen distinctly clustered alone, suggesting that they are not associated with any other group. If the assumption is correct that this group is not part of the fossil assemblage, then they are considered extrabasinal elements that were transported long distances from possibly cooler elevated regions, where they are more typically found.

The second association includes members of the Taxodiaceae and fungal elements, palynomorphs likely to have been derived from swamp forests similar to the Pacific coast *Sequoia*-forests or *Taxodium*-forests of southeastern U.S. (Florida Everglades and Okefenokee Swamp, Georgia).

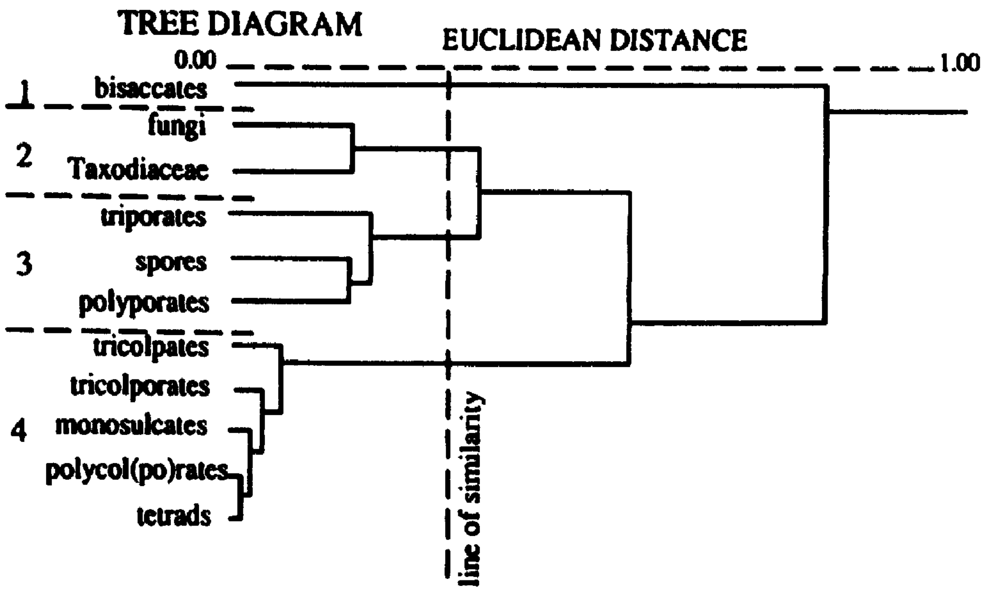


Figure 4.4. Group R-mode dendrogram utilizing the relative frequencies of nine palynomorph groups of the fossil assemblage. [Ward minimum variance method is used].

Associations 3 and 4 are typical of tree communities. The "triporate" association is dominated mostly by triporates and polyporates of Betulaceae (such as *Betula*-types, *Alnus*-types), secondly Juglandaceae (*Carya*-types, *Pterocarya*-types, *Platycarya-Plicatopollis*-types, *Engelhardtia*-types) and rarely Ulmaceae and other families of tree pollen. Spores are also fairly common, suggesting moss and ferns made up parts of the ground cover. Association 4 includes rare to uncommon non-triporate pollen taxa. Similarity in the pattern of relative frequencies shows the consistent association of these rare to infrequent palynomorphs in association 4. Amalgamation of associations 3 and 4 is conceivably more credible because they both represent tree communities with deciduous and hardwood elements (whether the pollen have a triporate condition or not). In actuality, many of the palynomorphs in either cluster are observed concurrently in some horizons. Based on the relative frequencies, these associations do not represent a distinct zone.

The familial cluster dendrogram (Fig. 4.5) shows the predominance and common occurrence of the Betulaceae family throughout the section since it clusters alone. Members of the ?Gentianaceae (*Pistillipollenites* spp.) make another distinct group that also clusters alone but is shown to be more similar to the third group, Juglandaceae and other families that cluster together.

On a species level, the triporate cluster dendrogram (Fig. 4.6) is more complicated and difficult to interpret. Clearly, *Alnipollenites verus* is an ubiquitous form in the section and has the highest relative frequencies among all triporates in virtually all horizons. Other species, *Trivestibulopollenites claripites, Momipites microfoveolatus, Myrica-Corylus*-types (*Myricipites annulites, Triatriopollenites* spp., and

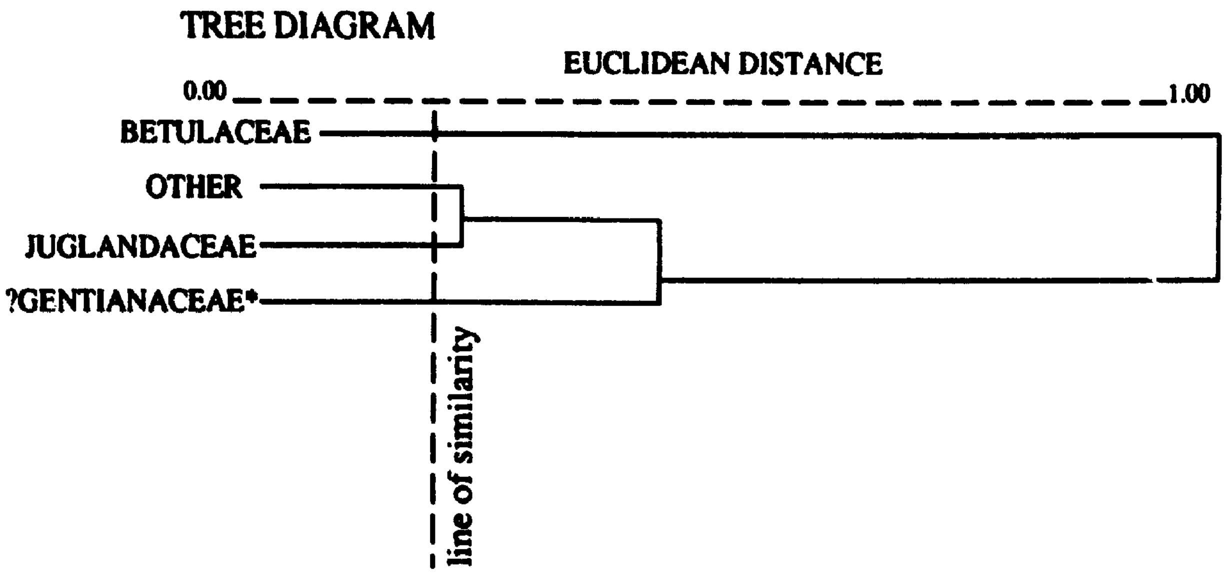
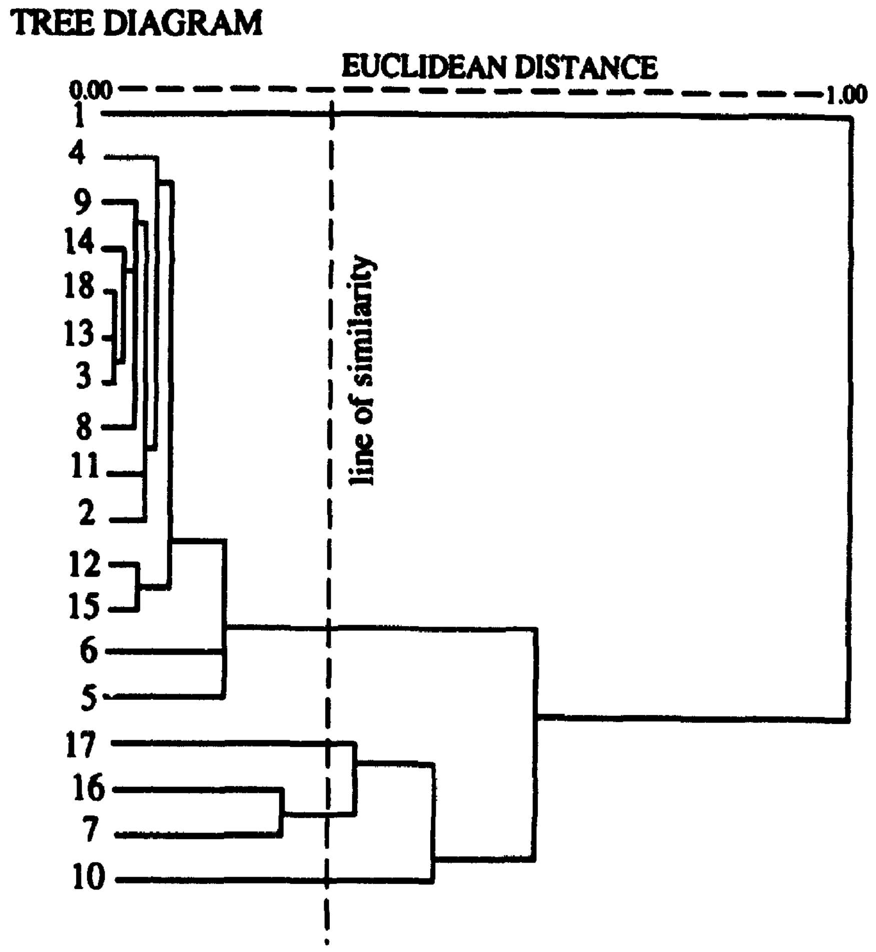


Figure 4.5. Family R-mode dendrogram utilizing relative frequencies of families with triporate members. [Ward minimum variance method is used].

* the fossil pollen, *Pistillipollenites*, is included in this family.



SPECIES:

1. *Alnipollenites verus*
2. *A. trina*
3. *A.* sp. A
4. *Carpinipites ancipites*
5. *Caryapollenites viridifluminipites*
6. *Momipites microfoveolatus*
7. *Myricipites annulites*
8. *Paraalnipollenites* sp.
9. *Platycaryapollenites* sp. cf. *P. platycaryoides*
10. *Pistillipollenites macgregorii*
11. *P.* sp. A
12. *Plicatopollis* sp. of the *P. plicata-* type
13. *Santalacites* sp.
14. *Subtriporopollenites anulatus*
15. *Triatriopollenites* spp. cf. *T. arboratus*
16. *Triporopollenites mullensis*
17. *Triivestibulopollenites claripites*
18. *Ulmipollenites undulosus*

Figure 4.6. Species R-mode dendrogram utilizing relative frequencies of eighteen triporate species. [Ward minimum variance method is used].

Triporopollenites spp.) and *Caryapollenites viridifluminipites* are also prevalent forms, clustering together based on similar lower frequencies.

The cluster analyses show that *Pistillipollenites macgregorii* also clusters alone because it is a very rare form in any horizon except in Nb, where relative frequencies reach 43% of the total palynomorphs counted. However, it is difficult to explain the clustering of *P.* sp. A with the large association of rare triporates except that it is also uncommon but is restricted to a single horizon, Nb.

CHAPTER 5. DISCUSSION

5.1 AGE

Based on the observed triporate palynomorphs in this study, an Early to Middle Eocene age, possibly Late Eocene is suggested for the Fossil Forest Hill area. This age is supported by the presence of triporate pollen *Pistillipollenites macgregorii*, *Plicatopollis* sp. of the *P. plicata*-type, *Platycaryapollenites* sp. cf. *P. platycaryoides*, *Thomsonipollis* sp., *Paraalnipollenites* sp., *Momipites coryloides* as well as with other non-triporate pollen types such as *Intratriporopollenites vescipites, I. crassipites, Tricolporopollenites kruschii, Faguspollenites* sp., *Juglanspollenites* sp. and *Tsugapollenites* sp. (Wodehouse, 1933; Hills, 1965; Hopkins, 1969; Rouse and Srivastava, 1970: Nichols, 1973; Elsik, 1974; Nichols and Ott, 1978; Frederiksen and Christopher, 1978; Choi, 1983; McIntyre, 1991). Though many of these elements are common in the Eocene and Oligocene (e.g. *Caryapollenites viridifluminipites, Intratriporopollenites vescipites*), distinctive Oligocene forms (e.g. *Boisduvalia clavatites, Saxonipollis saxonicus, Fisheripollis undulatus* and *Diervilia echinata*; Piel, 1971; Hopkins *et al.*, 1972; Rouse, 1977; Ioannides and McIntyre, 1980) are characteristically absent from the Fossil Forest Hill assemblages. McIntyre (1991) contends that, although many of the pollen taxa present in the fossil forest strata are important members of Eocene assemblages in the Arctic and farther south, they are not necessarily restricted to the Eocene. As well, many constituents of the Fossil Forest Hill assemblages are similar to those observed in the Eocene microfloral assemblages at Strand Fiord, Axel Heiberg Island and Strathcona Fiord, Ellesmere

Island (Choi, 1983; Ricketts and McIntyre, 1986).

Platycaryapollenites appears to be restricted to between the Late Paleocene and Middle Eocene throughout North America (Hopkins, 1969; Nichols and Ott, 1978; Choi, 1983), possibly as old as latest Cretaceous (Choi, 1983). *Platycarya*-like pollen first occurs in the fossil record at or slightly below the Paleocene-Eocene boundary (Frederiksen and Christopher, 1978; Wing and Hickey, 1984; Manchester, 1987) and then became abundant in the later Early Eocene (Wing and Hickey, 1984). Although not reported by McIntyre (1991), *Platycaryapollenites* was observed rarely in the Fossil Forest Hill samples in this study. It has also been reported to occur in very low frequencies at Strand Fiord, Axel Heiberg Island and Bay Fiord, Ellesmere Island (Choi, 1983).

Pistillipollenites macgregorii provides important evidence for an Eocene age because this species is not known from rocks younger than the Middle Eocene (Rouse, 1962; Hopkins, 1969; Rouse and Srivastava, 1970; Rouse, 1977), although some workers (Ricketts and McIntyre, 1986; Stockey and Manchester, 1988; Rouse and Mathews, 1988) have suggested a slightly extended range into the Late Eocene. The only reported Cretaceous *Pistillipollenites* is from the Cenomanian of Oklahoma (Hedlund, 1966) but this genus has been generally accepted as an early Tertiary form. The single occurrence of *Diervillapollenites* sp. at the base of the partial section is believed to be Eocene based on its association with *P. macgregorii*. The only other Eocene occurrence of fossil *Diervilla*-type pollen was reported by McIntyre (1991) also in the Geodetic Hills fossil forest succession. However, among Oligocene assemblages, Ioannides and McIntyre (1980) documented the significant occurrence of *Diervilla enchinata* which had not been recorded from pre-Oligocene rocks (Piel, 1971; Rouse, 1977; Ioannides and McIntyre, 1980). Other triporate genera that are common constituents of Early Eocene assemblages include *Thomsonipollis* (Elsik, 1968b, 1974; Srivastava, 1972b), *Momipites coryloides* (Wodehouse, 1933; Nichols, 1973; Frederiksen and Christopher, 1978), *Paraalnipollenites* (Rouse and Srivastava, 1972; Wingate, 1983) and *Plicatopollis* (Frederiksen and Christopher, 1978; Wingate, 1983). A similar form of *Paraalnipollenites* sp. was observed only in the Eocene of Nevada (Wingate, 1983). Ioannides and McIntyre (1980) reported *Paraalnipollenites alterniporus* from the Eocene of the Yukon, although Rouse and Srivastava (1972) strongly favoured a Paleocene age for their Yukon material based on palynomorph assemblages that included *Paraalnipollenites confusus*.

The presence of the spore *Cicatricosisporites* (Hopkins, 1969; Choi, 1983) and fungal elements *Striadiporites* (Elsik and Jansonius, 1974; Ioannides and McIntyre, 1980) and *Ctenosporites* (Elsik and Jansonius, 1974; Norris, 1986) also support an Eocene age. On the Pacific coast, *Cicatricosisporites* has a stratigraphic range from the Upper Eocene or Lower Oligocene (Hopkins, 1969), however, Frederiksen (1980), Srivastava (1972b) and Elsik (1968a) suggested that this genus has no stratigraphic value on the Gulf Coast and in South Carolina. *Cicatricosisporites* has also been considered to be a Cretaceous form in Arctic assemblages (Choi, 1983). Both fungal elements first appear in the Eocene: *Striadiporites* is Early Eocene to Recent (Elsik and Jansonius, 1974) and *Ctenosporites*, Middle or Late Eocene to

Early Oligocene (Elsik and Jansonius, 1974; Norris, 1986).

The absence of exclusively Cretaceous palynomorphs (e.g. *Aquilapollenites, Nudopollis, Expressipollis*) implies that the assemblage is younger than the Cretaceous (Ioannides and McIntyre, 1980; Choi, 1983). Marine dynoflagellate cysts (such as peridinioids and hystrichospheres) and acritarchs were not observed, although very rare reworked Cretaceous dynoflagellate cysts, spores and pollen were present (e.g. *Complexipollis*) at the top of the section (A horizon).

The strata of the fossil forest succession belong to the Buchanan Lake Formation (Ricketts, 1991) and the palynoflora within a few sections has been determined to be Middle Eocene age but not older, possibly early Late Eocene at the top of the section (Ricketts and McIntyre, 1986; McIntyre, 1991; Ricketts, 1991). There is no evidence to suggest that the leaf litter section is as young as the Oligocene. Based on structural and palynological evidence, Ricketts and McIntyre (1986) and Ricketts (1986, 1987, 1991) concluded that the deposition of the Buchanan Lake Formation occurred during the Middle or Late Eocene, coinciding with the thrusting and associated uplift of the Princess Margaret Arch. Bustin (1982) reported a Miocene or Pliocene age for strata just east of Geodetic Hills based on microfloral determinations but these assemblages were recently shown to be Middle Eocene in age (Ricketts and McIntyre, 1986). Hills and Bustin (1976) also considered a Miocene age for mummified wood and spruce cones of the Beaufort Formation near the fossil forest site. Fossil Forest Hill plant macrofossils are estimated to be of Eocene age (Basinger, 1987, 1991).

Vertebrate fossils have not been found at the fossil forest section at the Geodetic Hills Locality (Basinger, 1991). Fossil fauna found on Ellesmere Island are believed to have been derived from deposits of the Iceberg Bay Formation (stratigraphically directly below the Buchanan Lake Formation) which are estimated to be Early or early Middle Eocene in age (West *et al.*, 1977; McKenna, 1980; Estes and Hutchison, 1980). At Mokka Fiord, about 50 km southeast of the forest site, bone fragments were recovered from the Iceberg Bay Formation which are very similar to those found on Ellesmere Island (Basinger, 1991). No absolute ages are available because of the absence of igneous rocks in the area (Basinger, 1991). Vinson (1981), using paleomagnetic data, estimated a late Santonian to Middle Eocene age for the Eureka Sound Group at Bay Fiord area, Axel Heiberg Island.

5.2 ENVIRONMENT

Samples analyzed in this study were consistently devoid of marine palynomorphs, strongly suggesting that a non-marine depositional environment prevailed in the Fossil Forest Hill area during the early Tertiary. Since the modern counterparts of the fossil triporate genera represent an assemblage of plants that inhabit floodplains adjacent to large river systems (Farley, 1990; Francis, 1991; Basinger, 1991), it is probable that the paleoflora also occupied a similar environment. Palynological evidence for fluvial-floodplain deposition in the Eureka Sound deposits include the frequent occurrence of spores, tetrads (Ericaceae) and relatively large pieces of cuticle, considerable cellulosic material and relatively low frequencies of broken pollen grains (Batten, 1974). Q-mode cluster analyses support these conclusions, revealing a cyclical pattern to the sequence. Such a pattern is consistent with that of a floodplain.

An early successional forest (an alder- or gentian-type forest) was replaced by a climax-type forest (a taxodiaceous or birch/hickory-type forest) which was followed by a major period of erosion. The dominance of a particular forest-type depended on the prevailing moisture regime and the proximity of the vegetation to lakes or rivers. The cycle repeats about three to five times on the Q-mode hierarchial diagrams (Figs. 4.1, 4.2, 4.3), and according to Francis (1991), the cycle may have occurred as many as 30 times. During low flow levels of adjacent rivers, or large streams (a hiatus of stable hydrologic conditions), the vegetation probably grew uninterrupted from an early stage forest to a climax forest type (Francis, 1991; McIntyre, 1991). The erosional period that followed was possibly the result of severe flooding in the area. During high flow levels, the rivers would have overflowed their banks, depositing fine-grained sediments as crevasse splays and flooding the existing vegetation (Galloway and Hobday, 1983; Basinger, 1991; Ricketts, 1991). Such floods are stress factors that can shape the formation of the plant community (Riclefs, 1979) and provide many early successional sites. Periodic floods may have killed the trees and quickly buried the forests at the same time, sealing the forest from effects of decay, oxidation and redeposition (Francis, 1988, 1990). The exact nature and the extent of the flooding is unknown, but it was likely frequent and extensive, covering the entire vegetation (Francis, 1991).

The sedimentological evidence also suggests that the likely landscape is that of a floodplain (Ricketts and McIntyre, 1986; Francis and McMillan, 1987). Much of the sediment enclosing the leaf and woody layers is indicative of overbank deposition (Ricketts, 1986; 1991; McIntyre, 1991) on crevasse splays along main fluvial channels (Ricketts, 1991). The sediments are alternating shales and sandstones and suggest that fluctuations in the depositional surface relative to the surrounding uplands occurred regularly, causing complete changes in both the physical and floral landscape (Frances and McMillan, 1987).

The site of deposition is envisioned to have been covered with lowland deciduous trees interspersed with fairly widespread freshwater ponds or shallow lakes into which flood waters would have carried unsorted detritus, bisaccate pollen and other "upland" pollen grains (Spicer and Greer, 1986). Transport to the depositional site was probably accomplished largely by streams or rivers (Francis, 1991). The constantly changing local depositional environment was primarily responsible for the mixed mosaic nature of the deciduous forest and shrub association (McIntyre, 1991). Mixed evergreen forests (including the bisaccates *Picea* and *Pinus* and the triporates *Carya, Carpinus,* etc.) probably inhabited cooler, in more elevated, well-drained areas nearby (Fig. 5.1). It is likely that deposition occurred either under quiescent conditions or perhaps involved short transportation distances (Batten, 1974; Spicer and Greer, 1986). Well preserved plant macrofossils obtained from the fossil forest site also suggests limited transportation (Basinger, 1991). It is likely that the plant macrofossils were buried *in situ*, e.g. stumps, leaves, cones, fruits or deposited nearby

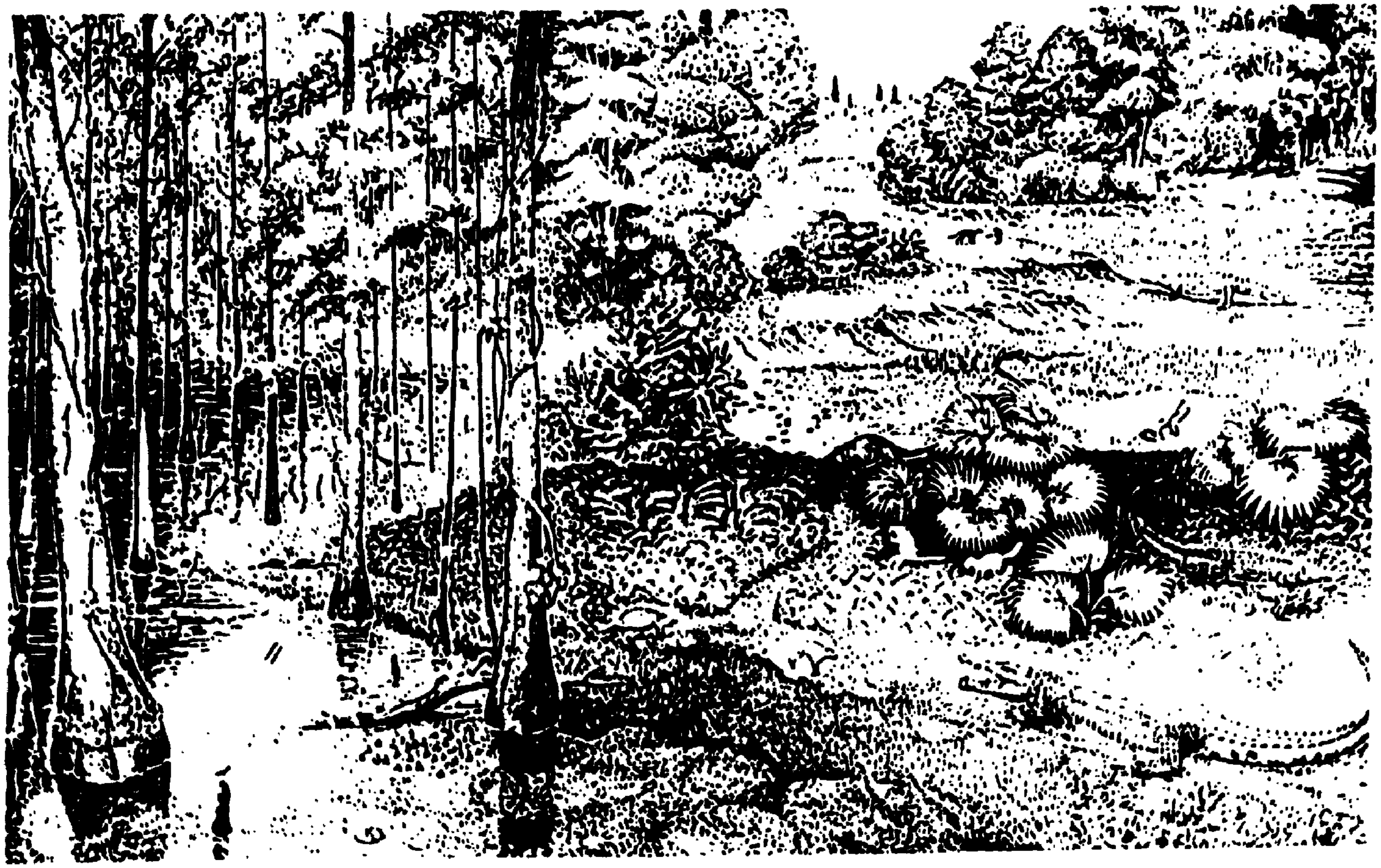


Figure 5.1. Paleoenvironmental reconstruction envisioned for the Fossil Forest Hill site (from Erickson, 1991). Deciduous and hardwood trees inhabit the moist lowlands (left background), with taxodiaceous trees dominating in or near the rivers or lakes (left foreground). Herbaceous plants are a significant part of the ground cover (right foreground). In the nearby uplands, pinaceous forests are important (right background).

their growth position (Francis, 1991; Basinger, 1991, Francis and McMillan, 1987).

Certain spores and pollen were apparently locally concentrated, deposited in nearby lakes, ponds and abandoned channels (Farley, 1990). The predominance of ferns (*Osmunda*-type, *Laevigatosporites*), fossil moss (*Sphagnum*-type), trees and shrubs of fossil triporate genera (*Plicatopollis, Alnipollenites, Ulmipollenites, Platycaryapollenites, Pistillipollenites*) suggests that there were numerous, local swampy depositional basins, most likely on major drainage floodplains, which supported their own local floras (Martin and Rouse, 1966; Spicer and Greer, 1986; Farley, 1990). The wide range, dominance and abundance of fossil *Alnus, Betula, Myrica, Carpinus, Corylus, Engelhardtia* (and rare *Diervilla)* over many horizons, suggest the presence of a shrubby woodland of marginal-type environments by streams or rivers (Grimm, 1957; Rouse, 1962; Martin and Rouse, 1966; Hopkins, 1969; Lewis *et al.*, 1983; Farley, 1990; McIntyre, 1991). Many taxodiaceous genera are members of the stream bank community (Chu and Cooper, 1950; Rouse, 1962; Martin and Rouse, 1966; Hou, 1983), while it has been suggested that the observed fungal elements were possibly waterborne (Day, *pers. comm.*, 1991). The presence of all these elements is strong evidence that the terrain was lowland, some of it covered by open water. Basinger (1991) suggested that the forest floor may have been saturated with water. Such an environment would most likely be subject to more frequent and/or prolonged flooding.

Rare bisaccate pollen in the assemblages is ecologically significant. Their generally low numbers and the lone clustering of this pollen as shown by the R-mode dendrograms (Fig. 4.4), support the idea that they are allochthonous elements in the fossil assemblages (Spicer and Greer, 1986; Farley, 1990). This strongly implies that the bisaccate pollen is not associated with the fossil assemblage and was likely derived from an external source and transported into the sedimentary basin. Plant taxa from local sources would probably dilute incoming "extrabasinal" taxa to such an extent that the latter would be rare or unlikely to be detected in a fossil assemblage (Spicer and Greer, 1986). By far the greatest number of these grains was derived from a species referable to modern *Picea* (and to a lesser extent *Pinus*, and rarely *Podocarpus, Tsuga, Abies, ?Larix*). Rare bisaccates and other upland pollen such as *?Ostrya, Carya, Carpinus, Corylus* and non-triporates such as *Quercus*, suggest relatively long distances of transportation (Hedlund, 1966; S.T. Andersen, 1974). Such "upland" pollen in the Fossil Forest Hill assemblages may suggest the importance of pinaceous forests mixed with deciduous trees, at least in the surrounding sedimentary basins. This environment is likely to have been cool, temperate, well-drained and less prone to flood disturbance and depositional events (Spicer and Greer, 1986). It is unlikely that "upland" pollen represent an *in situ* component of the fossil assemblage, because their ecological requirements and environmental preferences are different from those of the lowland flora.

5.3 CLIMATE

At present, triporate pollen taxa occur in a variety of habitats including uplands, swamps and stream margins (Table 5.1). Many of what are believed to be the modern-day analogues of the studied fossil triporate genera seem to favour a warm temperate climate bordering on subtropical. This subtropical influence is supported by the presence of *Myrica, Platycarya, Carya, ?Zelkova* and *Pistillipollenites*. The mixture of relatively cooler climate species (e.g. spruces, pines, ironwood, hopbeam) with relatively warmer climate species (e.g. swamp cypress) may suggest that a combination of vegetation grew on low moist ground and a portion of the pollen drifted in from areas of higher elevation (Spicer and Greer, 1986). Pinaceous trees and other such "upland" trees were excluded from the early Tertiary polar lowland floras (Basinger, 1991). However, if these cool temperate elements were part of the local vegetation, their presence in the palynoflora may imply a wider climatic and ecological tolerance for the parent plants in the Tertiary (Martin and Rouse, 1966; Hopkins, 1969; McIntyre, 1991).

Many of the triporate genera (e.g. *Ulmus, Carya, Corylus, Alnus*) are included in most modern temperate mixed forests or warm temperate wetland forests that now inhabit southeastern North America and eastern Asia, distributed over mid-latitudes (30° - 50° N; Martin and Rouse, 1966; Willis, 1973; Wolfe, 1979, 1980; Lewis *et al.*, 1983; Mabberley, 1987; McIntyre, 1991). Temperate deciduous forests reach their maximum development in areas with warm wet summers and relatively cold winters (Bartholomew *et al.*, 1983). Summers for the Arctic Tertiary region are suggested to

Table 5.1A. Ecological ranges and habitats of modern triporate genera whose fossil counterparts have been identified from the leaf litter succession, Buchanan Lake Formation (after Grimm, 1957; Simpson, 1961; Rouse, 1962; Hills, 1965; Martin and Rouse, 1966; Rouse and Srivastava, 1972; Hopkins, 1969; Willis, 1973; Hou, 1983; Srivastava, 1984; Wing and Hickey, 1984; Mabberley, 1987; Rouse and Mathews, 1988; Wing and Daghlian, 1989; Barnett, 1989; Farley, 1990; McIntyre, 1991).

TRIPORATE			**temperate**		**HABITAT AND**
TAXA	**trop**	**subtrop**	**warm**	**cool**	**GEOGRAPHIC RANGE**
Alnus			X	X	variable climate, north temperate swamps, wet woods, wet slopes, stream margins and banks, rivers, along streams or swamps; prefer moist soils, sites of early successional stages preceding forest development; forest margins or shrub vegetation; cosmopolitan Northern Hemisphere, south to central America, Andes Mts, Indo-China
Betula			X	X	moist uplands to bogs, wooded swamps; more coastal brackish waters; Northern Hemisphere, Malaysia, east Asia, western & eastern North America, Europe
Carpinus				X	moist upland woodlands to coastal swamps; north temperate Northern Hemisphere, North America, Europe, chiefly East Asia
Corylus			X	X	moist thickets, woodlands; north temperate Northern Hemisphere; Europe, Asia, North America
Engelhardtia			X		woodland and/or shrubland; more warm than temperate, Himalayas to Malaysia
Myrica		X	X	X	variable habitats, subcosmopolitan (not in the Mediterranean, Australia, central Europe, southwest Asia or North Africa)
Comptonia			X	X	eastern North America, moist sandy soils
Ostrya				X	uplands, open well-drained woods northern temperate

Table 5.1B.

TRIPORATE TAXA	**trop**	**subtrop**	**temperate**		**HABITAT AND GEOGRAPHIC RANGE**
			warm	**cool**	
Carya		X	X	X	variable habitat and climate; humid, summer rains, winters dry; relatively cooler and elevated areas, open forests, moist woodlands and stream banks; Northern America, Europe, chiefly east Asia
Platycarya		X	X	X	wetland, moist thickets, ephemeral habitats, open and early successional habitats; East Asia (Japan, China and Korea)
Thesium			X	X	subcosmopolitan; Old World (Europe, Africa, Asia, Australia)
Diervilla			X	X	shrubland, lowlands areas, temperate moist regions; along borders of woodlands, wayside thickets, dry rocky places throughout mountains and foothills. North America
gentian-type *(Pistillipollenites)*		X	X		ponds, swamps, backswamps, lowland areas of sedimentation, pondfills having few conifers, grassy areas; early successional niches humid climate, high rainfall, much fog, warm temperate bordering on subtropical
Planera			X		North America, southern United States
Ulmus			X	X	warmth loving, dry soil, relatively cooler and elevated areas, woodlands, northern temperate; Europe, Asia, northern Africa, eastern North America
Zelkova		X	X		moist woodlands; west and east Asia, Caucasus Mts., eastern Mediterranean, east to central China, Japan
Phyllostylon		X			Paraguay, west India
Celtis	X	X	X	X	cosmopolitan; wet lowlands to rock hills and barrens Northern Hemisphere, South Africa

have been very warm to hot (greater than 18° C; Wolfe, 1985; McKenna, 1980) with heavy rainfall (1000 -1500 mm; McIntyre, 1991), while winter temperatures may have dropped to as low as -3° C (McKenna, 1980; Wolfe, 1980; Schweitzer, 1980). Since taxodiaceous representatives have the narrowest ecological ranges, based on their present limited distribution (Chaney, 1948; Chu and Cooper, 1950; Schweitzer, 1980), their lowest temperature limits (an absolute low of -1.7° C, Chu and Cooper, 1950; a mean annual temperature range of 27° C, Wolfe and Tanai, 1980) represent the coolest minimum of the total floral assemblage.

The significant numbers of broad-leaved angiosperms in the Tertiary flora of Axel Heiberg Island, their deciduous habit and the wide growth rings indicate that precipitation fluctuated significantly seasonally, from being low or absent in the winter to heavy in the summer (Barron, 1984). The deciduous habit of the fossil plants may also be related to the unavailability of water during much of the winter (Raven and Curtis, 1970; Francis, 1988, 1990, 1991). It has been suggested that the moisture must have been abundant in both the soil and atmosphere, also based on the presence of the cypress trees (Chu and Cooper, 1950; Schweitzer, 1980).

The present-day *Metasequoia* forests of central China appear to closely resemble those believed to have occupied the Arctic during the Tertiary, but there are no modern analogues occurring in a similar warm, wet climatic regime, so close to the North Pole (Donn, 1982; Wolfe, 1985; Francis, 1988). These modern Asiatic forests occur at high altitudes (Chu and Cooper, 1950) although it is not known if altitude effects are significant. It is notable that the Sverdrup basin in which the fossil forests are found is 2000 to 3000 m above sea level (GSC Preliminary Map 36-1959). The fossil forests are characteristically rich in floristic composition, similar to polar fossil forests (Chaney, 1948; Schweitzer, 1980; Hsu, 1983; Hou, 1983; Tiffney, 1985) but there are slight vegetational differences, including the absence of beeches (Hou, 1983). Contemporary North American temperate forests (e.g. *Sequoia* forests of the Pacific coast, *Taxodium* forests of southeastern U.S.) are comparable but they lack significant constituents of the Arctic Tertiary forests, including *Metasequoia, Glyptostrobus, Platycarya, Pterocarya* (Chu and Cooper, 1950; Schweitzer, 1980), currently limited to eastern Asia. Natural stands of *Metasequoia* now occur with hardwoods on moist floodplains at high altitudes (Chaney, 1948; Chu and Cooper, 1950). Mountain ranges surround these relict communities of *Metasequoia*, and protect them from the climatic extremes which characterize other inland environments (Chu and Cooper, 1950). During early Tertiary time, these *Metasequoia* conifers with nearly the same genera of hardwoods were widely distributed at high latitudes, suggesting that they were parts of widespread contemporaneous flora (Axel Heiberg and Ellesmere Islands, Choi, 1983; Ricketts and McIntyre, 1986; McIntyre, 1991; Spitzbergen, Manum, 1962; Schweitzer, 1980; Banks Island, Doerenkamp *et al.*, 1976; Alaska, Wolfe, 1977; British Columbia, Martin and Rouse, 1966; west Greenland, Koch, 1964, etc.). The few existing sites of *Metasequoia* significantly suggest that the required climatic conditions and similar vegetational types now exist only in a single isolated valley in central China.

Many of the modern genera comparable to the observed fossil triporate genera occupy a small fraction of their former geographic and climatic ranges

(Simpson, 1961, Martin and Rouse, 1966; Hopkins, 1969; Choi, 1983). For example, *Carpinus* (Wodehouse, 1933; Hopkins, 1969), *Betula* (Hopkins, 1969), *Engelhardtia* (Nichols, 1973; Nichols and Ott, 1978), *Carya* (Hopkins, 1969; Nichols and Ott, 1978), *Platycarya* (Hopkins, 1969; Wing and Hickey, 1984; Manchester, 1987) and the taxodiaceous representatives occupy only a small portion of their former ranges. At present, *Platycarya* and *Engelhardtia* as well as *Metasequoia, Glyptostrobus,* and *Pterocarya* are considered contemporary Asian elements. The climatic cooling that began in the late Tertiary (Dorf, 1969), together with glaciation in the Pliocene (Frakes, 1979) may have resulted in the elimination and/or withdrawal of virtually all floral elements from the Arctic region (Wolfe, 1978; Basinger, 1991). Species of Arctic willow (*Salix arctophila, S. herbacea, S. planifolia,* Salicaceae, Porsild, 1973; Francis, 1990; Basinger, 1986), ground birch (Porsild, 1973; Francis, 1990) and heath (Ericaceae, Porsild, 1973) are the only remnants of the forests of Axel Heiberg Island. They occur as dwarf trees or shrubs, limited in growth primarily by frozen sterile soil and low air temperatures combined with strong Arctic winds (Porsild, 1973), but apparently not by sunlight (Francis, 1990).

Climatic deterioration (Dorf, 1969), either by declining winter temperatures (Basinger, 1991) or by declining summer temperatures (Wolfe, 1987) or both, and decrease in the amount of rainfall (Leopold and MacGinitie, 1972; Schweitzer, 1980), resulted in replacement of the temperate deciduous forest by hardier, better-adapted, pinaceous evergreen species and eventually by a tundra vegetation by the end of the Pliocene (Basinger, 1991). The fossil forest sequence likely represents a warmer interval, based on the main occurrence of warm temperate elements. Therefore, the Fossil Forest Hill flora suggests that the Geodetic Hills Locality experienced a climate that was significantly warmer and moister during the early Tertiary than it is today.

5.4 PALEOECOLOGY

Substantial forest growth, reflected in the large size and density of the trees (Francis and McMillan, 1987; Francis, 1988, 1990, 1991) indicates that optimal growing conditions must have existed during the Eocene (McKenna, 1980; Francis and McMillan, 1987; Francis, 1988, 1990, 1991). Winters were presumably mild with limited periods of temperatures below 0° C (Chaney, 1948; Chu and Cooper, 1950; Hou, 1983) and summers were warm (greater than 18° C) with a high rainfall (Francis, 1990; McIntyre, 1991). Fossil vertebrate fauna recovered from the early Tertiary deposits of Ellesmere Island includes alligators, lemurs, hippopotamus, rhinoceros, rodents, birds and tortoises, also supporting the warm temperature estimates (Dawson *et al.*, 1976; West *et al.*, 1977; McKenna, 1980; Estes and Hutchison, 1980; West *et al.*, 1981; Hickey *et al.*, 1983). During the relatively cold dark winters, the fauna could have hibernated or migrated to more southerly latitudes (Barron, 1984). In fact, many of the fossil fauna have modern representatives which do hibernate during times of cooler climate or adverse conditions (McKenna, 1980).

Assuming that the paleolatitude has remained nearly constant (Wynne *et al*, 1988; Embry and Osadetz, 1988; Irving and Wynne, 1991), a light regime similar to the present would have prevailed during the early Tertiary. The present-day photoperiods of the Arctic summers are essentially the same as those found at more southerly latitudes in a year (Francis, 1990; Basinger, 1991). The limited amount of light in the winter may not have been significant to the fossil flora because of the deciduous nature of most plants (Basinger, 1991; McIntyre, 1991).

Paleobiologic adaptations can help to explain the existence of these warm temperate forests at such high latitudes (Barron, 1984; Francis, 1988). Francis (1991) has suggested that the trees probably had a pronounced conical shape and were widely-spaced to allow interception of maximum incident light with minimum mutual shading. The fact that trees near the present-day treeline have adopted a pronounced conical shape (Francis and McMillan, 1987; Francis, 1988, 1991) supports this hypothesis. Physiognomic or leaf morphology suggests that fossil leaves found in high latitude areas possessed morphotypes (e.g. large leaf size) similar to those trees and plants adapted to reduced light, yet warm climate regimes (e.g. the dense tropical jungle understory; Dorf, 1969; Wolfe, 1985). The tree canopies are believed to have been very extensive, possibly closed, in order to intercept a maximum amount of light, thereby, allowing a small portion of incident light to reach the forest floor (Wolfe, 1985). Although, the light attenuation on the forest floor would have limited establishment and survival among the deciduous plants, low light levels could have been counteracted by relatively warm conditions (because respiration rates are depressed by cold; Spicer, 1989) and by the abundance for water and essential nutrients (Raven and Curtis, 1970). The development of understory growth is believed to have been limited by moisture (saturated soils and frequent flooding) not light, based on the absence of herbaceous remains in the fossil leaf litter in the area (Basinger, 1991). The undergrowth was probably sparse in the absence of winter light (Wolfe, 1985).

The deciduous habit may have been an adaptation to the reduced winter photoperiod, allowing the trees to conserve food and become dormant during the polar winters (Wolfe, 1979, 1985). Their survival probably depended highly on a combination of their frost hardiness (Basinger, *pers. comm.*, 1991) and their ability to metabolically "rest" during extended cold dark periods (Vaartaja, 1959). During the summer, they could have adapted to continuous daylight with fast and uninterrupted growth (Axelrod, 1984; Francis, 1986, 1990, 1991). There may have been no need for a dormancy response as in modern trees based on the absence of prominent late wood, indicating the lack of low winter temperatures (Basinger, 1991).

Certain woody plants such as beech, basswood, blackgum, hemlock, fir, spruce and sugar maple are considered shade tolerant (Raven and Curtis, 1970); all of these are believed to have been part of the fossil forest. Wing and Hickey (1984) suggested that living and fossil *Platycarya* colonized relatively open areas where low light levels did not limit growth.

Based on this scenario, it has been suggested that the fossil trees were photoperiodic ecotypes (Francis, 1988), i.e. were specially adapted to growing rapidly during continous daylight (Vaartaja, 1959).

CHAPTER 6. SUMMARY AND CONCLUSIONS

A palynological study of a fossil forest sequence from the Geodetic Hills locality, Axel Heiberg Island, N.W.T. was undertaken with its focus on the triporate pollen taxa. Previous work in the area has concentrated on plant macrofossils and fossil sediments. Although palynological investigations have been conducted, they have been preliminary and without adequate systematic treatment. This study has provided the first detailed palynological study of the research site. This study systematically describes and documents thirty-six species of eighteen triporate genera, obtained from six leaf litter horizons of the fossil forest sequence. Most of the triporate pollen taxa represent the Betulaceae, Juglandaceae, ?Gentianaceae and Myricaceae. Triporate pollen assemblages are estimated to be Early to Middle Eocene in age, possibly Late Eocene, in conjunction with other non-triporate forms. These assemblages are comparable to other Eocene assemblages of the Arctic, western Canada and southern United States. The absence of marine palynomorphs indicates a non-marine environment.

The palynoflora represents a tree community composed essentially of deciduous and hardwood elements, with shrubs a significant element on the forest floor. Many of the modern counterparts to the fossil triporate pollen genera represent an assemblage of woody plants that inhabits moist lowland areas near fluvial systems, such as fluvial-floodplains, with a prevailing warm temperate climate bordering on subtropical. Statistical analyses support the interpretation of a floodplain environment and suggest that swampy conditions prevailed. Nearby, mixed pinaceous forests inhabited cool uplands surrounding the sedimentary basin. Among the modern temperate forests of the Pacific coast, southeastern North America and eastern Asia, the *Metasequoia* forests of central China most resemble the Arctic Tertiary forests. It is likely that the climatic and environmental conditions in which these contemporary forests exist are similar to those that prevailed during the Eocene.

The fossil forests of eastern Axel Heiberg Island were composed of deciduous and hardwood trees and shrubs that lived on floodplains under a warm temperate climate during the early Tertiary. The few remnants of the fossil forests in the Arctic region, where only tundra currently exists, indicate that the climatic and environmental conditions of the area have changed drastically since the Middle Eocene. Global cooling and glaciation resulted in lower average temperatures and reduced moisture in the Arctic region, causing virtually all elements of the fossil forest either to be eliminated or to withdraw to the regions they now occupy. Conditions were considerably warmer and more humid than at present. Such conditions were amenable to the growth and proliferation of warm temperate forests, suggesting that the fossil forests existed during a warm interval in the early Tertiary.

REFERENCES

Andersen, S.T.
1974 Wind conditions and pollen deposition in a mixed deciduous forest. Grana, 14:57-63.

Anderson, R.Y.
1960 Cretaceous-Tertiary palynology, eastern side of the San Juan Basin, New Mexico. State Bureau of Mines and Minerals Resources. New Mexico Institute of Mining and Technology; Campus Station, Socorro, New Mexico, Memoir 6, p. 1-59.

Axelrod, D.I.
1984 An interpretation of Cretaceous and Tertiary biota in polar regions. Palaeogeography, Palaeoclimatology, Palaeoecology, 45:105-147.

Balkwill, H.R.
1978 Evolution of Sverdrup Basin, Arctic Canada. American Association of Petroleum Geologists Bulletin, 62:1004-1028.

Balkwill, H.F., and Bustin, R.M.
1975 Stratigraphic and structural studies, central Ellesmere Island and eastern Axel Heiberg Island, District of Franklin. Geological Survey of Canada, Paper 75-1A, p. 513-517.

Barnett, J.
1989 Palynology and paleoecology of the Tertiary Weaverville Formation, Northwestern California, U.S.A. Palynology, 13:195-246.

Barron, E.J.
1984 Climatic implications of the variable obliquity explanation of Cretaceous-Palaeogene high latitude floras. Geology, 12:595-598.

Bartholomew, J.C., Geelan, P.J.M., Lewis, H.A.G., Middleton, P., and Winkleman, (eds.).
1983 <u>The Time Atlas of the World, Comprehensive edition</u>. John Bartholomew & Sons Ltd. and Times Books Ltd., London, England, 227p.

Basinger, J.
1986 Our 'tropical' Arctic. Canadian Geographic, 106(6):28-37.

Basinger, J.
1987 Fossil flora of the Eocene Buchanan Lake Formation, Axel Heiberg Island, Canadian Arctic. Geological Association of Canada/Mineralogical Association of Canada, Annual Meeting, Saskatoon, Program with Abstracts, p. 23.

Basinger, J.
1991 The fossil forests of the Buchanan Lake Formation (Early Tertiary), Axel Heiberg Island, Canadian Arctic Archipelago: Preliminary Floristics and Paleoclimate. <u>In</u>: R.L. Christie and N.J. McMillan (eds.) <u>Tertiary Fossil Forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago</u>. Geological Survey of Canada, Bulletin 403, p. 39-65.

Bassett, I.J., Crompton, C.W., and Parmelee, J.A.
1978 Atlas of Airborne Pollen Grains and Common Fungus Spores of Canada. Biosystematics Research Institute, Ottawa, Ontario. Research Branch, Canada Department of Agriculture, Monograph No. 18, 321p.

Batten, D.J.
1974 Wealden palaeoecology from the distribution of plant fossils. Proceedings of the Geologists' Association, 85(Part 4):433-458.

Bratzeva, G.M.
1965 Pollen and spores in Maastrichtian deposits of the Far East. Geol. Inst. Trans. Akad. Nauk. SSSR 129, p. 1-42.

Bratzeva, G.M.
1969 Palynological studies of Upper Cretaceous and Paleogene of the Far East. Trudy Geol. Inst. Nauk, SSR, v. 207, 57p. [In Russian].

Brazier, M.D.
1980 Microfossils. George Allen & Unwin, Boston, p. 193.

Burdet, H.M., W.G. Chaloner, V. Demoulin, R. Grolle, D.L. Hawksworth, D.H. Nicolson, P.C. Silva, F.A. Stafleu, and E.G. Voss (eds.)
1987 International Code of Botanical Nomenclature. Fourteenth International Botanical Congress, Berlin, July-August, 1987. Koeltz Scientific Books.

Bustin, R.M.
1977 Eureka Sound and Beaufort Formations, Central Ellesmere and Axel Heiberg Islands, Canadian Arctic Archipelago. Unpublished M.Sc. dissertation, University of Calgary, 208p.

Bustin, R.M.
1982 Beaufort Formation, eastern Axel Heiberg Island, Canadian Arctic Archipelago. Bulletin of Canadian Petroleum Geology, 30:140-149.

Chaney, R.W.
1948 The bearing of the living *Metasequoia* on problems of Tertiary paleobotany. National Academy of Science Proceedings, 34:503-515.

Choi, D.K.
1983 Paleopalynology of the Upper Cretaceous-Paleogene Eureka Sound Formation of Ellesmere and Axel Heiberg Islands, Canadian Arctic Archipelago. Unpublished Ph.D. dissertation, The Pennsylvania State University, 580p.

Christie, R.L.
1988 Field studies at "Fossil Forest" sites in the Arctic Islands. In: Current Research, Part D, Geological Survey of Canada, Paper 88-1D, p. 57-60

Christie, R.L., and McMillan, N.J.
1991 Introduction. In: R.L. Christie and N.J. McMillan (eds.), Tertiary Fossil Forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Geological Survey of Canada, Bulletin 403, p. xiii-xvi.

Christopher, R.A.
1979 Normapolles and triporate pollen assemblages from the Raritan and Magothy Formations (Upper Cretaceous) of New Jersey. Palynology, 3:73-121.

Chu, K.L., and Cooper, W.S.
1950 An ecological reconnaissance in the native home of *Metasequoia glyptostroboides*. Ecology, 31:260-278.

Cookson, I.C., and Pike, K.M.
1954 Some dicotyledonous pollen types from Cainozoic deposits in the Australian region. Australian Journal of Botany, 2:197-219.

Crepet, W.L., and Daghlian, C.P.
1981 Lower Eocene and Paleocene Gentianaceae: floral and palynological evidence. Science, 214:75-77.

Crepet, W.L., Daghlian, C.P., and Zavada, M.
1980 Investigations of angiosperms from the Eocene of North America: a new juglandaceous catkin. Review of Palaeobotany and Palynology, 30:361-370.

Crepet, W.L., Dilcher, L., and Potter, F.W.
1975 Investigations of angiosperms from the Eocene of North America: a catkin with juglandaceous affinities. American Journal of Botany, 62:813-823.

Daghlian, C.P. and Crepet, W.L.
1986 Pollen structure and variability in *Pistillipollenites macgregorii*, a Paleogene gentian. American Journal of Botany, 73:698.

Dawson, M.R., West, R.M., Langston, W. Jr., and Hutchison, J.H.
1976 Paleogene terrestrial vertebrates: northernmost occurrence, Ellesmere Island, Canada. Science, 192:781-782.

Day, R.G.
1991 An overview of fossil fungi in the Geodetic Hills Fossil Forest, Axel Heiberg Island, N.W.T. In: R.L. Christie and N.J. McMillan (eds.), Tertiary Fossil Forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Geological Survey of Canada, Bulletin 403, p. 99-121.

Demchuk, T.
1988 A modified *Momipites - Caryapollenites* palynofloral lineage: Central Alberta Paleocene zonation. Palynology, 12:236. Abstract.

Doerenkamp, A., Jardine, S., and Moreau, P.
1976 Cretaceous and Tertiary palynomorph assemblages from Banks Island and adjacent areas (N.W.T.). Bulletin of Canadian Petroleum Geology, 24(3):372-417.

Donn, W.L.
1982 The enigma of high latitude paleoclimate. Palaeogeography, Palaeoclimatology, Palaeoecology, 40:199-212.

Dorf, E.
1969 Paleobotanical evidence of Mesozoic and Cenozoic climatic changes. Proceedings of North American Paleontological Convention, Chicago. Volume D, p. 323-346.

Edwards, K.J.
1981 The separation of *Corylus* and *Myrica* pollen in modern and fossil samples. Pollen et Spores, 22(2):205-218.

Elsik, W.C.
1968a Palynology of a Paleocene Rockdale lignite, Milam County, Texas. I: Morphology and taxonomy. Pollen et Spores, 10:265-313.

Elsik, W.C.
1968b Palynology of a Paleocene Rockdale Lignite, Milan County Texas. II: Morphology and taxonomy (end). Pollen et Spores, 10:599-664.

Elsik, W.C.
1969 An evaluation of *Engelhardtia* in the Gulf Coast Tertiary. Geological Society of America; Third Annual Meeting, South Central Section Program, p.10-11.

Elsik, W.C.
1974 Characteristic Eocene palynomorphs in the Gulf Coast, U.S.A. Palaeontographica Abt. B, v. 149:90-111.

Elsik, W.C., and Jansonius, J.
1974 New genera of Paleogene fungal spores. Canadian Journal of Botany, 52:953-958.

Embry, A.F., and Osadetz, K.G.
1988 Stratigraphy and tectonic significance of Cretaceous volcanism in Queen Elizabeth Islands, Canadian Arctic Archipelago. Canadian Journal of Earth Sciences, 25:1209-1219.

Erdtman, G.
1952 Pollen morphology and plant taxonomy: angiosperms - an introduction to palynology. Bol. Stockholm - Almqvist and Wiksell.

Erdtman, G.
1972 Pollen Angiosperms (An introduction to Palynology I). New York, Hafner, 553p.

Erickson, B.R.
1991 Flora and fauna of the Wannagan Creek Quarry: Late Paleocene of North America. Scientific Publications of the Science Museum of Minnesota, New Series, Volume 7, Number 3, 19p.

Estes, R., and Hutchison, J.H.
1980 Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. Palaeogeography, Palaeoclimatology, Palaeoecology, 30:324-347.

Faegri, K., and Iversen, J.
1964 Textbook of pollen analysis. Second edition, Hafner, New York, 237p.

Fairchild, W.W., and Elsik, W.C.
1969 Characteristic palynomorphs of the Lower Tertiary in the Gulf Coast. Palaeontographica Abt. B, 128(3-6):81-89.

Farley, M.B.
1990 Vegetation distribution across the early Eocene depositional landscape from palynological analysis. Palaeogeography, Palaeoclimatology, Palaeoecology, 79:11-27.

Fasbender, M.V.
1959 Pollen grain morphology and its taxonomic significance in the Emherstieae, Cynometreae, and Sclerolobieae (Caesalpiniaceae) with special reference to American genera. Lloydia (Cincinnati), 22:107-162.

Fischer, B.F.G.
1984 Stratigraphic and structural geology of the region surrounding Bunde and Bukken fiords, Axel Heiberg Island, Canadian Arctic. In: Current Research, Part A. Geological Survey of Canada, Paper 84-1A, pp. 309-314.

Fishbein, E., and Patterson, R.T. [*in press*]
Error weighted maximum likelihood (EWML): A statistically-based method to cluster quantitative micropaleontological data. Journal of Paleontology.

Forsyth, D.A., Asudeh, I., and Green, A.G.
1986 Alpha Ridge and Iceland - products of the same plume? Journal of Geodynamics, 6:197-214.

Fortier, Y.O., Blackadar, R.G., Glenister, B.F., Greiner, H.R., McLaren, D.J., McMillan, N.J., Norris, A.W., Roots, E.F., Souther, J.G., Thorsteinsson, R., Tozer, E.T. (eds.).
1963 Geology of the North-central Part of the Arctic Archipelago, N.W.T. (Operation Franklin). Geological Survey of Canada, Memoir 320.

Frakes, L.A.
1979 Climates throughout geological time. Elsevier Scientific Publishing Co., Amsterdam, 310p.

Francis, J.E.
1988 A 50-million-year-old fossil forest from Strathcona Fiord, Ellesmere Island, Arctic Canada: Evidence for a warm polar climate. Arctic, 41(4):314-318.

Francis, J.E.
1990 Polar fossil forests. Geology Today. May-June, p. 92-95.

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 (eds.). Tertiary Fossil Forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Geological Survey of Canada, Bulletin 403, p. 29-38.

Francis, J.E., and McMillan, N.J.
1987 Fossil forests in the Far North. Geos, 16(1):(winter)6-9.

Frederiksen, N.O.
1979 Paleogene sporomorph biostratigraphy, northeastern Virginia. Palynology, 3: 129-167.

Frederiksen, N.O.
1980 Paleogene sporomorphs from South Carolina and quantitative correlations with the Gulf Coast. Palynology, 4: 125-179.

Frederiksen, N.O.
1988 Sporomorph biostratigraphy, floral change and paleoclimatology, Eocene and earliest Oligocene of the eastern Gulf Coast. United States Geological Survey Professional Paper 1448, 68p.

Frederiksen, N.O., and Christopher, R.A.
1978 Taxonomy and biostratigraphy of Late Cretaceous and Paleogene triatriate pollen from South Carolina. Palynology, 2:1-145.

Galloway, W.E., and Hobday, D.K.
1983 Terrigenous clastic depositional systems: Applications to petroleum, coal and uranium explorations. Springer-Verlag, New York, 421p.

Gladkova, A.N.
1965 Iskopaemye Myricaceae Zapadnoi Sibiri (Fossil Myricaceae from western Siberia). Trudy Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Instituta, number 239:142-190.

Gonzalez Guzman, A.E.
1967 A palynological study on the Upper Cuervos and Mirador Formations (Lower and Middle Eocene) Tibu area, Columbia. Leiden, E.J. Brill, 68p.

Greely, A.W.
1886 Report of Sergeant D.L. Brainard on a petrified forest discovered May 20, 1883, near Cape Baird, 81°30' N, 64°30' W. In: Three years of Arctic Service, v. 2, Appendix 14, Charles Scribner's Sons, New York, p. 419, 420.

Grimm, W.C.
1957 The Book of Shrubs. The Stackpole Company, Harrisburg, Pennsylvania. 521p.

Groot, J.J., and Groot, C.R.
1962 Some plant microfossils from the Brightseat Formation (Paleocene) of Maryland. Palaeontographica, Abt. B, 111:161-171.

Gruas-Cavagnetto, C.
1968 Etude palynologique des divers gisements du Sparnacien du bassin de Paris. Soc. Geol. de France, Mem., n.s., 47(2):1-144 (Mem. No. 110).

Hail, W.J., and Leopold, E.B.
1960 Paleocene and Eocene age of the Coalmont Formation, North Park, Colorado. United States Geological Survey Professional Paper, 400-B:260-261.

Heer, O.
1878 Note on fossil plants discovered in Greinnell Land. Geological Society of London, Quarterly Journal, 34:66-72.

Hedlund, R.W.
1966 Palynology of the Red Branch Member (Woodbine Formation). Bulletin Oklahoma Geological Survey, 112:1-62.

Hickey, L.J., West, R.M., Dawson, M.R., and Choi, D.K.
1983 Arctic terrestrial biota: paleomagnetic evidence of age disparity with mid-northern latitudes during the late Cretaceous and early Tertiary. Science, 221:1153-1156.

Hills, L.V.
1965 Palynology and age of early Tertiary basins, interior British Columbia. Unpubl. Ph.D Thesis, University of Alberta, Edmonton.

Hills, L.V., and Bustin, R.M.
1976 *Picea banksii* Hills and Ogilvie from Axel Heiberg Island, District of Franklin. In: Report of Activities, Part B, Geological Survey of Canada Paper 76-1B, p. 61-63.

Hills, L.V., and Wallace, S.
1969 *Paraalnipollenites*, a new form genus from uppermost Cretaceous and Paleocene rocks of Arctic Canada and Russia. Geological Survey of Canada, Bulletin 182, p. 139-145.

Hopkins, W.S. Jr.
1969 Palynology of the Eocene Kitsilano Formation, southwestern British Columbia. Canadian Journal of Botany, 47:1101-1132.

Hopkins, W.S. Jr., Rutter, N.W., and Rouse, G.E.
1972 Geology, paleoecology, and palynology of some Oligocene rocks in the Rocky Mountain Trench of British Columbia. Canadian Journal of Earth Sciences, 9:460- 470.

Hou, H.Y.
1983 Vegetation of China with reference to its geographical distribution. Annals of the Missouri Botanical Garden, 70:509-548.

Hsu, J.
1983 Late-Cretaceous and Cenozoic vegetation in China, emphasizing their connections with North America. Annals of the Missouri Botanical Gardens, 70:490-508.

Ioannides, N.S., and McIntyre, D.J.
1980 A preliminary palynological study of the Caribou Hills outcrop section along the MacKenzie River, District of MacKenzie. In: Current Research, Part A, Geological Survey of Canada, Paper 80-1A, p. 197-208.

Irving, E., and Wynne, P.J.
1991 The paleolatitude of the Eocene fossil forests of Arctic Canada. In: R.L. Christie and N.J. McMillan (eds.). Tertiary Fossil Forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Geological Survey of Canada, Bulletin 403, p. 209-212.

Jansonius, J., and Hills, L.V.
1976 Genera file of fossil spores and pollen: University of Calgary, Department of Geology, Special Publication, 3431 cards; with Supplements 1-7, (1977-1983).

Kalguktar, R.M., and McIntyre, D.J.
1991 Helicosporous fungi and Early Eocene pollen, Eureka Sound Group, Axel Heiberg Island, Northwest Territories. Canadian Journal of Earth Sciences, 28(3):364-371 (March).

Kedves, M.
1988 Paleophytogeography of the Angiosperm pollen grains during the Upper Cretaceous and the Tertiary II. Acta Biol. Szeged., 34:45-57.

Kirchheimer, F.
1932 Uber Pollen aus der juntertiaren Braunkohle von Salzhausen (Oberhessen). N. Jahrb. Mineralogie, 67: 304-312.

Koch, E.
1964 Review of fossil floras and non-marine deposits of West Greenland. Geological Society of America Bulletin 75:535-548.

Kremp, G.O.W.
1965 Morphologic encyclopedia of palynology (An international collection of definitions and illustrations of spores and pollen). University of Arizona Press, Tucson, 263p.

Krutzsch, W.
1960 Uber *Thomsonipollis magnificus* (Thomson and Pflug 1953) n.f.gen. n. comb. und. Bemerkungen Zur regionalen Verbreitung einiger Pollen gruppen im alterer Palaogen. Freiberger Forschungshefte, pt. C86, p. 54-65.

Krutzsch, W.
1961 Beitrag zur. Sporenpalaontologie Tertiarablagerungen Brandenburgs: Geol. Gesell. DDR Ber. 5:590-343.

Krutzsch, W.
1962 Stratigraphisch bzw botanisch wichtige neue sporen- und pollenformen aus dem deutschen Tertiar: Geologie 11(3):265-306.

Kulkova, I.A.
1968 Pollen *Pistillipollenites mcgregorii* Rouse 1962 in the Eocene deposits of Yakut. Doklady. Akad. Nauk. SSSR, 182:1410-1412; [In Russian].

Leffingwell, H.A.
1971 Palynology of the Lance (Late Cretaceous) and Fort Union (Paleocene) Formations of the type Lance area, Wyoming. Geological Society of America Special Paper, 67:B22-B28.

Leopold, E.B., and MacGinitie, H.D.
1972 Development and affinities of Tertiary floras in the Rocky Mountains. In: A. Graham (ed.). *Floristics and paleofloristics of Asia and eastern North America*. Elsevier Publishing Co., Amsterdam, p. 147-200.

LePage, B.A., and Basinger, J.F.
1989 Early Tertiary *Larix* from the Canadian High Arctic. The Musk-ox: Student Research in Canada's North, Proceedings of the Second National Student Conference on Northern Studies, Ottawa, 39:103-109.

LePage, B.A., and Basinger, J.F.
1991 Early Tertiary *Larix* from the Buchanan Lake Formation, Canadian Arctic Archipelago and a consideration of the phytogeography of the genus. In : R.L. Christie and N.J. McMillan (eds.), *Tertiary Fossil Forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago*. Geological Survey of Canada, Bulletin 403, p. 67-82.

Lewis, W.H., Vinay, P., and Zenger, V.E.
1983 *Airborne and Allergenic POLLEN of North America*. The Johns Hopkins University Press, Baltimore, 254p.

Mabberley, D.J.
1987 *The Plant Book (a portable dictionary of higher plants)*. Cambridge University Press, Cambridge, 707p.

Manchester, S.R.
1987 The Fossil History of the Juglandaceae. Monographs in Systematic Botany. Missouri Botanical Garden, Lawrence, Kansas, 137p.

Manum, S.
1962 Studies in the Tertiary flora of Spitzbergen, with notes on Tertiary floras of Ellesmere Island, Greenland and Iceland. Norsk Polarinstitutt skrifter, no. 125, 127p.

Martin, H.A., and Rouse, G.E.
1966 Palynology of late Tertiary sediments from Queen Charlotte Islands, British Columbia. Canadian Journal of Botany, 44:171-208.

McIntyre, D.J.
1974 Palynology of an Upper Cretaceous section, Horton River, District of MacKenzie, N.W.T. Geological Survey of Canada, Paper 74-14, 57p.

McIntyre, 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 (eds.). *Tertiary Fossil Forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago*. Geological Survey of Canada, Bulletin 403, p. 83-98.

McKenna, M.C.
1980 Eocene paleolatitude, climate, and mammals of Ellesmere Island. Palaeogeography, Palaeoclimatology, Palaeoecology, 30:349-362.

McMillan, N.J.
1986 Tertiary Fossil Forests in the Arctic. Episodes, 9(3):169-170.

Miall, A.D.
1984a Variations in fluvial style in the lower Cenozoic synorogenic sediments of the Canadian Arctic Islands. Sedimentary Geology; 38:499-523.

Miall, A.D.
1984b Principles of Sedimentary Basin Analysis. Springer-Verlag, New York, 490p.

Miall, A.D.
1986 The Eureka Sound Group (Upper Cretaceous-Oligocene), Canadian Arctic Islands. Bulletin of Canadian Petroleum Geology, 34:240-270.

Miall, A.D.
1988 The Eureka Sound Group: alternative interpretations of the stratigraphy and paleogeographic evolution - Discussion. In: Current Research, Part D, Geological Survey of Canada, Paper 88-1D, Interior Plains and Arctic Canada, p. 143-148.

Nagy, E.
1969 Palynological investigations of the Miocene in Mecseck Mountains. Magyar Allami Foldtani Intezet Evkonyve, 52:235-649.

Nagy, E., and Rakosi, L.
1964 Magyar All. Foldtani intezetevi jelentese az, Evrol: 269, 276.

Nichols, D.J.
1973 North American and European species of *Momipites* ("*Engelhardtia*") and related genera. Geoscience and Man 7:103-117.

Nichols, D.J., and Ott, H.L.
1978 Biostratigraphy and evolution of *Momipites-Caryapollenites* lineage in the early Tertiary in the Wind River Basin, Wyoming. Palynology 2:93-112.

Nilsson, S.
1968 Pollen morphology in the genus *Macrocarpaea* (Gentianaceae) and its taxonomic significance. Svensk Botanisk Tidskrift, 62:338-353.

Norris, G.
1986 Systematic and stratigraphic palynology of Eocene to Pliocene strata in the Imperial Nuktak C-22 well, MacKenzie Delta region, District of MacKenzie, N.W.T. Geological Survey of Canada, Bulletin 340, 89p.

Norton, N.J., and Hall, J.W.
1969 Palynology of the upper Cretaceous and lower Tertiary in the type locality of the Hell Creek Formation, Montana, U.S.A. Palaeontographica, Abt B, 125, pp. 1-64.

Obst, J.R., McMillan, N.J., Blanchette, R.A., Christensen, P.J., Faix, O., Han, J.S., Kuster, T.A., Landucci, L.L., Newman, R.H., Petersen, R.C., Schwandt, V.H., and Wesolowski, M.F.
1991 Characterization of Canadian Arctic fossil woods. In: R.L. Christie and N.J. McMillan (eds.). Tertiary Fossil Forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Geological Survey of Canada, Bulletin 403, p. 123-146.

Pflug, H.
1953 Zur Entstehung und Entwicklung des angiospermiden Pollens in der Erdgeschichte. Palaeontographica Abt. B, 95:60-171.

Plauchut, B.P.
1971 Geology of the Sverdrup Basin. Bulletin of Canadian Petroleum Geology, 19:659-679.

Piel, K.M.
1971 Palynology of Oligocene sediments from central British Columbia. Canadian Journal of Botany, 49:1885-1920.

Porsild, A.E.
1973 Illustrated flora of the Canadian Arctic Archipelago (1957). Bulletin #146. National Museum of Canada. Ottawa.

Pokrovskaya, I.M. (ed.)
1956 [Atlas of Oligocene spore and pollen complexes from various regions of the U.S.S.R.]. Vsesoyuz. Nauchno-Issledovatel. Geol. Inst., Materialy, new ser., n 16, 312p. [In Russian].

Pokrovskaya, I.M., and Stelmak, N. (eds.)
1960 Atlas of Upper Cretaceous, Paleocene, and Eocene spores and pollen from some regions of U.S.S.R.: Tr. Vses. Nauchn. Issled. Geol. Inst., v.30, 572p., [In Russian].

Potonie, R.
1931 Pollen formen aus tertiaren Braunkohlen, III. Jahrb. Preuss. Geol. Landesanst. (Berl.), 52 (1932):1-7.

Potonie, R.
1934 Zur Mikrobotanik des eozanen Humodils des Geiseltals. Inst. Palaobot. Petrogr. Brennsteine Arb. 4:25-117.

Potonie, R.
1958 Synopsis der Gattungen der Sporae dispersae II. Teil: Sporites (Nachtrage), Saccites, Aletes, Praecolpates, Polyplicates, Monocolpates; Beihefte Zum Geologischen Jahrbuch, v. 31, ll4p.

Potonie, R.
1960 Synopsis der Gattungen der Sporae dispersae III. Teil: Nachtrage Sporites, Fortsetzung Pollenites mit General register su teil I-II: Beih. Geol. Jahrb., Heft 39, 189p.

Raatz, G.
1938 Midrobotanisch-stratigraphische Untersuchung der Braunkohle des. Muskauer Bogens: Preuss. Geol. Landesanst., Abh., v. 183, 48p.

Raven, P.H. and Curtis, H.
1970 Biology of plants. Worth Publishers, Inc., New York, 706p.

Riediger, C.L., and Bustin, R.M.
1987 The Eureka Sound Formation, southern Ellesmere Island. Bulletin of Canadian Petroleum Geology, 35:123-142.

Ricketts, B.D.
1986 New formations in the Eureka Sound Group, Canadian Arctic Islands. In: Current Research, part B. Geological Survey of Canada, Paper 86-1B, pp. 363-374.

Ricketts, B.D.
1987 Princess Margaret Arch: re-evaluation of an element of the Eurekan Orogen, Axel Heiberg Island, Arctic Archipelago. Canadian Journal of Earth Sciences, 24:2499-2505.

Ricketts, B.D.
1988 The Eureka Sound Group: alternative interpretations of the stratigraphy and paleogeographic evolution -Reply. In: Current Research, Part D, Geological Survey of Canada, Paper 88-1D, Interior Plains and Arctic Canada, p. 149-152.

Ricketts, B.D.
1991 Sedimentation, Eurekan tectonism and the fossil forest succession on eastern Axel Heiberg Island, Canadian Arctic Archipelago. In: R.L. Christie and N.J. McMillan (eds.). Tertiary Fossil Forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Geological Survey of Canada, Bulletin 403, p. 1-27.

Ricketts, B.D., and McIntyre, D.J.
1986 The Eureka Sound Group of eastern Axel Heiberg Island: new data on the Eurekan Orogeny. In: Current Research, Part B, Geological Survey of Canada, Paper 86-1B:405-410.

Riclefs, R.E.
1979 Ecology. Second Edition. Chiron Press Inc. New York, 1979, 966p.

Roche, E.
1969 Etude palynologique de sediments du Montien continental et du Landenien superieur en Hainaut. Soc. Belge Geol. Paleont. Hydrol., Bulletin, 78:131-146.

Rouse, G.E.
1962 Plant microfossils from Burrard Formation of western British Columbia. Micropaleontology, 8(2):187-218.

Rouse, G.E.
1977 Paleogene palynomorph ranges in western and northern Canada. American Association of Stratigraphic Palynologists, Contribution Series, 5A:48-65.

Rouse, G.E., Hopkins, W.S., Jr., and Piel, K.M.
1971 Palynology of some Late Cretaceous and early Tertiary deposits in British Columbia and adjacent Alberta. Geological Society of America, Special Paper, 127:213-246.

Rouse, G.E., and Mathews, W.H.
1961 Radioactive dating of Tertiary plant-bearing deposits. Science, 133:1079-1080.

Rouse, G.E., and Mathews, W.H.
1988 Palynology and geochronology of Eocene beds from Cheslatta Falls and Nazko areas, central British Columbia. Canadian Journal of Earth Sciences, 25(8):1268-1276.

Rouse, G.E., and Srivastava, S.K.
1970 Detailed morphology and taxonomy and distribution of *Pistillipollenites mcgregorii*. Canadian Journal of Botany, 48:287-292.

Rouse, G.E., and Srivastava, S.K.
1972 Palynological zonation of Cretaceous and early Tertiary rocks of the Bonnet Plume Formation, northeastern Yukon, Canada. Canadian Journal of Earth Sciences, 9:1163-1179.

Schweitzer, H.J.
1974 Die Tertiaren: Koniferen Spitzbergens. Palaeontographica, Abt. B, 149:1-89.

Schweitzer, H.J.
1980 Environment and climate in the early Tertiary of Spitsbergen. Palaeogeography, Palaeoclimatology, Palaeoecology, 30:297-311.

Simpson, J.B.
1936 Fossil pollen in Scottish Tertiary coals. Proceedings of the Royal Society, Edinburgh, 56:90-108, Pt. II.

Simpson, J.B.
1961 The Tertiary pollen-flora of Mull and Ardnamurchan. Transactions of the Royal Society of Edinburgh, 64:179-384.

Skarby, A.
1968 *Extratriporopollenites* (Pflug) *emend.* from the Upper Cretaceous of Scania, Sweden. Stockholm Contribution in Geology, (Acta Universitans Stockholmiensis), 16:1-60.

Sohl, N.F.,and Mello, J.F.
1970 Biostratigraphic analysis. In: J.P. Owen, *et al.*, (eds). Stratigraphy of the outcropping post Magoth Upper Cretaceous Formations in Southern New Jersey and Northern Delmarva Peninsula, Delaware and Maryland. U.S. Geological Survey Professional Paper 674; pp. 28-55.

Souther, J.G.
1963 Geological traverse across Axel Heiberg Island from Buchanan Lake to Strand Fiord. In: Y.O Fortier, *et al.*, (eds.). Geology of the North-central Part of the Arctic Archipelago, N.W.T. (Operation Franklin). Geological Survey of Canada, Memoir 320, p. 74-95.

Spicer, R.A.
1989 Plants at the Cretaceous-Tertiary boundary. Phil. Transactions of the Royal Society Lond B325, 291-305.

Spicer, R.A., and Greer, A.G.
1986 Plant taphonomy in fluvial and lacustrine systems. In: R.A. Gastaldo (ed.) Land plants - notes for a Short Course. University of Tennessee, Department of Geological Science, Stud. Geol., 15:10-26.

Srivastava, S.K.
1966 Upper Cretaceous microflora (Maastrichtian) from Scollard, Alberta, Canada. Pollen et Spores, 8(3):497-552.

Srivastava, S.K.
1969 Assorted angiosperm pollen from Edmonton Formation (Maastrichtian) Alberta, Canada. Canadian Journal of Botany, 47: 975-989.

Srivastava, S.K.
1972a Taxonomic notes on pollen genera: *Callistropollenites, Tricolporites* and *Carpinipites*. Canadian Journal of Botany, 50:9-12.

Srivastava, S.K.
1972b Some spores and pollen from the Paleocene Oak Hill member of the Naheola Formation, Alabama., U.S.A. Review of Palaeobotany and Palynology, 14:217-285.

Srivastava, S.K.
1975 Maastrichtian microspore assemblages from the interbasaltic lignites of Mull, Scotland. Palaeontographica, Abt. B, 150:125-156.

Srivastava, S.K.
1984 Palynology of the Monterey Formation (Miocene) Phosphatic Facies at Lions Head, Santa Maria, California. Palynology, 8:33-49.

Stanley, E.A.
1965 Upper Cretaceous and Paleocene plant microfossils and Paleocene dinoflagellates and hystrichosphaerids from northwestern South Dakota, Bulletin of American Paleontology, 49(222):179-384.

Stephenson, R.A., Embry, A.F., Nakiboglu, S.M., and Hastaoglu, M.A.
1987 Rift-initiated Permian - Early Cretaceous subsidence in the Sverdrup Basin. In: C. Beaumont and A. Tankard (eds). Sedimentary basins and basin-forming mechanisms. Canadian Society of Petroleum Geologists, Memoir 12, p. 213-231.

Stockey, R.A., and Manchester, S.R.
1988 A fossil flower with *in situ Pistillipollenites* from the Eocene of British Columbia. Canadian Journal of Botany, 66:313-318.

Stone, D.E., and Broome, C.R.
1975 Juglandaceae. A. Rich. ex Kunth. World Pollen and Spore Flora, 4:1-35.

Sung, T.C., and Tsao, L.
1976 The Paleocene spores and pollen grains from the Fushun coal field, northeast China. Acta Palaeontologica Sinica, 15(2):147-162.

Takahashi, K., and Kim, B.K.
1979 Palynology of the Miocene Formation in the Yeoungill Bay District, Korea. Palaeontographica, Abt. B, Bd. 170, 80p

Tarnocai, C., and Smith, C.A.S.
1991 Paleosols of the fossil forest area, Axel Heiberg Island. In: R.L. Christie and N.J. McMillan (eds.) Tertiary Fossil Forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Geological Survey of Canada, Bulletin 403, p. 171-188.

Thiergart, F.
1940 Die mikropalaontologie als pollenanalyses im dienst der. Braunkohlenforschung. Von Ferdinand Enke, Stuttgart, 13 Heft.

Thomson, P.W., and Pflug, H.
1953 Pollen und sporen des mitteleuropaischen Tertiars. Palaeontographica, Abt. B., 94:1-138.

Thorsteinsson R. and Tozer, E.T.
1957 Geological investigations in Ellesmere and Axel Heiberg Islands, 1956. Arctic, 10(1):3-31.

Tiffney, B.H.
1985 Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. Journal of the Arnold Arboretum, 66:73-94.

Tozer, E.T.
1960 Summary account of Mesozoic and Tertiary stratigraphy, Canadian Arctic Archipelago. Geological Survey of Canada, Paper 60-5, 24p.

Tozer, E.T.
1963 Mesozoic and Tertiary stratigraphy. In: Y.O Fortier, R.G. Blackadar, B.F. Glenister, H.R. Greiner, D.J. McLaren, N.J. McMillan, A.W. Norris, E.F. Roots, J.G. Souther, R. Thorsteinsson, E.T. Tozer (eds.). Geology of the North-central Part of the Arctic Archipelago, N.W.T. (Operation Franklin). Geological Survey of Canada, Memoir 320, p. 74-95.

Traverse, A.
1988 Paleopalynology. Unwin Hyman Ltd., Boston, 600p.

Trettin, H.P.
1989 The Arctic Islands. In: Bally, A.W., and Palmer, A.R., (eds.), The Geology of North America - An overview. Boulder, Colorado, Geological Society of America, The Geology of North America, volume A, p. 349-370.

Troelson, J.C.
1950 Contributions to the geology of northwest Greenland, Ellesmere Island, and Axel Heiberg Island. Meddelelser om Gronland, 149(7):1-86.

Tschudy, R.H.
1973 Stratigraphic distribution of significant Eocene palynomorphs of the Mississippian embayments. U.S. Geological Survey Professional Paper, 743-B:B1-B24.

Tschudy, R.H.
1975 Normapolles pollen from the Mississippi embayment. U.S. Geological Survey, Professional Paper 865, 40p.

Tschudy, R.H., and Van Loenen, S.D.
1970 Illustrations of plant microfossils from the Yazoo Clay (Jackson Group, Upper Eocene), Mississippi. United States Geological Professional Paper 543-E:5p.

Vaartaja, A.
1959 Evidence of photoperiod ecotypes in trees. Ecological Monographs, 29(2):911.

Vinson, T.E.
1981 A paleomagnetic study of the Upper Cretaceous to Lower Eocene Eureka Sound Formation, Strathcona Fiord, Ellesmere Island, Canada. Unpublished M.Sc. dissertation, University of Wisconsin, Milwaukee, 119p.

West, R.M., and Dawson, M.R.
1977 Mammals from the Paleogene of the Eureka Sound Formation, Ellesmere Island, Arctic Canada. Geobios Mem. Special 1, p. 107-124.

West, R.M., Dawson, M.R., Hickey, L.J., and Miall, A.D.
1981 Upper Cretaceous and Paleogene sedimentary rocks, eastern Canadian Arctic and related North Atlantic areas. In: Kerr, J.M., Fergusson, A.J., and Machan, L.C., (eds.) Geology of the North Atlantic borderlands. Canadian Society of Petroleum Geologists, Memoir 7:279-298.

West, R.M., Dawson, M.R., and Hutchison, J.H.
1977 Fossils from the Paleogene Eureka Sound Formation, N.W.T., Canada: Occurrence climatic, and paleogeographic implications. In: West, R.M. (ed.) Paleontology and Plate Tectonics: Milwaukee Public Museum, Special Publ. Biol. Geol., no.2, p. 77-93.

West, R.M., Dawson, M.R., Hutchison, J.H. and Ramaekers, P.
1975 Paleontologic evidence of marine sediments in the Eureka Sound Formation of Ellesmere Island, Arctic Archipelago, N.W.T., Canada. Canadian Journal of Earth Sciences, 12:574-579.

Whitehead, D.R.
1963 Pollen morphology in Juglandaceae I: pollen size and pore number variation. Journal of the Arnold Arboretum, 44:101-110.

Whitehead, D.R.
1965 Pollen morphology in Juglandaceae II: survey of the family. Journal of the Arnold Arboretum, 46(4):369-410.

Willis, J.C. (revised by H.K. Airy Shaw)
1973 A Dictionary of Flowering Plants and Ferns, Eighth edition. Cambridge University Press, London, 1214p.

Wilson, M.A.
1978 Palynology of three sections across the uppermost Cretaceous/Paleocene boundary in the Yukon Territory and District of Mackenzie, Canada. Palaeontographica, Abt. B, 66:99-182.

Wilson, L.R., and Webster, R.M.
1946 Plant microfossils from a Fort Union Coal of Montana. American Journal of Botany, 33:271-278.

Wing, S.L., and Daghlian, C.P.
1989 Paleogene *Pistillipollenites* were produced by early successional rosids of uncertain familial affinity. Botanical Society of America - ABSTRACTS; 40th Annual Meeting -Toronto, Canada. Supplement to American Journal of Botany, 76(6):177-178. June 1989.

Wing, S.L., and Hickey, L.J.
1984 The *Platycarya* perplex and the evolution of the Juglandaceae. American Journal of Botany, 71: 388-411.

Wingate, F.H.
1983 Palynology and age of the Elko Formation (Eocene) near Elko, Nevada. Palynology, 7:93-132.

Wodehouse, R.P.
1933 Tertiary pollen II. The oil shales of Eocene Green River Formation. Torrey Bot. Club Bull., 60(7):479-525.

Wodehouse, R.P.
1935 Pollen grains, their structure, identification and significance in science and medicine. McGraw-Hill Book Co., Inc., N.Y., 574p. [1965 edition].

Wolfe, J.A.
1977 Paleogene floras from the Gulf of Alaska region. U.S. Geological Survey Professional Paper 997, 108p.

Wolfe, J.A.
1978 A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. American Scientist, 66:694-703.

Wolfe, J.A.
1979 Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia. U.S. Geological Survey Professional Paper 1106, 37p.

Wolfe, J.A.
1980 Tertiary climates and floristic relationships at high latitudes in the Northern Hemisphere. Palaeogeography, Palaeoclimatology, Palaeoecology, 30:313-323.

Wolfe, J.A.
1985 Distribution of major vegetation types during the Tertiary. In: E.T. Sundquist, and W.S. Broecker (eds.). The Carbon Cycle and Atmospheric CO_2: Natural Variations Archean to Present. Geophysical Monograph, 32:357-375.

Wolfe, J.A.
1987 An overview of the origins of the modern vegetation and flora of the northern Rocky Mountains. Annals of the Missouri Botanical Garden, 74:785-803.

Wolfe, J.A., and Tanai, T.
1980 The Miocene Seldovia Point flora from the Kenai Group, Alaska. U.S. Geological Survey Professional paper 1105, 52p.

Wolff, H.
1934 Mikrofossilien des Pliozanen Humodils der Grube Freigericht bei Dettingen a. Main und Verleich mit alteren Schichten des Tertiars sowie posttertiaren Ablagerungen. Arb. Inst. Palaobot. Petrog. Brennstein, 5:55-101.

Wynne, P. J., Irving, E., and Osadetz, K.G.
1988 Paleomagnetism of Cretaceous volcanic rocks of the Sverdrup Basin - magnetostratigraphy, paleolatitudes, and rotations. Canadian Journal of Earth Sciences, 25: 1220-1239.

Young, G.S.
1991 Microscopic characterization of fossil wood from Geodetic Hills, Axel Heiberg Island. In: R.L. Christie and N.J. McMillan (eds.), Tertiary Fossil Forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Geological Survey of Canada, Bulletin 403, p. 171-188.

Zaklinskaya, E.D.
1963 Angiosperm pollen and their significance for the stratigraphy of the Upper Cretaceous and Paleogene. Trudy Geol. Inst. Akad. Nauk. S.S.R., v.74, 256p., [In Russian].

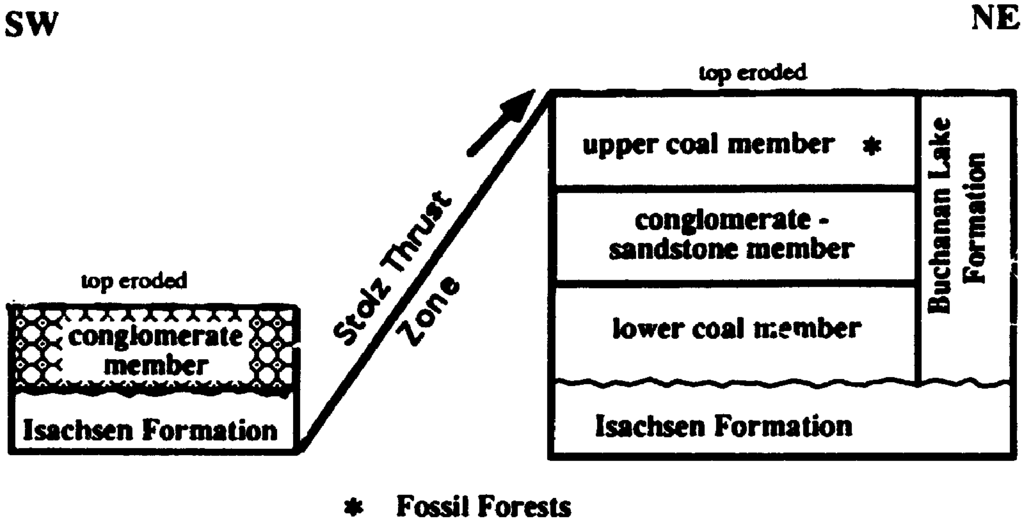
APPENDICES I-III

APPENDIX IA. Leaf litter layers of the partial fossil forest succession under study and their descriptions (after Day, *pers. comm.*, 1991; Day, 1991; Francis 1991; Basinger, 1991), following the nomenclature of Francis and McMillan (1987). (Informal divisions of K and N; Day, 1991).

LEAF-LITTER LAYERS	LEAF LAYER DESCRIPTIONS
A	Relatively poorly-preserved mixed broad-leaved litter (with minor *Metasequoia*), about 15 to 20cm thick, (composition to be later determined). Fruits (such as *Carya*) have also been recovered from this layer (Basinger, *pers. comm.*, 1991).
I	Relatively poorly preserved unit of carbonized "woody peat", principally of *Metasequoia* (needles and cones), *Larix*, and *Alnus*, about 10 to 20 cm thick.
J	Leaf mat unit principally composed of *Metasequoia* needles and *Alnus* leaves, about 20cm thick.
Ka	Ka is the upper portion of the "K" unit (about 10cm thick), more diverse than Kb. A mixture of *Alnus*, *Carya*, *Gingko*, *Betula* and *Osmunda*. Mixed unit of *Alnus* leaves and *Metasequoia* needles and minor miscellaneous broad leaves (to be determined).
Kb	Well-preserved mixed leaf litter, 10 to 20 cm thick, at the bottom of level K, consisting mainly of *Alnus* and *Osmunda*. Also minor *Betula*, *Ginkgo* and *Carya*.
M	Coarse litter horizon, mainly of *Metasequoia* foliage, about 15 cm thick and containing abundant rootlet and woody fragments.
Nb	Lower part of the "N" level (which is a stump level with large woody stumps fully exposed). It appears to represent relatively undisturbed forest floor conditions; Francis, 1991. Basinger (1991) has observed the rare plant macrofossil taxa in N, a paleoecologically distinct layer with abundant taxodiaceous leaf litter mats). Nb is a thin, well-preserved litter mat almost monospecific in nature with *Metasequoia* dominating, in contrast to the upper part of level, Na where *Metasequoia* is mixed with a variety of broad-leaved angiosperms.

Appendix IB.

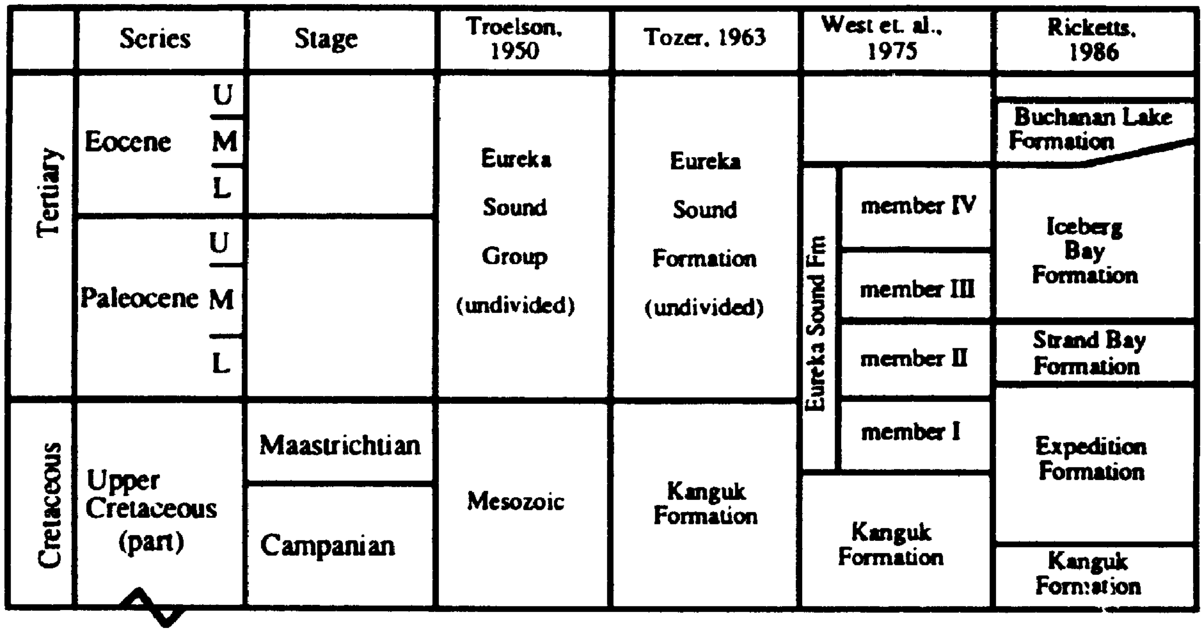
Schematic summary of lithostratigraphy of the fossil-forest bearing strata, Geodetic Hills area. Note that the conglomerate member in the hanging wall of the Stolz Thrust contains an interfingering sliver of lower coal member strata (after Ricketts, 1991). The Isachsen Formation is Lower Cretaceous in age.



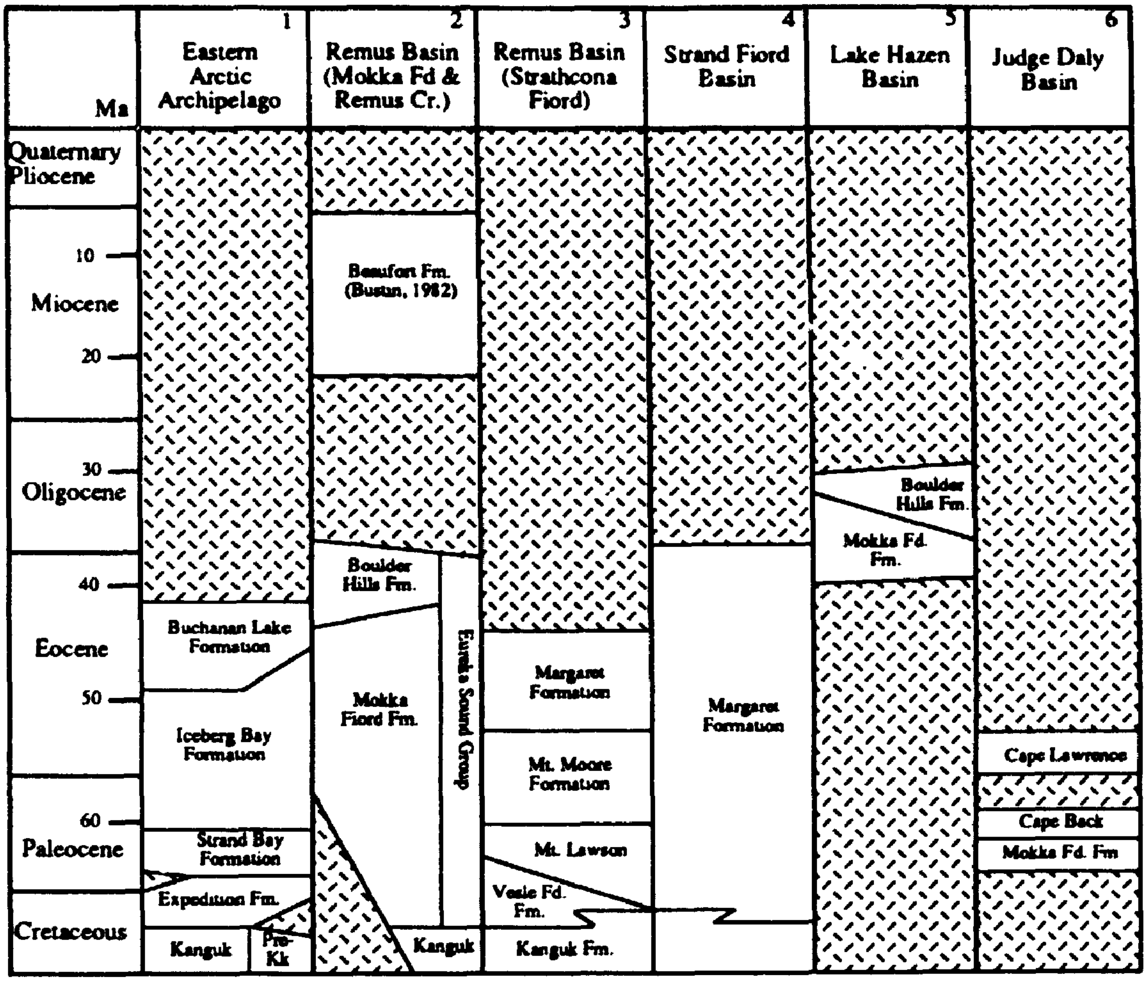
Appendix IC. Informal divisions of the unit of fine-grained sediments which contain the fossil forest remains; (note: these divisions are made for the convenience of paleobotanical description and are not meant to imply stratigraphic significance; from Basinger, 1991). These subunits are in the *upper coal member* of Ricketts' lithostratigraphic scheme of the fossil-forest bearing strata, Geodetic Hills area in Appendix IB. The leaf litter layers under study herein (see Appendix IA), derive from the middle unit (Day, *pers. comm.*, 1991). *

	Description
upper	coarser unit, nearly 100m thick, which is composed mainly of sand and includes many "channel sands assemblages" but few litter mats
middle *	heterogeneous unit with a moderate proportion of crossbedded sands, also about 50m thick, which contains most of the litter mats and stumps
lower	finer grained unit, about 50m thick, containing some leaf-litter mats and tree stumps

Appendix IIA. Comparison of stratigraphic schemes for the Eureka Sound Group (after Ricketts, 1986).



Appendix IIB. Comparison of current stratigraphic schemes for the Eureka Sound Group. Column 1 from Ricketts (1986, 1988); columns 2-6 from Miall (1986, 1988).



APPENDIX IIIA. REGISTER OF TRIPORATE POLLEN SPECIMENS

Slide No.	Leaf Horizon	Neg.	Plate # fig. #	EFS	Size µm	taxa
4	A	test-3	I-1,2	D44-D44/3	29.64	Alnipollenites verus
20	Ka	test-11	I-3	K21-K21/3	21.84	A. verus - 3
16	Ka	20-29	I-5	M51/2	21.84	" - 3
18	Ka	22-29	I-6	S10/3	24.18	" - 3
26	M	22-12	I-7	E8	21.84	" - 4
4	A	24-13a	I-8	C42-C42/1	27.30	" - 6
4	A	24-35a	I-9,10	S32/1	20.28	" - 4 - ring
16	Ka	23-25	I-4	W26	20.28	Alnipollenites trina
16	Ka	19-32	I-11	Y39/3	21.06	A. sp. A - 4
20	Ka	14-16	I-12	G12/2	20.28	" - 3
20	Ka	19-28	I-13	T24/4	21.06	" - 3
20	Ka	14-12	I-14	H11	22.62	" - 3
21	Kb	18-26	I-15	V38/2	21.06	" - 4
16	Ka	22-32	IV-6	M22/1	25.74	Annutriporites sp.
4	A	6-20a	IV-5	P42	29.64	
2	A	24-30a	I-18	S40/1	27.30	Carp. ancipites - 3
21	Kb	19-6	II-4	O8	21.81	" - 3
5	A	19-22	II-6	M10-M10/2	35.88	" - 4
14	J	23-33	II-5	O21	26.52	Carpinipites sp. - 3
4	A	6-8a	III-1	P30/3	28.08	Carya. virid.
4	A	22-25	III-2	L23/4-M23/2	35.88	
1	A	23-5	III-3	U49/1-U48/2	32.70	Carya. juxta.
1	A	24-8A	III-4	R45/1	35.88	Carya. inelegans
4	A	6a-6	III-5	C35/1	38.22	Carya. veripites
4	A	7-22	III-6	P9/4	35.88	
4	A	7-30	III-11	K22/3	22.62	M. coryloides
4	A	6-31a	III-12	M52/4	19.94	
4	A	11-11	III-13	G40	18.76	M. microfov.
14	J	20-23	III-19	S21-S21/3	31.20	Momipites ?tenuipolis
1	A	20-15	IV-5	R47/2-R47/4	23.40	M. annulites
2	A	24-31a	IV-6	S40/1	22.62	
28	M	20-2	I-16	O20	35.10	Paragl. sp.
11	J	23-21	I-17	J29-J29/1	26.52	
31	Nb	18-17	V-9	T16	18.72	Pist. macr. - s
29	M	22-27	V-10	S18/2	25.74	" - p
33	Nb	17-27	V-11	Z43/3	27.30	" - 3,p
33	Nb	17-29	V-12	F15/4	23.40	" - n
33	Nb	17-5	V-13	P45	23.40	Pist. sp. A - p
33	Nb	22-28	V-15	S19/1-S19/3	24.18	" - r/n
31	Nb	17-0	V-16	R29/2-R29/4	28.08	" - dense
35	Nb	17-9	V-14	J40-J40/3	24.96	" - n
4	A	24-5a	III-8	H35	18.72	Platycarya. sp.
35	Nb	17-12	III-9	X51	21.06	
31	Nb	20-35a,36a	III-14,15	N23/3	27.30	Plicatopollis plicata
8	I	8-1,3	III-17,18	Z33/1-Z33/3	25.74	
33	Nb	17-30	III-16	O8/3	30.40	Plicatopollis sp. A
28	M	16-12	IV-3	X20/3	23.40	Sant. sant.
18	Ka	23-30	IV-4	O8/1-O8/3	24.18	
4	A	7-4a	IV-17	G21/3	32.76	Sub. anulatus
5	A	20-5	IV-18	O52	33.44	
5	A	20-19	IV-19	P51	26.52	Sub. nanus
5	A	20-6	IV-20	R14/3	28.08	
4	A	24-11a	IV-1	V8/3	31.98	Thomsonipollis sp.
4	A	24-1a	IV-2	T28/2	32.76	
28	M	19-2	IV-4	L20	24.96	Triat. subtriangulus
4	A	14-28	IV-1	O26/4-P26/2	24.96	Triat. sp. A
29	M	20-30	IV-2	G49/1	29.64	
28	M	20-27	IV-3	V52/3	32.76	"
1	A	21-0,20-0	IV-7,8	G15/1	30.1	Triat. sp. B
18	Ka	22-30	IV-9	N9/2	32.63	T. arboratus
5	A	23-2	IV-10	R30/4	30.42	
5	A	20-4	IV-11	F51	34.43	"
26	M	20-8	IV-12	P41/2-P42/1	23.40	Triporo. mullensis
4	A	7-19	IV-16	D50/1	31.98	
11	J	10-21	IV-14	L43-L43/1	27.30	Triporo. sp. A
4	A	test-14	IV-15	H38	24.18	
4	A	14-34	IV-13	Q49/4	22.62	"
11	J	22-14	II-1	S25/1	24.95	T. claripites - arci
1	A	19-10	II-2	U17-U17/1	29.64	
11	J	22-16	II-3	K14-K14/1	26.52	T. betuloides
4	A	22-24	II-9	W13/2-V13/4	29.64	U. undulosus - 4
4	A	22-23	II-10	S27/2-S28/1	28.86	" - 3
4	A	22-26	II-11	K43/3	29.64	" - 5
4	A	22-21	II-7	U44/1	31.98	" - 5
28	M	22-3	II-18	U42/2	29.64	U. tricostatus
26	M	22-4	II-12	S36/1	23.40	U. krempii - 3
12	J	22-8	II-15	N42/3-O42/1	27.30	" - 4
4	A	22-19	II-13	L38/2	30.40	" - 4
12	J	23-32	II-14	S15/3	28.86	" - 4
29	M	22-22	II-17	R43/1	26.52	" - 4
REGISTER OF NON-TRIPORATE POLLEN SPECIMENS						
5	A	24-3	V-8	R31	35.54	Tilia-type
4	A	6-14a	V-17	P42-P42/4	38.48	Pterocarya-type
29	M	24-34a	V-18	J28-J28/3	29.64 (papilla 4.7)	Metasequoia-type
11	J	10-22	V-19	U25	28.86	Taxodium-type
11	J	10-25	V-20	J44/3	35.5 X 43.3	Ctenosporites

APPENDIX IIIB. GROUP/TAXA ABUNDANCE (ABSOLUTE COUNTS)

sample	polycol-(po)rates	tetrads	tricol-pates	tricol-porates	fungi	spores	triporates	Taxodi-aceae	mono sulcates	bisaccates	poly porates	TOTAL COUNTS
A1	2	29	93	22	140	114	44	143	3	27	35	652
A2	4	21	81	42	127	120	36	129	9	38	33	641
A3	3	28	116	20	168	114	50	160	4	33	35	731
A4	1	16	83	12	129	90	12	95	4	22	14	464
A5	11	11	72	15	102	82	12	108	4	18	26	461
I1	1	0	6	5	309	25	9	180	7	2	112	656
I2	0	0	3	4	205	15	18	186	7	1	93	532
I3	0	0	11	2	310	22	11	169	2	4	121	652
I4	0	1	5	1	313	23	16	151	4	5	134	653
I5	1	0	7	7	315	19	16	156	4	3	131	659
J1	1	1	19	23	365	12	6	178	4	34	55	698
J2	0	0	13	43	234	19	1	179	10	22	42	563
J3	0	0	13	48	236	23	4	156	4	17	48	549
J4	1	0	19	37	194	19	4	170	13	23	38	518
J5	0	0	13	45	234	23	2	127	7	29	51	531
Ka1	0	0	6	0	31	76	61	21	18	4	215	432
Ka2	0	0	13	3	39	56	51	13	13	8	188	384
Ka3	0	0	7	1	32	89	59	14	13	3	185	403
Ka4	0	1	12	2	32	83	41	23	7	5	197	403
Ka5	0	0	6	1	33	86	57	17	2	2	201	405
Kb1	0	0	6	1	147	104	30	16	7	2	81	394
Kb2	1	0	2	1	103	103	33	12	3	3	105	366
Kb3	0	0	4	0	138	149	17	18	6	6	107	445
Kb4	0	0	4	0	114	115	28	19	5	4	112	401
Kb5	0	0	3	0	89	109	20	11	3	4	107	346
M1	2	1	19	15	94	21	10	179	2	12	74	429
M2	3	3	18	11	103	19	7	169	3	10	72	418
M3	5	1	27	11	102	19	19	178	6	12	82	462
M4	3	0	25	16	77	19	13	184	6	7	77	427
M5	3	1	24	13	82	16	10	178	5	9	80	421
Nb1	1	1	6	14	84	11	130	63	3	5	56	374
Nb2	1	4	10	6	36	18	149	61	0	7	58	350
Nb3	0	1	10	6	69	17	147	71	2	5	95	423
Nb4	1	0	9	9	73	11	130	86	2	8	95	424
Nb5	1	2	4	5	60	16	139	91	4	9	47	378

APPENDIX IIIC FAMILY ABUNDANCE (ABSOLUTE COUNTS)

sample	BETULACEAE	JUGLANDACEAE	?GENTIANACEAE	OTHER	SUM	TOTAL COUNT
A1	31	2	0	0	33	652
A2	7	4	2	11	34	640
A3	14	2	0	8	24	731
A4	10	2	1	1	14	464
A5	8	2	0	4	14	461
I1	5	0	0	1	6	656
I2	12	0	0	0	12	532
I3	16	0	0	0	16	652
I4	15	0	0	1	16	653
I5	15	1	0	1	16	659
J1	4	3	0	0	7	698
J2	0	0	0	0	1	563
J3	2	1	0	0	3	549
J4	1	0	0	3	4	518
J5	1	0	0	1	2	531
Ka1	61	1	1	3	65	432
Ka2	54	0	1	1	55	384
Ka3	48	2	0	1	51	403
Ka4	38	0	0	3	41	403
Ka5	56	0	1	2	58	405
Kb1	30	0	0	0	30	394
Kb2	32	0	1	0	33	366
Kb3	17	0	0	0	17	445
Kb4	27	0	0	0	27	401
Kb5	19	0	1	0	20	346
M1	10	0	0	0	10	429
M2	6	0	0	1	8	418
M3	17	0	1	1	19	462
M4	9	0	0	4	13	427
M5	7	3	0	0	10	421
Nb1	14	0	115	1	130	374
Nb2	17	0	137	0	154	350
Nb3	12	0	135	0	147	423
Nb4	8	0	120	2	130	424
Nb5	7	0	132	0	139	378

APPENDIX IIID. SPECIES ABUNDANCE (ABSOLUTE COUNTS)

	BETULACEAE						JUGLANDACEAE				?GENTIANACEAE	OTHER								
sample	A. verus	A. trina	A. sp. A	Triv. clar.	Carp. ancip.	Paraal. sp.	Mom. micro.	Carya. virid	Plicat. plicat	Platy. sp.	Pist. macg.	Pist sp. A	Myr ann	Sant sant	Sub anul	Triat arbor	Trip mol.	Pint ural	SM	[illegible]
A1	1	0	0	23	1	0	6	2	0	0	0	0	0	0	0	0	0	0	33	652
A2	0	0	0	15	0	0	2	3	1	1	2	0	2	0	3	3	2	0	34	640
A3	1	0	0	10	0	0	3	0	0	2	0	0	3	0	0	2	3	0	24	731
A4	1	0	0	7	0	0	2	1	0	1	1	0	0	0	0	0	1	0	14	464
A5	1	0	0	5	0	0	2	1	0	1	0	0	0	0	1	1	2	0	14	461
I1	3	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	6	656
I2	11	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	552
I3	13	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	16	652
I4	12	0	0	1	0	0	2	0	0	0	0	0	0	0	0	1	2	0	16	653
I5	13	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	16	659
J1	0	0	0	3	0	1	0	3	0	0	0	0	0	0	0	0	0	0	7	698
J2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	563
J3	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	3	549
J4	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	2	0	4	518
J5	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	531
Ka1	55	2	3	0	1	0	0	1	0	0	1	0	1	1	0	0	1	0	65	432
Ka2	46	6	0	1	0	0	2	0	1	0	0	1	0	0	0	0	0	0	55	384
Ka3	48	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	51	403
Ka4	35	2	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0	41	403
Ka5	51	1	0	3	0	0	1	0	0	0	1	0	2	0	0	0	0	0	58	405
Kb1	26	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	30	394
Kb2	30	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	33	366
Kb3	14	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	445
Kb4	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27	401
Kb5	18	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	20	346
M1	7	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	10	429
M2	1	0	0	5	0	0	2	0	0	1	0	0	0	0	0	0	1	0	8	418
M3	5	0	0	7	0	0	5	0	0	0	1	0	0	0	0	0	1	0	19	462
M4	5	0	0	4	0	0	0	0	0	0	0	0	4	0	0	0	2	0	13	427
M5	4	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	10	421
Nb1	8	1	0	2	0	0	3	0	0	0	108	7	0	0	1	0	0	0	130	374
Nb2	9	0	0	4	0	0	2	0	0	0	128	9	0	0	0	0	0	0	154	390
Nb3	7	1	0	3	0	0	1	0	0	0	116	19	0	0	0	0	0	0	147	423
Nb4	2	1	0	4	0	0	1	0	0	0	103	17	2	0	1	1	0	0	130	424
Nb5	3	2	0	0	0	0	2	0	0	0	116	16	0	0	0	0	0	0	139	378

PLATES 1-5

PLATE ONE

Betulaceae

All specimens magnified x 1500, unless otherwise stated.

1, 2 *Alnipollenites verus*. 1, specimen at low focus showing wall structure, possibly three layers; vestibulate pore structure; 2, high focus showing granulate surface sculpture; x 1000.

3 *Alnipollenites verus*. Triporate form with weak vestibula.

4 *Alnipollenites trina*. Weak or absent vestibula and straight arci that parallel sides.

5-8 *Alnipollenites verus*. 5, abnormal form with curved and bent arci; 6, another abnormal form with curved and bent arci that extend to the equator. The second set of arci on the other hemisphere is visible; 7, common tetraporate; 8, uncommon six-pored form; x 1200.

9, 10 *Alnipollenites verus*. 9, at low focus, aberrant form showing arci; 10, at high focus showing unusual polar ring on one pole, more typical of *Paraalnipollenites* species and *Triporopollenites mullensis*; x 1400.

11 *Alnipollenites* sp. A. Triporate form showing unusual arci, most resembles *A. verus*.

12 *Alnipollenites* sp. A. Specimen showing two sets of wavy arci, one on each pole.

13 *Alnipollenites* sp. A. Pores weakly or non-vestibulate, usually obscured by arci.

14 *Alnipollenites* sp. A. Arci extend to the equator and may encircle aperture.

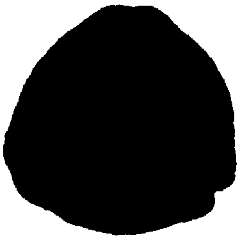
15 *Alnipollenites* sp. A. Off polar view. Uncommon four-pored type.

16 *Paraalnipollenites* sp. with strongly convex sides, weakly developed arci and polar ring; x 1000.

17 *Paraalnipollenites* sp. Subtriangular type showing stronger exinal features; x 1250.

18 *Carpinipites ancipites*. Specimen with slight labra and tumescence; x 1000.

PLATE 1

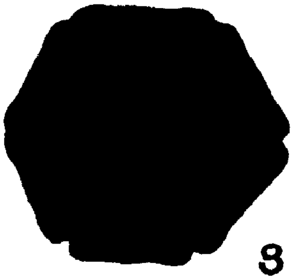

1

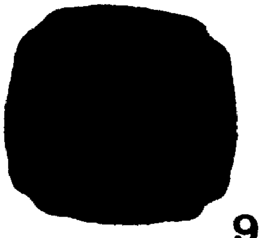

2

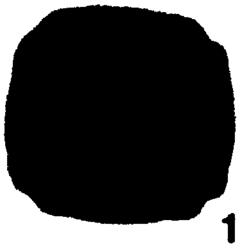

3

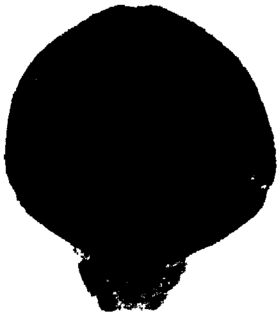

4


6


8


9


10


16


17

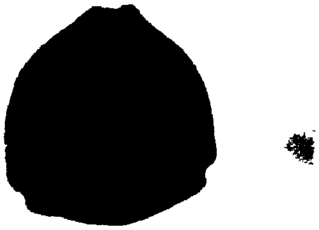

18

PLATE TWO

Betulaceae and Ulmaceae

All specimens magnified x 1000, unless otherwise stated.

1, 2 *Trivestibulopollenites claripites* with weakly developed arci; x 1300; 2, form with small distinct vestibula and no arci.

3 *Trivestibulopollenites betuloides*. Subcircular specimen with small vestibulate pores; x 1300.

4 *Carpinipites ancipites*. Specimen with slight labra and tumescence; x 1500.

5 *Carpinipites* sp. Intermediate form verging onto the form-genus *Triporopollenites*; wall structure and atria indistinct.

6 *Carpinipites ancipites*. Large tetraporate form with slight labra.

7, 8 *Ulmipollenites undulosus*. 7, at low focus, specimen showing details of the weak annulate pore structure and absent arci; 8, at high focus, showing irregular reticulate sculpture.

9 *Ulmipollenites undulosus*. Tetraporate specimen with distinct annuli and irregular reticulate to brevirugulate surface sculpture.

10 *Ulmipollenites undulosus*. Triporate specimen with rugulate sculpture.

11 *Ulmipollenites undulosus*. Five-pored form with brevirugulate to rugulate exine, lacking arci.

12 *Ulmipollenites krempii*. Rare triporate with ulmoid (verrucate) sculpture; x 1500.

13,14 *Ulmipollenites krempii*. Specimen slightly torn, with brevirugulate to reticulate surface sculpture; 14, subpolygonal shaped specimen having distinct arci and brevirugulate ornamentation; x 900.

15-17 *Ulmipollenites krempii*. 15, at low focus, form showing slight annuli; 16, at high focus, showing reticulate surface sculpture and slight subequatorial pores; x 1200, 17, subpolygonal form with distinct arci and reticulate exine; x 1150.

18 *Ulmipollenites tricostatus*. Straight arci more or less parallel to sides of grain.

PLATE 2

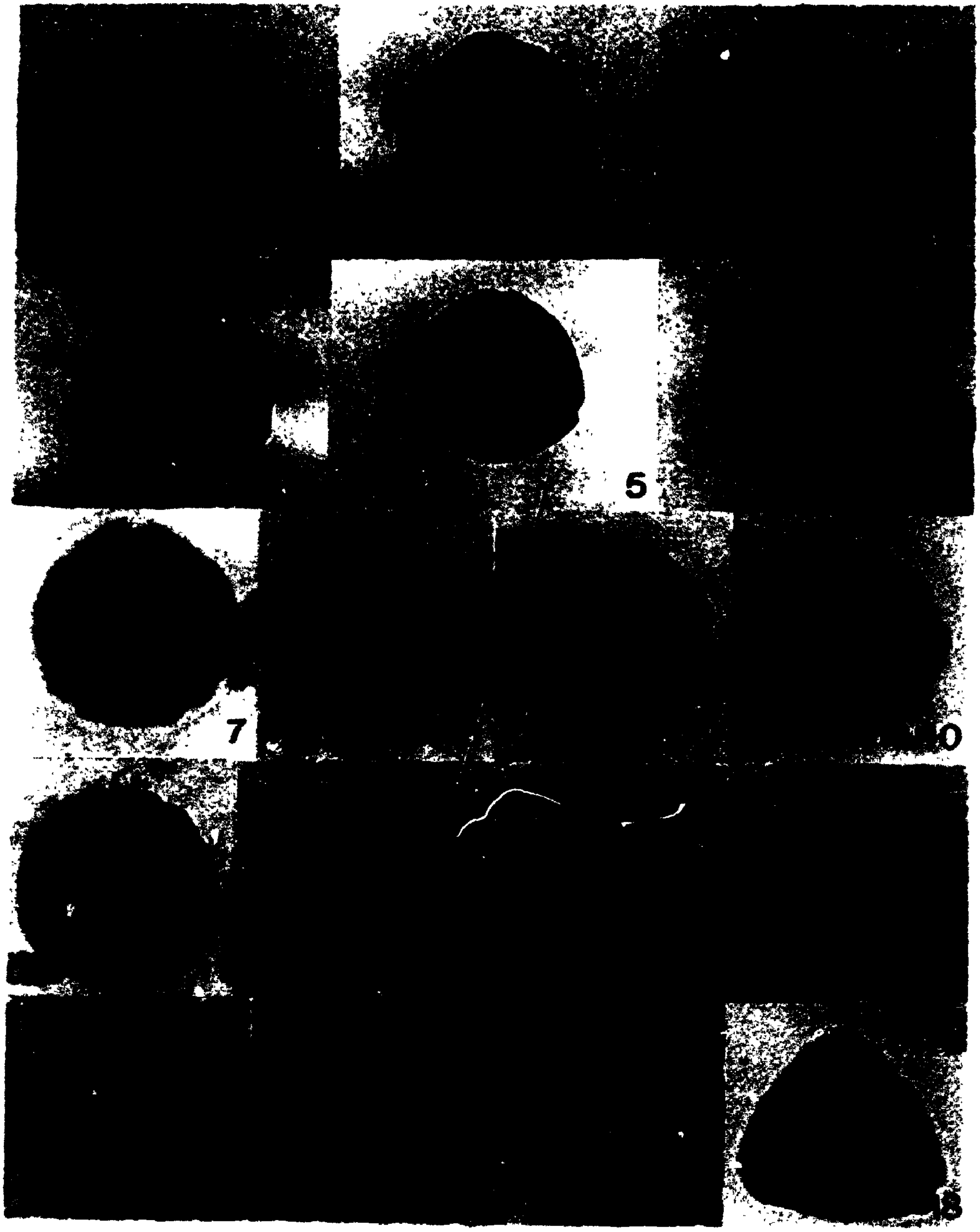


PLATE THREE

Juglandaceae

All specimens magnified 1000 X, unless otherwise stated.

1, 2 *Caryapollenites viridifluminipites*. 1, folded specimen with nearly all subequatorial pores and psilate exine; 2, larger specimen with slightly subequatorial pores.

3 *Caryapollenites juxtaporipites*. Specimen with small subequatorial pores and finely granulate surface sculpture.

4 *Caryapollenites* sp. cf. *C. inelegans*. Form with large, subequatorial pores.

5, 6 *Caryapollenites* sp. cf. *C. veripites*. 5, specimen with polar thinned area without a polar island; 6, specimen with slight folding and exinal elaboration.

7, 8 *Platycaryapollenites* sp. cf. *P. platycaryoides*. 7, form showing two interwoven pseudocolpi; 8, showing weak atria and possibly three pseudocolpi; x 1500.

9, 10 *Caryapollenites* sp. A. 9, specimen with coarse granules in pore region and slightly subequatorial pores; 10, folded specimen with tarsus pore pattern.

11, 12 *Momipites coryloides*. 11, strongly convex form with wide atria and slight tumescence; 12, specimen with less convex sides and slight tumescence; x 1500.

13 *Momipites microfoveolatus*. Small grain, less than 20μm, with foveolate surface sculpture; x 1500.

14, 15 *Plicatopollis* sp. of the *P. plicata*-type. 14, at high focus, specimen show "rolled up" folds extending to the equator; 15, at low focus, showing wall structure (possibly three layers) and distinct atria.

16 *Plicatopollis* sp. A. Form with triradiate structure extending only to atria, most resembles *P. triradiatus (=Momipites triradiatus)* and only *P. cretacea* in part.

17, 18 *Plicatopollis* sp. of the *P. plicata*-type. 17, at low focus, subtriangular specimen showing details of pores and wall structure; 18, at high focus, showing curved or bent arci with no associated thinned spots; x 1500.

19 *Momipites ?tenuipolis*. Poorly-preserved specimen with exinal elaborations on one pole, polar ring and island; most resembles *Momipites tenuipolis* except in size, about 10μm larger. [not described]

3 of/de 3

PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT

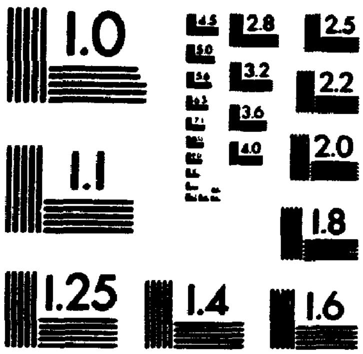


PLATE 3

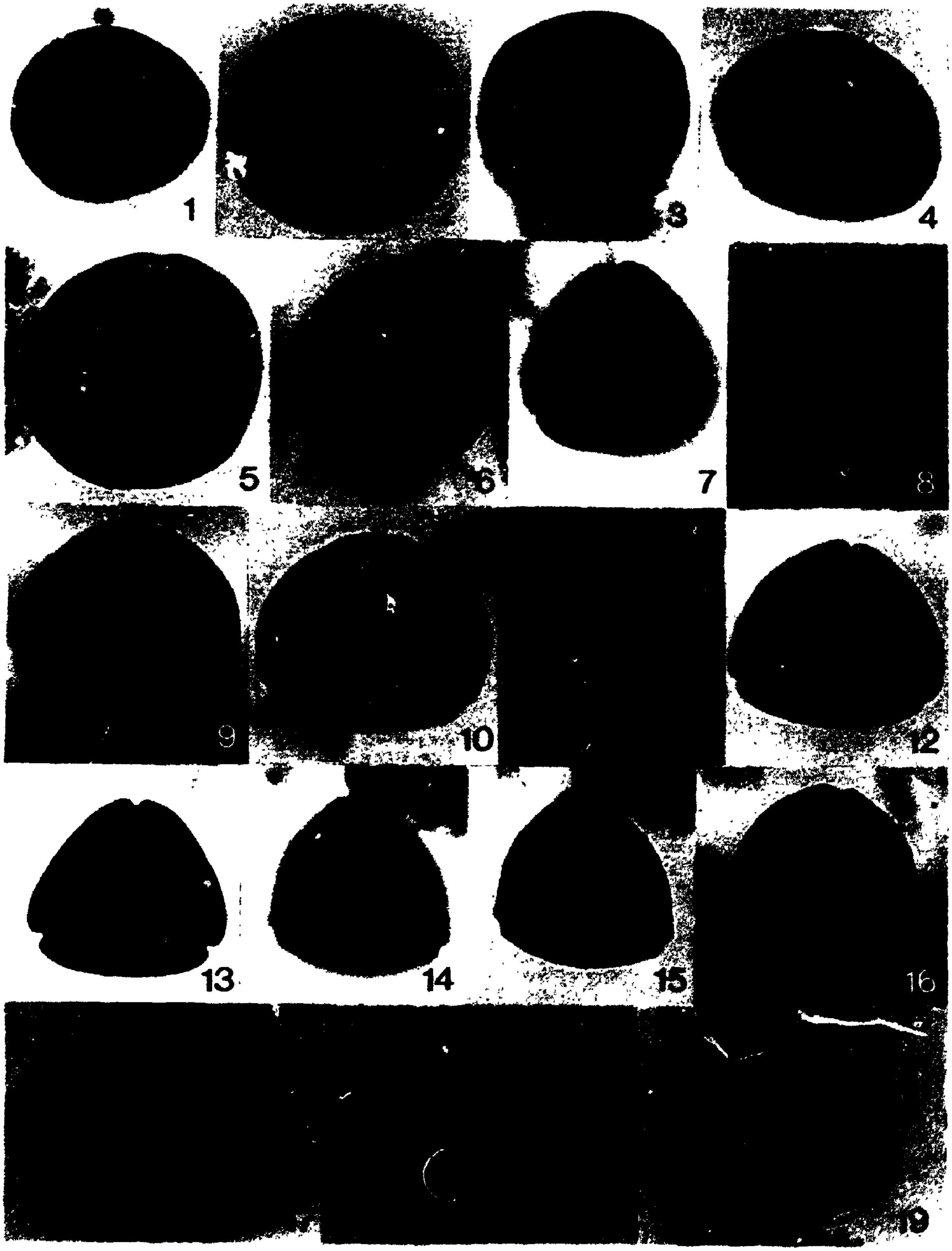


PLATE FOUR

Form-taxa

All specimens magnified x 1000, unless otherwise stated.

1-3 *Triatriopollenites* sp. A. All specimens with convex sides, small, distinct atria but variable outlines; 1, subtriangular specimen with slightly protruding pores and possible arci, x 1500; 2, subtriangular form; 3, rounded triangular form with strongly convex sides, x 900.

4 *Triatriopollenites subtriangulus*. Rounded subtriangular grain with slight tumescence, most resembles *Myricipites*, a rounded triangular form with protruding pores and pore thickenings; x 1500.

5, 6 *Annutriporites* sp. Specimens showing distinct dark ring or collar, corresponding to ektexinal thickening (annuli); 5, dark ring outlines possible atrium, x 1150; 6, slightly corroded with apparent arci.

7, 8 *Triatriopollenites* sp. B. 7, specimen showing unusual exinal elaborations, arci and a polar ring, more characteristic of *Paraalnipollenites*; 8, same specimen magnified x 1650, showing distinct atrium.

9-11 *Triatriopollenites* spp. cf. *T. arboratus*. 9, specimen with subcircular outline showing 2 wall layers; 10, subspheroidal specimen; 11, rounded triangular form with distinct labra, x 850.

12 *Triporopollenites mullensis*. Form showing two wall layers and simple pore pattern lacking annuli, vestibula and atria; x 1200.

13-15 *Triporopollenites* sp. A. 13, spheroidal form (probably as in nature) with distinct arci, x 1400; 14, oblately flattened form showing distinct arci that appears to encircle apertures, double wall structure and simple pore condition as in "*Corylus*"-type pattern (Wodehouse, 1933) verging onto a vestibulate condition, x 1500; 15, similar specimen to 14 but with a regularly pitted surface sculpture; x 1300.

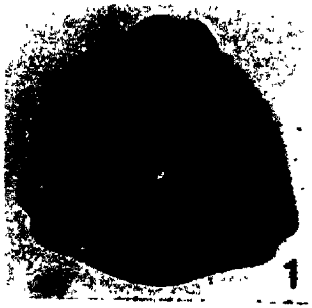
16 *Triporopollenites mullensis*. Specimen with a simple pore pattern, lacking exinal features; x 1100

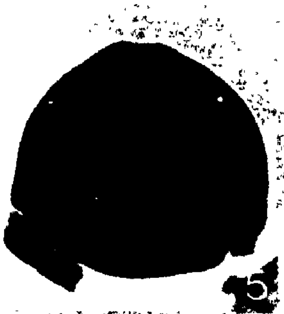
17 *Subtriporopollenites anulatus*. Specimen showing multilayered (three) wall and lolongate pores.

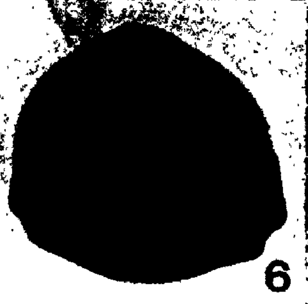
18 *Subtriporopollenites anulatus*. Possibly another form because it is more circular in outline and has circular to lalongate pores. Three wall layers are discernable.

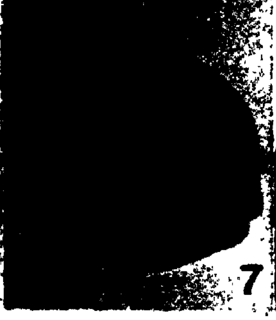
19, 20 *Subtriporopollenites nanus*. 19, round specimen with small subequatorial pores, all in one hemisphere; 20, showing equatorial to slightly subequatorial pores.

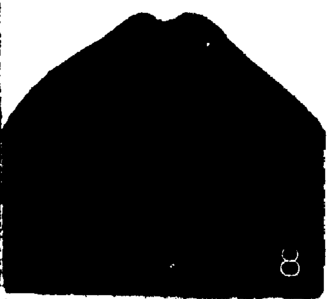
PLATE 4

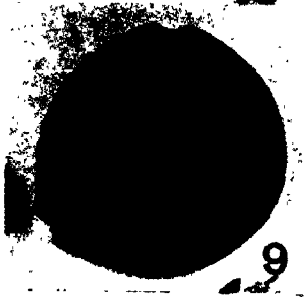

1

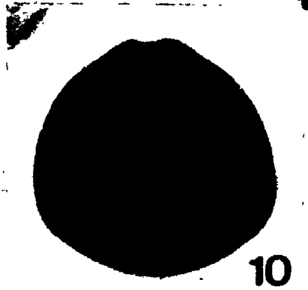

5

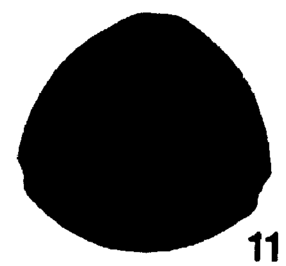

6

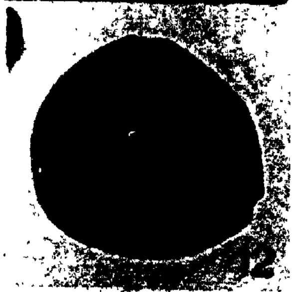

7

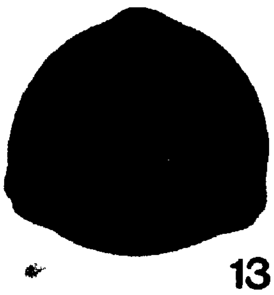

8

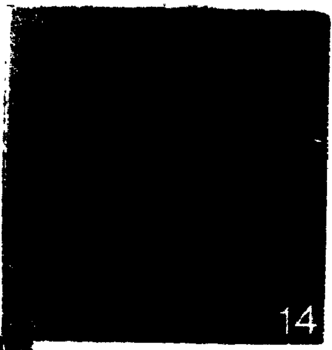

9

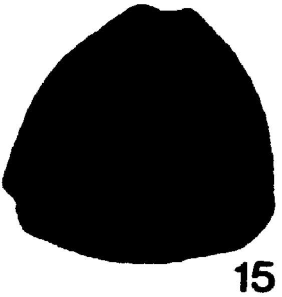

10

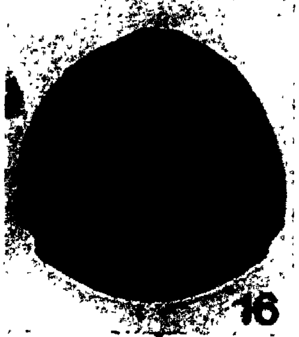

11


12

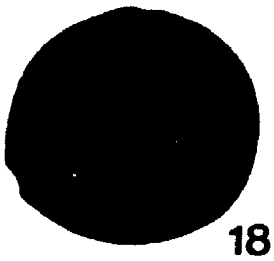

13


14


15


16


17


18


19


20

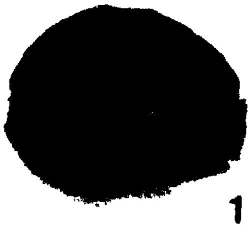
PLATE FIVE

Other triporate and non-triporate pollen

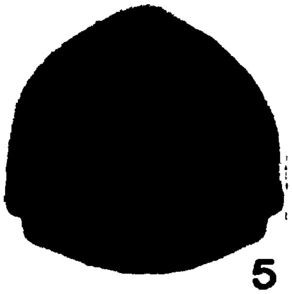
All specimens magnified x 1000, unless otherwise stated.

1, 2	*Thomsonipollis* sp. Only tetraporates were observed; 1, specimen showing slight nexinous thickenings and finely scabrate exine; 2, showing relatively weaker nexinous invaginations.
3, 4	*Santalacites* sp. cf. *S. santaloides*. 3, specimen showing details of apertures and wall structure, both simple, x 1250; 4, showing discontinuous arcuate folds, only extending to each pore, x 1400.
5, 6	*Myricipites annulites*. Both specimens show atria, tarsus pattern (Wodehouse, 1933) and slight pore thickenings. 5, spheroidal specimen showing details of finely granulate surface, x 1500; 6, subtriangular form with slightly protruding pores.
7	*Diervillapollenites* sp. Large grain with baculate processes and reduced ornaments in the pore region; x 750.
8	*Tiliaepollenites* sp. Specimen showing details of dense irregularly reticulate surface sculpture; resembles modern *Tilia*.
9-12	*Pistillipollenites macgregorii*. Variable ornamentation characterize specimens; 9, with gemmae, x 1500; 10, with pistils or baculae; 12, nearly none with reduced secondary gemmae/pistils, x 1500; 11, possibly four-pored form with a variety of different shaped ornaments (baculae and gemmae).
13-16	*Pistillipollenites* sp. A. 13, specimen with non-random arrangement of pistils, ornaments absent in interapertural regions, x 1500; 14, form showing pistils arranged directly on "triradiate structure" with nexine pulling away from sexine, x 1400; 15, form showing strong tumescent pores, possibly thicker nexine and few reduced or secondary ornaments, x 1250; 16, form showing a densely ornamented triradiate structure, x 1150.
17	*Polyatriopollenites* sp. Six-pored form, resembles modern *Pterocarya*.
18	*Taxodiaceaepollenites* sp. B. Specimen with papilla extending about 4.6μm long, resembling modern *Metasequoia*.
19	*Taxodiaceaepollenites* sp. A. Inaperturate gymnosperm pollen showing scabrate exine, split along a line of weakness, resembling modern *Taxodium*.
20	*Ctenosporites* sp. Common fungal element showing details of the wall structure and septa; x 1200.

PLATE 5

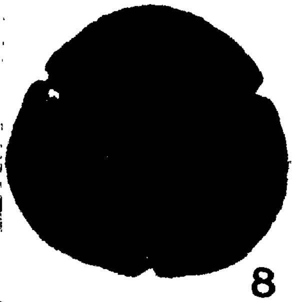

1

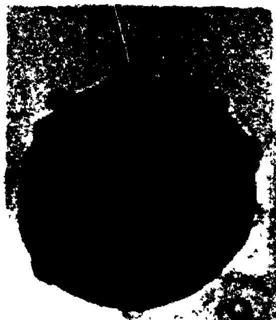

2

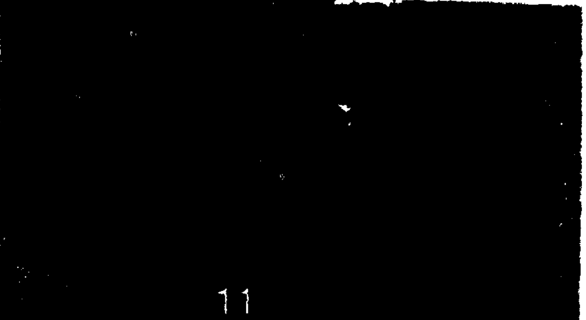

5

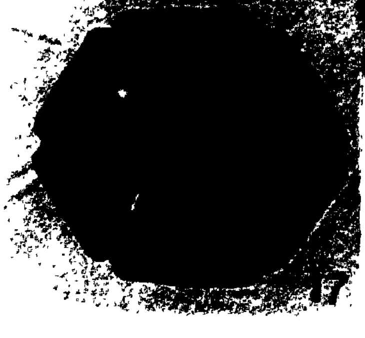

6


7


8


9


11


17


18


20

END

24-12-92

FIN